N° d'ordre : 2714

THÈSE

présentée à

L'UNIVERSITÉ BORDEAUX 1

ÉCOLE DOCTORALE DE : SCIENCES DU VIVANT, GÉOSCIENCES, SCIENCE DE L'ENVIRONNEMENT

Par **FONTANIER Christophe**

POUR OBTENIR LE GRADE DE

DOCTEUR

SPÉCIALITÉ : **OCÉANOGRAPHIE, PALÉO-OCÉANOGRAPHIE**

ÉCOLOGIE DES FORAMINIFÈRES BENTHIQUES DU GOLFE DE GASCOGNE :
ÉTUDES DE LA VARIABILITÉ SPATIALE ET TEMPORELLE
DES FAUNES DE FORAMINIFÈRES BENTHIQUES
ET DE LA COMPOSITION ISOTOPIQUE ($\delta^{18}O$, $\delta^{13}C$) DE LEURS TESTS

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Soutenue le **7 octobre 2003**

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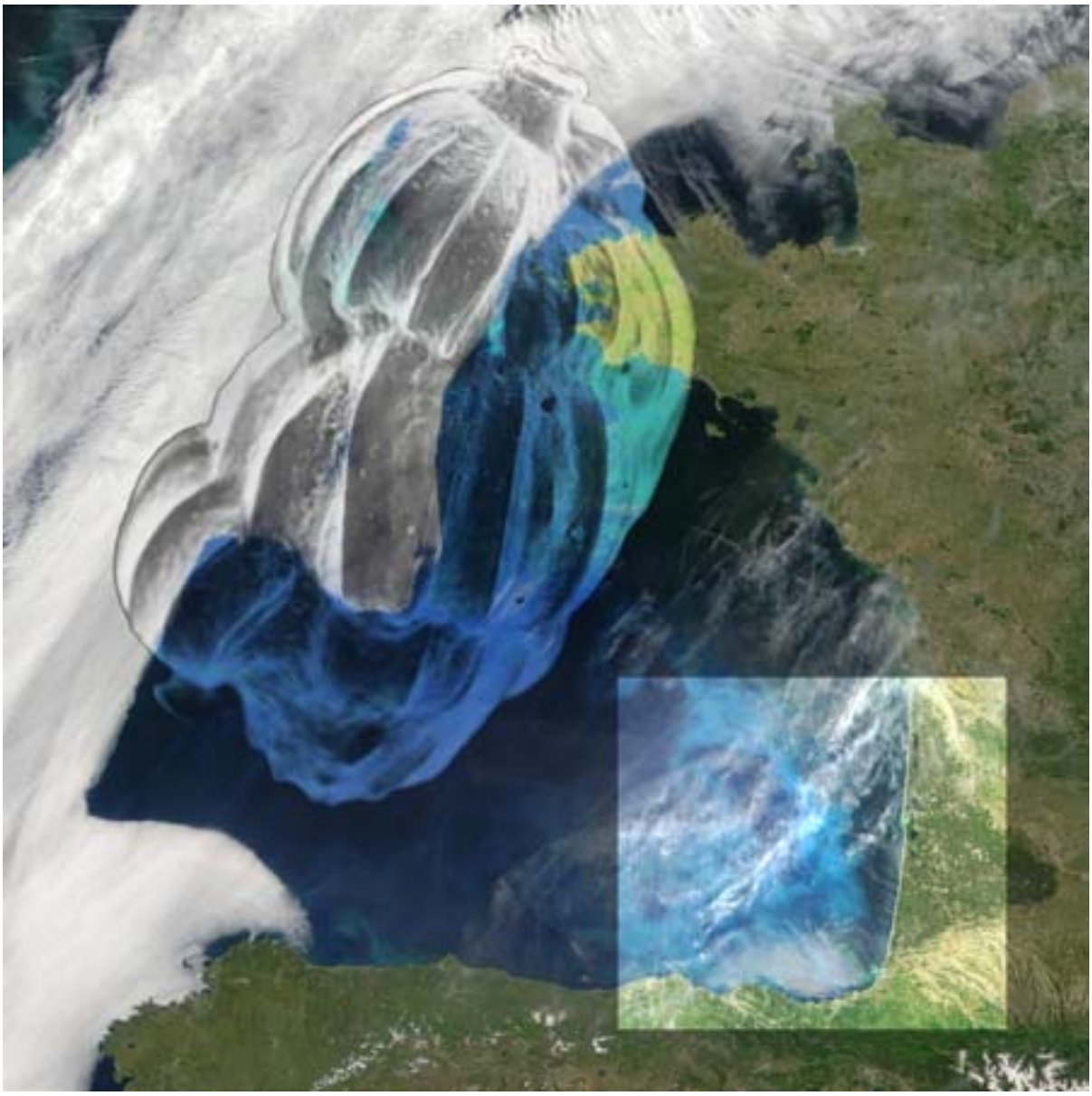
---2003---

« Je me lève en ce jour dans l'énergie des Cieux : lumière du soleil, éclat de la lune, splendeur du feu, vitesse de l'éclair, rapidité du vent, profondeur de la mer, stabilité de la terre, fermeté du roc. »

Incantation protectrice
Attribuée à saint Patrick (V^{e} s.)



REMERCIEMENTS

Voici sûrement le partie la plus difficile de cette thèse, à savoir trouver assez de synomymes de « je gratifie, je présente ma reconnaissance…et cetera » pour pouvoir adresser mes remerciements les plus chaleureux aux personnes qui, d'une façon ou d'une autre, ont été autant de soutiens ou d'aides précieuses lors de ces trois années de thèse.

Il s'agit avant tout de remercier gracieusement l'ensemble des chefs de mission du programme OXYBENT. Ils se sont évertués à entretenir et à faire fructifier ce projet. Merci donc Pierre Carbonel, Jean-Claude Sorbe, Pierre Anschutz et Frans Jorissen. Sans eux, le programme OXYBENT n'aurait pas pu exister.

Je veux tout particulièrement gratifier mon superviseur, à savoir Fransciscus Josephus Jorissen, pour m'avoir laissé travailler sur cette thèse. Je le remercie pour son honnêteté, son encadrement, l'ensemble de ses suggestions et des corrections sur les travaux présentés (il y en a eu !) et son soucieux intérêt pour mon futur proche.

J'aimerais également remercier les membres du jury de cette thèse et tout particulièrement les deux rapporteurs qui ont révisé le manuscript.

Il me semble également important de louer les travaux multiples et variés d'un certain nombre d'étudiants du Département de Géologie et d'Océanographie. Ils purent réaliser, dans le cadre du projet OXYBENT et sous la supervision de Frans Jorissen, des stages et des rapports ô combien utiles et pertinents pour la réalisation de cette thèse (DEUG, Licence, Maîtrise, DES, DEA, thèse). Pour être plus précis, je remercie Anne Alexandre, Laetitia Licari, Julie Morvan, Vanessa Maurin, Violette Venet, Claude David et Nicolas Maréchal Abram.

Je remercie très chaleureusement Alexandra Coynel, Filipa Naughton, Cecilia Laprida, Maite, Stéphanie Caradec et Antoine Marache du bâtiment Recherche Géologie pour leur bonne humeur, leurs suggestions et les bonnes soirées qu'on a passées ensemble.

Je remercie Laure Corbari, Laetitia Pichevin et Nadia Sénéchal, anciennes camarades de DEA, pour leur vitalité et leur énergie.

De l'étage « micropal », je tiens tout particulièrement à féliciter pour leur joie de vivre et leurs sourires Edith Dufour et Françoise Cigrand. Vive la retraite!

Je voudrais maintenant adresser ma plus profonde reconnaissance à l'ensemble des personnes qui ont physiquement ou mentalement collaboré à l'édification et/ou la correction des chapitres et des papiers présentés. Merci donc Gwennaëlle Chaillou, Emmanuelle Geslin, Clémentine Griveaud, Silvia Hess, Hélène Howa, Virginie Lafon, Sandra Langezaal, Kazuyo Tachikawa, Pierre Anschutz, Pierre Carbonel, Jean-Pierre Debenay, Sander Ernst, Russel Frew, Jacques Giraudeau, Pierre Laborde, Andreas Mackensen, Luis Lampert, Jean-Jacques Pichon, Ralf Schiebel, Gerhard Schmiedl, Olivier Weber, Jean-Marie Jouannneau et les reviewers anonymes qui ont critiqué les chapitres 1, 2 et 4.

Je re-remercie particulièrement l'équipe jeune et dynamique d'Utrecht, à savoir, Sandra Langezaal et Sander Ernst, pour leur convivialité, leur bonne humeur et les échanges fructueux d'opinion sur la problèmatique des foraminifères benthiques.

Merci Myriam Sibuet et Jean-Caude Sorbe pour vos aides respectives et vos conseils concernant le macro et le supra-benthos. Votre disponibilité et votre ouverture d'esprit m'ont été plus que profitable.

Je tenais également à faire un gros clin d'œil à l'ensemble des membres du Département pour l'Etude des Bio-Indicateurs Récents et Fossiles de l'Université d'Angers (Ils se reconnaîtront !)…avec une particulière reconnaissance pour Emmanuelle Geslin, Julie Morvan, Valérie Le Cadre, Erica Bicchi, Clémentine Griveaud, Florence Sylvestre, Hélène Howa, Gérald Duchemin, Fabrice Redois, Eric Armynot du Châtelet, Jean-Pierre Debenay.

Je remercie également Christine Audrain, du Service Commun d'Imageries et d'Analyses Microscopiques, pour m'avoir pleinement aider dans la réalisation des photos MEB des foraminifères benthiques.

Voilà maintenant le plus gros morceau ! Certains diront que ce sont de basses flagorneries, d'autres diront que c'est bien normal, mais il faut que maintenant je remercie « les ami(e)s ». Camarades de l'obscure et du lumineux, je vous remercie des moments ô combien intenses que l'on passe ensemble lorsqu'on le peut ! Merci donc Agathe, Aleta, Armelle, Audrey, Cathy, Juju (-dicaëlle), Vanina, Manue, David, Eduardo, Erwan (R-1 D2), Farid (Poseur de Rail), Hervé, Jean-Luc, Jérôme (mon frère et/ou Orlok), Julien, Karim, Loïc (« ouHHH un MacDo ! ») Matthieu (« Aime bien le WISKY ! »), Medi (« on va pas y arriver !»), Sébastien (Robert Sleg !). Je remercie Georges Lucas pour son soutien indirect et bien involontaire et Georges Buch pour avoir calibré le zéro de l'échelle relative de la stupidité mondiale.

Un merci très amical à M. et Mme Nafati pour leur bonne humeur et leur simplicité !

J'embrasse tendrement Stéphanie Desprat, ma douce moitié, pour m'avoir supporté dans tous les sens durant ces trois années. Merci de tes sourires, de ton amour, des moments merveilleux que nous avons partagés et de ceux que nous partagerons encore. Pourvu que les dieux et la Fortune nous prêtent vie aussi longtemps que possible!

Finalement, je remercie très (très, très !) fortement mes parents Martine et Fabrice et mon frère Jérôme pour leur présence et leur soutien.

J'embrasse tendrement ma mamie.

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Casford J.S.L., Rohling E.J., Abu-Zied R., Cooke S., Fontanier C., Leng M.J. et V. Lykousis (2002), *Paleoceanography*, **17**, no 2.

A dynamic concept for eastern Mediterranean circulation and oxygenation during sapropel formation.

Casford J.S.L., Rohling E.J., Abu-Zied R., Fontanier C., Jorissen F.J., M.J. Leng, Schmiedl G. et J. Thomson (2003), *Palaeogeography*, *Palaeoclimatology and Palaeoecology,* **190**.

INTRODUCTION

Écologie des foraminifères benthiques du Golfe de Gascogne : Études de la variabilité spatiale et temporelle des faunes de foraminifères benthiques et de la composition isotopique ($\delta^{13}C$, $\delta^{18}O$) de leurs tests.

Cette thèse a pour principal objectif de préciser les caractéristiques écologiques majeures des communautés de foraminifères benthiques peuplant actuellement diverses stations situées sur la bordure de plate-forme et sur la pente de la marge aquitaine dans le Golfe de Gascogne. Elle a été réalisée dans le cadre des projets OXYBENT et FORAMPROX (PROOF, PNEDC).

Ce travail s'articule sur deux axes d'étude : (1) préciser la dynamique spatiale et temporelle des diverses populations de foraminifères benthiques en relation avec les paramètres majeurs environnementaux que sont le flux de matière organique exportée depuis les eaux de surface et l'oxygénation des eaux de fond et des eaux interstitielles dans le sédiment, (2) préciser les variations du signal géochimique des tests ($\delta^{13}C$ et $\delta^{18}O$) de certaines espèces de foraminifères benthiques en écho à la dynamique saisonnière et spatiale des communautés benthiques.

L'intérêt de ce travail est donc double. D'un point de vue écologique, il s'agit de mieux connaître le rôle écologique joué par les foraminifères benthiques au sein des écosystèmes benthiques profonds dans les transferts d'énergie et de matière et les cycles biogéochimiques. Alternativement, de par le potentiel avantageux de fossilisation des faunes de foraminifères benthiques, l'étude des peuplements actuels de foraminifères est indispensable pour une utilisation optimale et juste des assemblages fossiles de foraminifères benthiques en tant qu'outils de reconstruction des paléo-environnements benthiques.

Une approche pluridisciplinaire est fondamentalement nécessaire pour ce travail de thèse. Aussi, ce travail se découpe-t-il principalement en 6 chapitres ayant fait l'objet de publication ou en soumission après des travaux très fructueux de collaboration entre des laboratoires de diverses universités.

Les foraminifères benthiques

Une classification phénétique

Les foraminifères benthiques (classe FORAMINIFERA, règne PROTOCTISTA, embranchement GRANULORETICULOSA; selon Sen Gupta, 1999) sont des organismes unicellulaires eucaryotes dotés d'une capacité d'adaptation exceptionnelle. En effet, au travers de peuplements variés, ils occupent des environnements marins aussi variés que les plaines abyssales oligotrophes, les aires de résurgences hydrothermales et les zones hypersalines lagunaires (Murray, 1970 ; Coull et al., 1977 ; Steineck et Bergstein, 1979 ; Debenay, 1990 ; Sen Gupta et Aharon, 1994), et ont également colonisés certains environnements d'eaux saumâtres et d'eaux douces (Pawlowski, 2000).

Une caractéristique remarquable des foraminifères benthiques (et planctoniques) est leur capacité à protéger leur cellule protoplasmique dans une enveloppe plus ou moins rigide appelée test. Les tests des foraminifères benthiques sont soit de nature organique, soit faits de particules terrigènes et biogènes agglutinées, soit constitués de biocristaux d'aragonite et de calcite (carbonate de calcium) biominéralisés par les organismes. Ils ont un fort potentiel de fossilisation qui dépend tant de leur nature propre que des conditions physico-chimiques du milieu sédimentaire où ils sont enfouis. Les tests de foraminifères benthiques retrouvés dans les archives sédimentaires constituent donc un outil micropaléontologique majeur dans les reconstitutions des paléo-environnements benthiques en paléo-océanographie et dans l'établissement d'échelles biostratigraphiques.

La classification actuelle des foraminifères en divisions taxonomiques distinctes est essentiellement basée sur des critères morphologiques du test (Loeblich et Tappan, 1988 ; Sen Gupta, 1999). La composition et les microstructures du test sont de première importance pour classifier les foraminifères en divers ordres. La composition chimique et les arrangements granulaires des biocristaux sont utilisés comme critères discriminants secondaires afin de définir et distinguer les sous-ordres et les super-familles. Le mode d'addition des chambres d'habitation, la nature des cloisons et les ouvertures sont également pris en compte. Finalement, la forme et l'arrangement des chambres ainsi que la nature sessile ou vagile des organismes sont considérées (Sen Gupta, 1999). Dans la mesure où cette classification ne tient pas compte des analyses génétiques nécessaires pour actuellement classer les organismes vivants en espèces dites biologiques, les espèces de foraminifères actuellement répertoriées

sont des espèces dites morphologiques, hiérarchisées dans une classification purement phénétique. Les foraminifères planctoniques et benthiques représentent près de 40.000 espèces fossiles et vivantes dont près de 3.000 espèces vivent actuellement dans nos mers, majoritairement des espèces benthiques.

L'établissement d'une classification phylogénétique des foraminifères benthiques (basée sur la reconnaissance de séquences de gènes) est en cours depuis quelques années et tend à démontrer une diversité spécifique beaucoup plus grande que le laisse supposer la classification morphologique actuellement en vigueur (e.g. Pawlowski, 2000 ; Pawlowski et al., 2002).

Quelques éléments de biologie

Les foraminifères benthiques présentent un corps protoplasmique unique pourvu d'un noyau le plus souvent sphérique. Le test est produit par la partie extérieure du protoplasme appelée ectoplasme ainsi que par un réseau de pseudopodes. Les pseudopodes sont de très longues extensions granuloréticulées du protoplasme. Ils se projettent par diverses ouvertures à travers le test dans l'environnement immédiat. Les pseudopodes permettent de saisir les particules sédimentaires environnantes. Ils permettent d'évacuer également les déchets du métabolisme. Ils aident à la construction du test en rassemblant les particules terrigènes et biogènes au contact de l'ectoplasme. Ils permettent une fixation temporaire ou semi-permanente au substrat et permettent également aux foraminifères de se déplacer sur et dans le sédiment.

Dans les environnements benthiques à sédimentation pélagique ou hémipélagique, les foraminifères benthiques peuvent vivre soit dans les premiers centimètres du sédiment en position endopélique, soit en position épibiote ou épilithe sur des supports biogènes et terrigènes émergents dans les eaux de fond. La distribution verticale d'une espèce de foraminifères benthiques par rapport à l'interface eau-sédiment permet de définir son microhabitat. Le microhabitat répond à un ensemble composite de paramètres physico-chimiques et biologiques inhérents à l'environnement benthique.

En ce qui concerne leurs exigences trophiques, les foraminifères benthiques d'environnements benthiques marins profonds sont généralement considérés comme des organismes organohétérotrophes détritivores capables de se nourrir (1) soit de particules organiques en suspension au-dessus du sédiment (suspensivores), (2) soit de détritus organiques déposés sur et dans le sédiment (dépositivores), (3) soit de bactéries endopéliques

organohétérotrophes et chimiolithotrophes variées présentes dans leur microhabitat (bactériophages).

Alors que les modes de reproduction et les cycles de vie de certaines espèces de foraminifères benthiques d'environnements benthiques margino-littoraux sont bien compris et largement illustrés (Loeblich et Tappan, 1988), la dynamique des populations de foraminifères benthiques des environnements marins profonds est très mal connue. Les études sur les communautés benthiques profondes le plus souvent fragmentaires et limitées dans le temps ne permettent d'estimer que d'une façon très fragmentaire les taux de renouvellement des populations ainsi que les périodes précises de reproduction des individus.

Les écosystèmes benthiques des environnements marins profonds

Un écosystème est l'association d'un milieu physico-chimique aux limites bien définies (= biotope) et de l'ensemble des organismes vivants qui le peuplent (= biocénose). Selon la définition de la Convention sur la Diversité Biologique (CDB, 1994), l'écosystème est « un complexe dynamique constitué de communautés de plantes, d'animaux et de micro-organismes, et de leur interaction, formant une unité fonctionnelle » (Lévêque et Mounolou, 2001). Au sein de ces systèmes, des réseaux trophiques complexes permettent des transferts de matière et d'énergie intégrés dans des cycles biogéochimiques majeurs.

Les environnements benthiques profonds : Rôle de la matière organique détritique

Les environnements benthiques dits « profonds » sont définis comme les biotopes des fonds océaniques où les processus photosynthétiques sont impossibles de par l'absence d'énergie lumineuse utilisable. Ils s'étalent dans la zone aphotique des océans, depuis les bordures de plate-forme jusque dans les fosses océaniques les plus profondes. Dans de tels environnements benthiques, seules les bactéries chimiolithotrophes sont capables de synthétiser leur propre matière organique. Pour se faire, elles utilisent le carbone inorganique dissous prélevé dans leur milieu de vie (le plus souvent sous forme de CO_2) et l'énergie libérée lors de l'oxydation dans le sédiment d'espèces chimiques réduites (e.g. Singleton, 1999 ; Jørgensen, 2000). La biocénose des environnements benthiques profonds est principalement constituée de groupes d'organismes organohétérotrophes dont les liens trophiques, la structure spatiale et la dynamique saisonnière sont largement tributaires du flux

de matière organique exportée depuis les sources de production primaire des eaux de surface (e.g. Graf, 1989 ; Snelgrove et al., 1997).

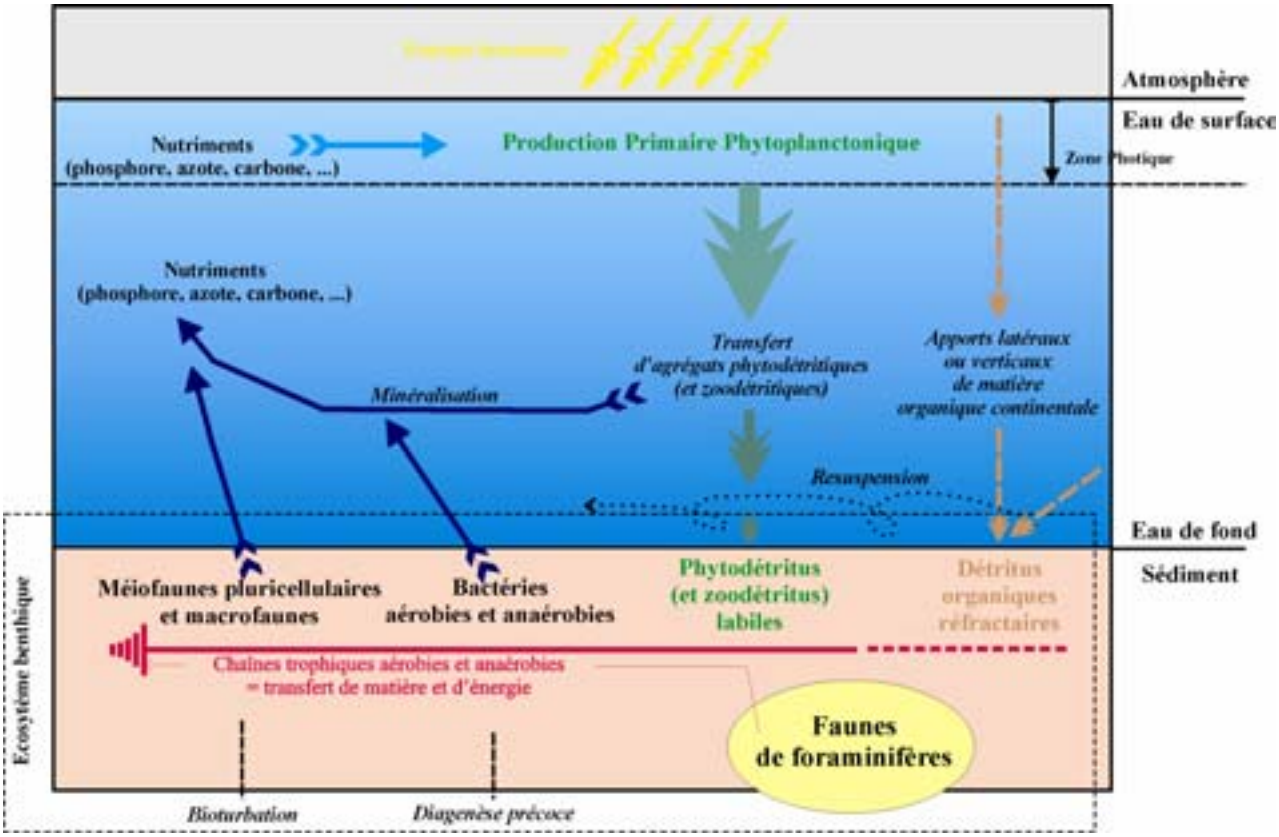

Fig. 1. Couplage entre la production primaire des eaux de surface et la structure des écosystèmes benthiques des environnements profonds. Notez que la méiofaune pluricellulaire et la macrofaune participent amplement aux processus de bioturbation dans le sédiment superficiel. Notez également que les bactéries aérobies et anaérobies catalysent les réactions chimiques majeures caractérisant la diagenèse précoce.

Cette matière organique consiste le plus souvent en des agrégats pluri-millimétriques ou pluri-centimétriques de micro-algues phytoplanctoniques (prymnésiophycées, cyanophycées et bacillariophycées) qui constituent, une fois déposés sur le fond, le phytodétritus. La figure 1 présente d'une façon très simplifiée les principales caractéristiques de ce couplage qui existe entre le pélagos et le benthos. De par leur richesse en éléments biolimitants tel que le carbone, l'azote et le phosphore, les phytodétritus constituent une source indispensable de matière organique pour pourvoir à l'ensemble des besoins métaboliques des organismes benthiques hétérotrophes. Les lipides et les acides aminés constitutifs de cette manne organique sont très facilement hydrolysables et assimilables par les organismes benthiques (e.g. Grémare et al.,

2002). Par conséquent, les particules phytodétritiques sont rapidement dégradées dans les boucles trophiques aérobies du sédiment superficiel bioturbé, et sont considérées comme des détritus organiques très réactifs dits labiles (e.g. Carney, 1989) (Fig. 2). L'énergie extraite de cette matière organique lors de la respiration aérobie et anaérobie assure, entre autre, la reproduction, la croissance des individus, et l'entretien des processus complexes et énergiquement coûteux de la biominéralisation des groupes d'organismes calcifiants.

La seconde source importante de matière organique détritique est d'origine continentale (e.g. Bruland et al., 1989). Les détritus organiques transportés par les vents et les fleuves dans le domaine marin sont de nature variable. Il s'agit, entre autres, de cuticules de feuilles, des fragments de tissus vasculaires de plantes supérieures, des grains de pollens respectivement riches en lignine, cutine et sporopollénine. Pour le biologiste marin, cette matière organique le plus souvent inerte et difficilement hydrolysable par les organismes benthiques est définie comme la matière organique dite réfractaire (e.g. Bruland et al., 1989 ; Grémare et al., 2002). D'un point de vue biochimique, elle est essentiellement constituée de biomolécules polymériques très résistantes à la dégradation. Seuls certains consortia bactériens benthiques organohétérotrophes sont capables, via l'utilisation d'exo-enzymes, de dépolymériser et de labiliser cette matière organique résistante et de consécutivement s'en nourrir (e.g. Carney, 1989 ; Jorgensen, 2000) (Fig. 2). A la différence des phytodétritrus d'origine marine, la matière organique dite réfractaire est dégradée lentement dans le sédiment et participe le plus souvent aux boucles trophiques dites anaérobies du sédiment profond.

Une source non particulaire de matière organique potentiellement utilisable par les organismes organohétérotrophes benthiques est la matière organique dissoute. Cette matière organique est advectée dans les divers biotopes benthiques au grès des déplacements de masses d'eau profonde. Alors que pour certains auteurs cette source de matière organique serait inerte et inutilisable (e.g. Williams et Druffel, 1987), pour d'autres, elle jouerait un rôle important sur la dynamique et la structure des microflores bactériennes benthiques des environnements profonds (Duursma, 1961 ; Sugirima et Suzuki, 1991 ; Bruland et al., 1989 ; Kirchman et al., 1991). Cependant, l'incertitude sur la quantification de ses concentrations dans les eaux de fond et les eaux porales ainsi que le manque de donnée concernant sa composition chimique ne permettent pas encore d'estimer l'importance du rôle de cette source de matière dissoute sur les cycles biogéochimiques des écosystèmes benthiques marins (Middelburg et al., 1993).

Il est à noter que des processus de resuspension, associés à des courants de fond intenses ou des évènements turbiditiques, peuvent affecter les particules organiques phytodétritiques fraîchement déposées. Ils entraînent, à moyen terme, une « réfractorisation » progressive des composés organiques en suspension dans la mesure où les composantes les plus labiles de la matière organique détritique sont rapidement et préférentiellement consommées dans les eaux de fond. Lors de leur dépôt final, ces détritus organiques remaniés sont difficilement hydrolysables.

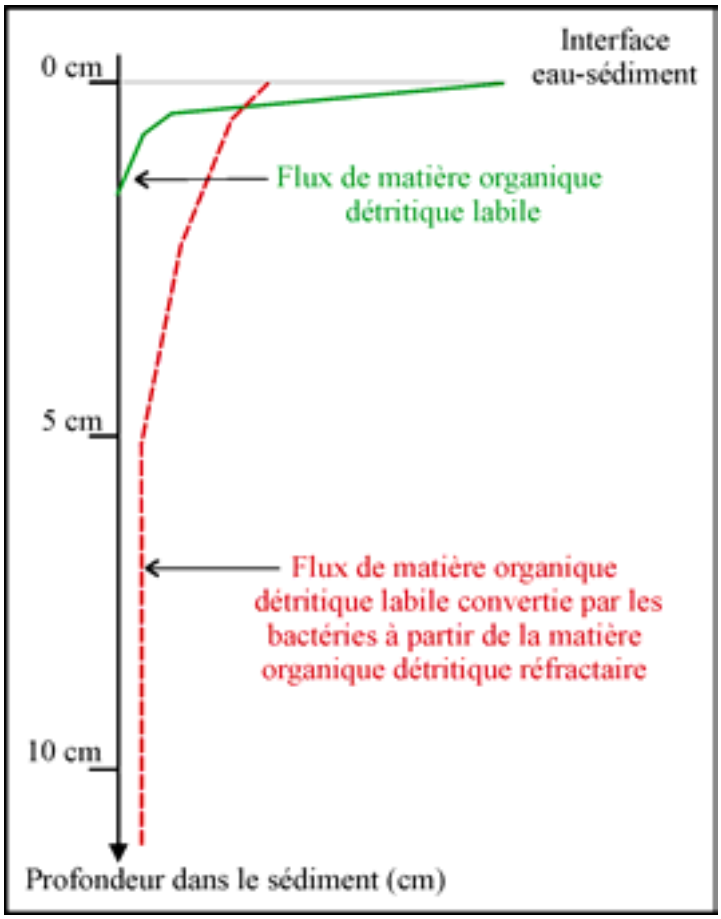

Fig. 2. Répartition de la matière organique détritique dans le sédiment en fonction du caractère labile ou réfractaire des détritus organiques. Les bactéries seraient responsables de la « labilisation» de composés organiques réfractaires enfouis plus ou moins profondément dans le sédiment (d'après Carney, 1989).

Des processus biogéochimiques importants : la diagenèse précoce.

Les apports de matière organique particulaire dans les écosystèmes benthiques profonds induisent des modifications significatives des conditions biogéochimiques dans les premiers décimètres du sédiment, caractérisant partiellement ce que les géochimistes appellent la diagenèse précoce. La diagenèse précoce est essentiellement contrôlée par des processus biologiques tels la bioturbation, la décomposition bactérienne de la matière organique détritique et les phénomènes de précipitation/dissolution (Cojan et Renard, 1999).

Les apports de matière organique particulaire labile à l'interface eau-sédiment sont rapidement reminéralisés au sein des boucles trophiques aérobies du sédiment superficiel. L'oxygène, qui est le premier accepteur d'électron utilisé lors de la respiration dite aérobie, est l'oxydant le plus énergétique. Il permet la dégradation très rapide des détritus organiques les plus labiles. Cela se traduit généralement par une diminution de la concentration en oxygène dissous des eaux interstitielles dans les premiers millimètres ou centimètres du sédiment. La limite entre le sédiment superficiel oxygéné et le sédiment profond, où l'oxygène est totalement absent, est communément appelé « limite oxygène zéro ». Néanmoins, les processus de dégradation de la matière organique détritique ne s'arrêtent pas à cette limite. Dans le sédiment profond d'autres oxydants prennent le relais de l'oxygène et permettent au sein d'une chaîne trophique, dite anaérobie, la dégradation des détritus organiques plus ou moins résistants en matière organique soluble assimilable par les bactéries (Middelburg et al., 1993). Il s'agit principalement des nitrates, des oxydes-hydroxydes de manganèse et de fer et des sulfates que seuls certains consortia bactériens hétérotrophes et certains groupes d'organismes unicellulaires peuvent utiliser lors de processus respiratoires anaérobies (e.g. Froelich et al., 1979 ; Finley et al., 1983 ; Jorgensen, 2000 ; Hyacinthe et al., 2001) (Fig. 3). L'ensemble de ces processus biogéochimiques catalysés principalement par des consortia bactériens très diversifiés crée au sein du sédiment superficiel des gradients très marqués de concentration d'espèces chimiques dissoutes ainsi que des environnements chimiques où les phénomènes de précipitation et de dissolution sont exacerbés. Il est cependant à noter que la « limite oxygène zéro » séparant un sédiment oxique d'un sédiment anoxique n'est pas uniquement une simple interface nette et plane. Nombreux sont les microenvironnments oxiques, dysoxiques ou suboxiques associés le plus souvent à des terriers macrofaunaux égrainant les parties profondes et anoxique du sédiment et créant une mosaïque tridimensionnelle complexe de gradients géochimiques

L'intensité des processus diagénétiques ainsi définis est largement fonction de la quantité et de la qualité des détritus organiques exportés à l'interface eau-sédiment, de la facilité à l'enfouissement des détritus organiques les plus labiles via les processus de bioturbation, et de la nature même des particules sédimentaires terrigènes. L'utilisation préférentielle des particules organiques facilement hydrolysables dans le sédiment superficiel contraste par rapport à l'enfouissement et la préservation des composés organiques les plus résistants très lentement convertis en composés organiques assimilables par les bactéries (Carney, 1989) (Fig. 2).

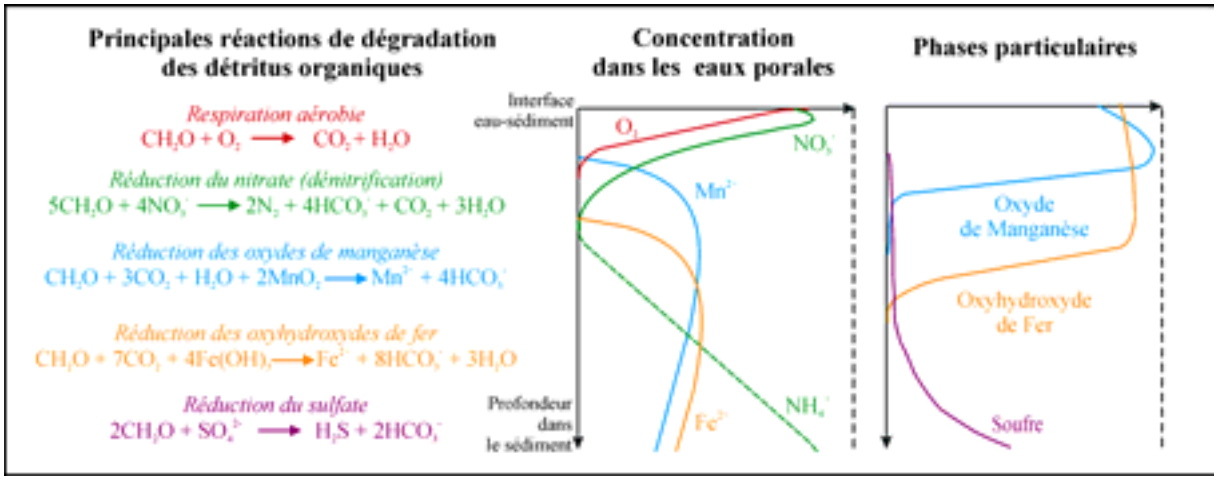

Fig. 3 Principales réactions de dégradation bactérienne des détritus organiques dans le sédiment durant la diagenèse précoce. La molécule de sucrose (= CH_2O) est utilisée comme le substrat organique décomposé. Ces réactions diagénétiques conduisent à la création de gradients chimiques et de zones de précipitations préférentielles de certaines phases minérales. (D'après Froelich et al., 1979).

Les biocénoses benthiques profondes : rôle des bactéries et des foraminifères benthiques

Loin d'être des milieux désertiques, les écosystèmes benthiques profonds présentent une biodiversité étonnante (e.g. Sanders, 1968 ; Grassle, 1989 ; Grassle et Maciolek, 1992 ; May, 1992 ; Snelgrove et al., 1997).

Comme suggéré précédemment, les bactéries hétérotrophes benthiques constituent le groupe majeur de consommateurs primaires des détritus organiques déposés dans le sédiment (e.g. Lochte et Turley, 1988 ; Jumars et al., 1989 ; Thiel et al., 1990 ; Delle Groce et al., 1996 ; Jørgensen, 2000 ; Turley, 2000). Elles participent à une partie importante de la minéralisation de la matière organique particulaire labile et réfractaire exportée jusque dans

les biotopes benthiques. Aussi, se développent à l'interface eau-sédiment les consortia bactériens qui adoptent des comportements opportunistes lors de dépôts saisonniers de phytodétritus. Ils montrent des augmentations remarquables de densité en profitant des fortes concentrations de lipides et d'acides aminés hydrolysables constitutifs des phytodétritus (e.g. Lochte et Turley, 1988). Les bactéries benthiques endopéliques anaérobies qui occupent des niches plus profondes dans le sédiment sont moins réactives aux apports soudains de phytodétritus, mais entretiennent cependant par les processus respiratoires importants une minéralisation accrue de la matière organique détritique plus résistante (e.g. Moodley et al., 2002).

Les foraminifères benthiques, de par leur taille (~100µm), leur biomasse importante et leur taux de croissance potentiellement élevé, sont une composante essentielle de la méiofaune benthique interstitielle (e.g. Altenbach et Sarnthein, 1989 ; Gooday et al., 1992). Ils semblent constituer un maillon important des chaînes trophiques des écosystèmes benthiques en participant amplement à la fixation et au recyclage du carbone, de l'azote ou du phosphore issus de la matière organique détritique (e.g. Altenbach et Sarnthein, 1989 ; Gooday et al., 1992 ; Moodley et al., 2000 ; Moodley et al., 2002). A ce titre, il est généralement suggéré que la composition, la densité des communautés de foraminifères benthiques des environnements profonds ainsi que les microhabitats des espèces sont influencés par la qualité et la quantité de matière organique exportée au sédiment (e.g. Altenbach et Sarnthein, 1989 ; Corliss et Emerson, 1990 ; Corliss, 1991 ; Herguera and Berger, 1991 ; Rathburn and Corliss, 1994 ; Jorissen et al., 1995 ; Fariduddin et Loubere, 1997 ; Jorissen et al., 1998 ; Loubere et Fariduddin, 1999b ; De Rijk et al., 2000 ; Licari et al., 2003). La salinité, la température et la pression, autres variables abiotiques majeures caractérisant les environnements benthiques profonds, n'exerceraient, semble-t-il, que des rôles mineurs sur les communautés de foraminifères benthiques. Il est également suggéré que les foraminifères benthiques endopéliques superficiels ont une dynamique saisonnière fortement influencée par les apports intermittents de phytodétritus (e.g. Gooday, 1988 ; Barmawidjaja et al., 1992 ; Silva et al., 1996 ; Gooday et Rathburn, 1999 ; Gooday et Hughes, 2002 ; Kitazato et al., 2000). Certaines espèces opportunistes de foraminifères benthiques qui vivent près de l'interface eau-sédiment seraient extrêmement sensibles aux apports d'une matière organique labile. Les réponses des faunes de foraminifères benthiques profonds à une forte variabilité des apports phytodétritiques demeurent très mal connues. Aussi, le rôle et la dynamique des foraminifères benthiques au sein d'un écosystème benthique profond ne peuvent-ils pas être correctement compris sans une connaissance exhaustive de la biocénose

benthique et une appréciation optimale des paramètres abiotiques définissant le biotope. En effet, il serait simpliste de considérer les foraminifères benthiques comme affranchis des chaînes trophiques benthiques complexes qui prévalent entre les divers groupes d'organismes benthiques. Pour exemple, il a été démontré que les foraminifères benthiques profonds subissent une pression prédatrice de la part d'un certain nombre d'organismes méiofaunaux et macrofaunaux tels que les isopodes (Elizehalde et al., 1999 ; Gudmundsson et al., 2000). De plus, nombreux sont les paramètres physico-chimiques pouvant exercer des limitations exclusives sur les communautés de foraminifères benthiques. Ainsi, après le flux de matière organique exportée, la concentration d'oxygène dissous dans les eaux de fond et dans les eaux interstitielles pourrait jouer un rôle fondamental sur la structure et la dynamique des faunes de foraminifères benthiques (e.g. Mackensen et Douglas, 1989 ; Sen Gupta et Machain-Castillo, 1993 ; Alve et Bernhard., 1995 ; Jorissen et al., 1995 ; Bernhard et Sen Gupta, 1999 ; Kitazato et al., 2000).

Le modèle conceptuel TROX (TRophic condition and Oxygen concentration) présenté par Jorissen et al. (1995) tend à donner des idées sur le double contrôle qu'exerce le flux de matière organique exportée depuis la production primaire des eaux de surface et les concentrations en oxygène dissous des eaux de fond et des eaux interstitielles, sur la densité, la composition et surtout les microhabitats des faunes de foraminifères benthiques. En tenant compte de la décroissance de la densité des faunes relative à la diminution du flux de matière organique, le modèle explique que, dans des situations oligotrophes, la distribution des faunes de foraminifères benthiques est contrôlée par les faibles flux de carbone organique. L'ensemble des populations benthiques présente des microhabitats endopéliques très superficiels afin de profiter d'une façon optimale des apports limités de phytodétritus à l'interface eau-sédiment. Dans des situations eutrophes, la profondeur réduite de la pénétration d'oxygène dans le sédiment via des processus diagénétiques exacerbés limite la majorité des espèces de foraminifères benthiques à des microhabitats endopéliques peu profonds et oxygénés. Seuls certaines espèces tolérantes à des conditions anoxiques adoptent des niches endopéliques profondes. La pénétration des faunes de foraminifères benthiques dans les premiers centimètres du sédiment est maximale dans des situations trophiques intermédiaires où la bonne pénétration de l'oxygène est associée avec des apports relativement importants de phytodétritus. Les niches endopéliques intermédiaires et profondes s'étendent à une profondeur maximale (plusieurs centimétres) et peuvent être occupées par des espèces oxyphiles qui y trouvent la manne organique labile nécessaire à leur activité métabolique.

Les travaux récents de de Rijk et al. (1999 ; 2000) en Mer Méditerranée montrent le rôle majeur que jouent les flux exportés de carbone organique depuis des eaux de surface sur la répartition bathymétrique de plusieurs espèces de foraminifères benthiques le long de divers transects. Ces études suggèrent que l'absence/présence de nombreuses espèces le long des pentes semble répondre à des gammes de tolérance bien délimitées en terme d'apport de matière organique.

L'étude des écosystèmes benthiques profonds

Les biocénoses benthiques profondes sont des associations complexes d'organismes extrêmement variés dont la structure et la dynamique sont dépendantes (1) des limites de tolérance des diverses espèces par rapport aux variables abiotiques environnementales et (2) des relations inter et intra-spécifiques au sein et entre les diverses communautés. Le manque d'observations in situ à une résolution temporelle adéquate ainsi que les problèmes expérimentaux de mise en culture de biocénoses benthiques profondes dans les conditions optimales du biotope originel ne permettent malheureusement pas d'éprouver, d'une façon scientifiquement correcte, l'ensemble des relations biotiques existant entre les divers grands groupes d'organismes (bactéries, foraminifères, méiofaune et macrofaune pluricellulaire). Une évaluation des relations de compétition inter et intra-spécifique, de prédation, d'amensalisme, de commensalisme, de coopération et de mutualisme nécessiterait des investigations pluridisciplinaires poussées qui sont malheureusement d'un point de vue logistique encore impossible à l'heure actuelle.

L'étude écologique des communautés de foraminifères benthiques : relation au biotope

Si l'étude des relations entre les foraminifères et les autres groupes d'organismes benthiques peut sembler délicate, la détermination des limitations et des tolérances des espèces de foraminifères benthiques aux conditions physico-chimiques du biotope est beaucoup plus aisée. Parmi la multitude de facteurs environnementaux abiotiques définissant ce biotope, la température, la salinité, la pression, l'oxygénation des eaux de fonds, les processus diagénétiques dans le sédiment superficiel, l'oxygénation des eaux porales, la nature du substrat sédimentaire, la dynamique des courants, les apports sédimentaires terrigènes et les apports de particules organiques sont autant de variables qu'il est possible

d'étudier grâce aux méthodes et matériels actuellement utilisés dans la recherche océanographique. Seule une approche pluridisciplinaire peut donc aboutir à une précision plus exhaustive de l'impact de l'essentiel de ces paramètres environnementaux sur les faunes de foraminifères benthiques. C'est dans cette optique que cette thèse est traitée.

Le programme OXYBENT : une approche pluridisciplinaire pour préciser l'écologie des foraminifères benthiques et des ostracodes du Golfe de Gascogne

Le projet OXYBENT (*OXYgénation et BENThos*), rattaché au programme national *PROcessus biogéochimiques dans l'Océan et Flux* (PROOF) défini par l'Institut National des Sciences de l'Univers (INSU), rassemble les équipes de recherche des trois laboratoires constitutifs de l'Unité Mixte de Recherche 5805 de l'Université de Bordeaux 1. Ces trois laboratoires sont le Département de Géologie et d'Océanographie (DGO), le Laboratoire d'Océanographie Biologique (LOB) et le Laboratoire d'Ēcophysiologie et d'Ēcotoxicologie des Systèmes aquatiques (LEESA). De nombreux laboratoires étrangers à l'Université de Bordeaux 1, se sont également impliqués dans le programme OXYBENT. C'est le cas du Department of Stratigraphy and Paleontology de l'Université d'Utrecht (Pays-Bas), de l'Alfred Wegener Institute de Bremerhaven (AWI, Allemagne), du Department of General Genetics et de l'Institüt für Geologie und Paläontologie de l'Université de Tübingen (Allemagne).

Le programme OXYBENT a permis, entre octobre 1997 et avril 2001, d'effectuer une quantité remarquable de prélèvements à diverses stations benthiques du Golfe de Gascogne. 15 stations s'étalant entre 140 et 2800 mètres de profondeur ont été échantillonnées à l'aide d'un carottier multitube au cours de 11 campagnes océanographiques à bord du bateau scientifique de l'INSU Côtes de la Manche. Ces stations correspondent pour la plupart à des environnements de pente ouverte, certaines d'entre elles se situant dans des environnements de canyon. Le carottier multitube de type Barnett (Barnett, 1984) présente la caractéristique avantageuse de pouvoir collecter en une seule fois 8 carottes de sédiment dont les interfaces eau-sédiment et les eaux de fond surnageantes sont préservées lors des prélèvements. Le carottage ne perturbe en aucun cas le sédiment collecté et conserve admirablement bien les structures sédimentaires relevant de la bioturbation (terriers) ou de processus de dépôts gravitaires (turbidites). En fin de compte, le carottier multitube permet de collecter des portions fidèles de l'écosystème benthique (biocénose et biotope) sur lequel une batterie d'analyses géochimiques, sédimentologiques et faunistiques est alors envisageable.

L'un des buts principaux du programme OXYBENT était d'établir les relations existant entre la méiofaune uni- et pluricellulaire vivant aux diverses stations échantillonnées et les conditions physico-chimiques de ces mêmes environnements benthiques. Il s'agit entre autres de préciser la dynamique des communautés du méiobenthos fossilisable que sont les faunes de foraminifères benthiques et les faunes d'ostracodes en relation aux données biogéochimiques à l'interface eau-sédiment et dans le sédiment. La pluridisciplinarité de ce projet tient du fait qu'en complément des analyses faunistiques, de nombreuses analyses chimiques et sédimentologiques ont été effectuées durant ou à l'issu de chaque campagne océanographique afin de quantifier d'une façon exhaustive les caractéristiques physico-chimiques des stations échantillonnées et notamment les processus diagénétiques.

« Ēcologie des foraminifères benthiques du Golfe de Gascogne : Ētudes de la variabilité spatiale et temporelle des faunes de foraminifères benthiques et de la composition isotopique ($\delta^{18}O$, $\delta^{13}C$) de leurs tests. »

La thèse intitulée « Ēcologie des foraminifères benthiques du Golfe de Gascogne : études de la variabilité spatiale et temporelle des faunes de foraminifères benthiques et de la composition isotopique ($\delta^{18}O$, $\delta^{13}C$) de leurs tests. » s'inscrit parfaitement dans une des problématiques soulevées par le projet OXYBENT à savoir celle d'étudier les relations existant entre le flux de matière organique et le fonctionnement d'écosystèmes benthiques du Golfe de Gascogne. Pour se faire, sept stations du Golfe de Gascogne ont fait l'objet d'analyses faunistiques poussées concernant les foraminifères benthiques ainsi que de la quantification de la diagenèse précoce dans les sédiments (Fig. 4 ; Tableau 1). Des analyses isotopiques $\delta^{13}C$ et $\delta^{18}O$ ont été réalisées sur les tests des espèces dominantes de certaines stations.

Les buts de cette thèse se déclinent en 5 grands points :

1. Eprouver les grandes lignes du modèle TROX (Jorissen et al., 1995) en étudiant la répartition bathymétrique des communautés des foraminifères benthiques dans le Golfe de Gascogne en relation avec le niveau trophique et le niveau d'oxygénation de diverses stations et en précisant les facteurs limitants majeurs contrôlant la densité, la composition et les microhabitats des faunes de foraminifères benthiques. Proposer une adaptation régionale au niveau spécifique de ce modèle.

2. Préciser la dynamique saisonnière et inter-annuelle des communautés de foraminifères benthiques en réponse aux variations saisonnières d'apports de phytodétritus et des changements hypothétiques de la diagenèse précoce, et comparer cette saisonnalité temporelle avec la variabilité spatiale à micro- et méso-échelle.
3. Appréhender la structure des communautés de foraminifères benthiques dans les zones préférentielles d'accumulation de matière organique réfractaire telles que les environnements de canyon.
4. Apprécier les variations chimiques $\delta^{13}C$ et $\delta^{18}O$ du test d'espèces dominantes de foraminifères benthiques en fonction des paramètres environnementaux afin de calibrer des outils paléo-océanographiques.
5. Estimer la pertinence de l'utilisation de certaines espèces de foraminifères benthiques en tant qu'outils de reconstruction qualitative et quantitative de paramètres paléo-environnementaux.

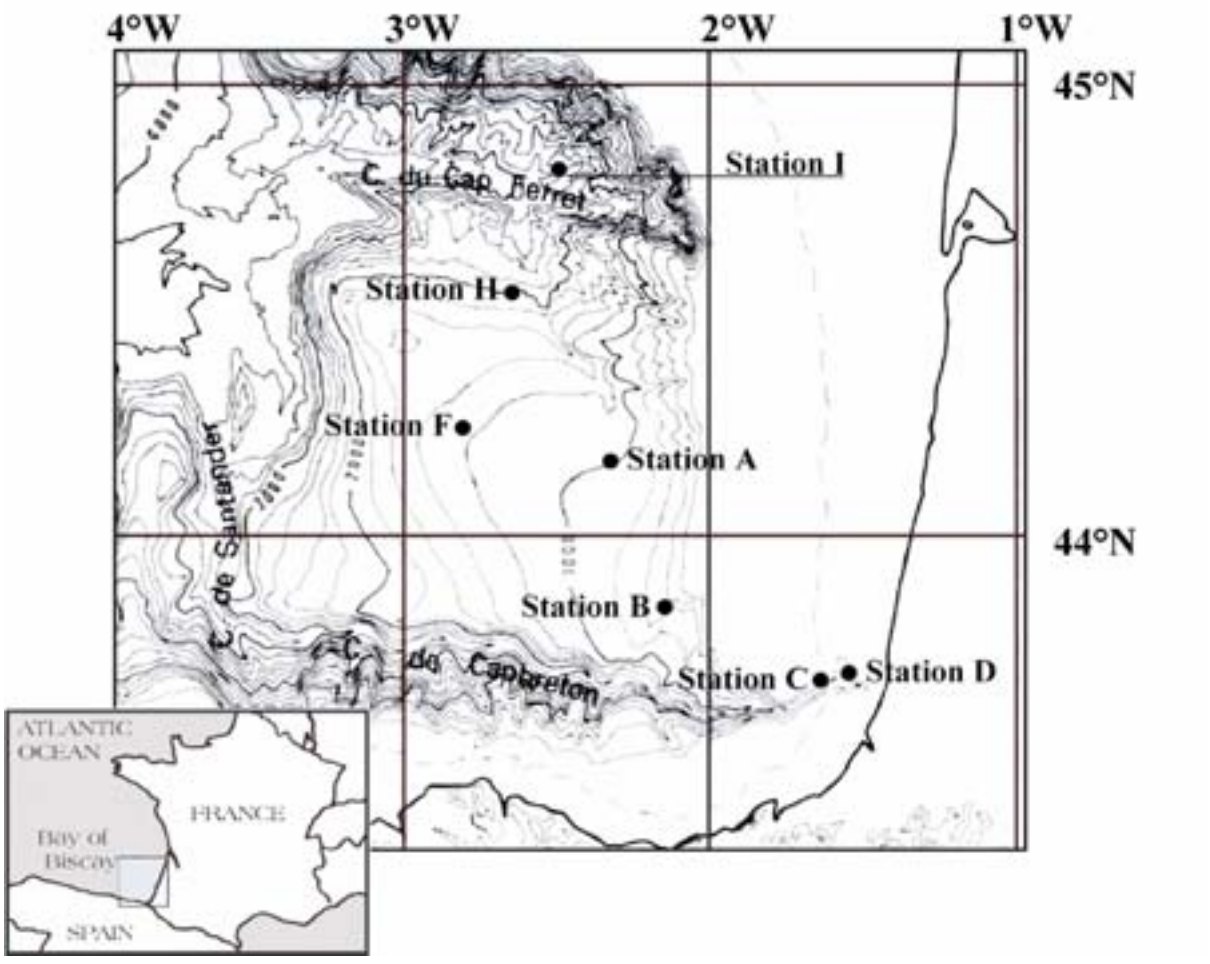

Fig. 4 Zone d'étude du projet OXYBENT et situation géographique des sept stations présentées dans cette thèse

Station	Profondeur (m)	Latitude	Longitude	Date de prélèvement	Nombre de campagnes	Nombre de carottes
D	140	43°41'93N	1°34'10W	Octobre 1997	1	1
C	235	43°40'08N	1°38'87W	Octobre 1997	1	1
B	~550	43°49'98N	2°23'04W	D'octobre 1997 à avril 2000	10	15*
A	~1000	44°09'78N	2°20'27W	D'octobre 1997 à avril 2001	10	12*
F	1264	44°17'10N	2°44'95W	Janvier 1998	1	1
H	1993	44°17'10N	2°44'95W	Octobre 1998	1	1
I	~2800	44°49'46N	2°33'78W	De janvier 1999 à avril 2000	3	4*

Table 1. Profondeur, localisation et date de prélèvement des 7 stations étudiées dans cette thèse. Le nombre de missions océanographiques OXYBENT correspondant et le nombre total de carottes prélevées sont également mentionnés. L'astérisque indique que des duplicata de carottes sont disponibles pour certains prélèvements

Dans le premier chapitre de cette thèse, l'accent est porté sur l'impact que joue le flux exporté de carbone organique, l'oxygénation des eaux de fond et des eaux interstitielles ainsi que les conditions diagénétiques dans le sédiment sur la structure des faunes de foraminifères benthiques de 5 stations de la marge aquitaine. Ces stations s'étalent entre 150 et 2000 mètres de profondeur dans le Golfe de Gascogne (stations D, B, A, H et F). Les apports de matière organique ont une incidence supputée sur les processus diagénétiques et la disponibilité d'oxygène au sein du sédiment. Ils constituent également une source primordiale de nourriture pour les organismes benthiques organohétérotrophes. Aussi, cette étude porte-elle préférentiellement sur les variations de densité, de composition faunistique et de microhabitat des foraminifères benthiques le long du transect bathymétrique défini par les 5 stations en réponse à l'état d'eutrophisation et d'oxygénation des différents biotopes benthiques. Un des buts primordiaux de ce chapitre est notamment d'éprouver les idées soutenues par le modèle TROX (Jorissen et al., 1995) et de créer, si possible, une adaptation locale au niveau spécifique de cette approche conceptuelle.

Dans les second et troisième chapitres, les variations saisonnières des faunes de foraminifères benthiques de deux stations du haut de pente sont envisagées (stations A et B). Ces deux stations se trouvent à 550 et 1000 mètres de profondeur sur la marge aquitaine du Golfe de Gascogne ; elles ont été échantillonnées pendant près de 3 ans (entre septembre 1997 et avril 2001). Grâce à l'utilisation d'images SeaWIFS, il est possible de suivre les variations saisonnières de production primaire dans les eaux de surface durant ces périodes d'échantillonnage. Aussi, notre zone d'étude, marquée par des blooms phytoplanctoniques au printemps et en automne, est-elle idéale pour suivre l'impact des apports saisonniers de

phytodétritus sur la dynamique saisonnière des faunes de foraminifères. Ainsi, dans ces deux chapitres, sont présentés des modèles conceptuels traitant de la dynamique de certaines populations de foraminifères benthiques et des couplages hypothétiques existant entre les productions primaires pélagiques et les réponses des foraminifères benthiques. L'utilisation de duplicata de carottes permet d'évaluer également la variabilité spatiale à méso-échelle des communautés de foraminifères benthiques (« patchiness ») ainsi que l'impact de cette variabilité sur la justesse des analyses concernant les changements saisonniers des faunes benthiques.

Dans le quatrième chapitre sont décrites les faunes de foraminifères benthiques échantillonnées à trois reprises dans une station de canyon située à 2800 mètres de profondeur (station I). Le canyon de Cap-Ferret est actuellement une zone de dépôt centre où se concentre et sédimente préférentiellement une grande quantité de détritus organiques en suspension, transportés depuis les pentes adjacentes. Aussi, la densité, la composition et la distribution verticale dans le sédiment des communautés de foraminifères benthiques de la station I sont-elles comparées avec les caractéristiques de faunes collectées dans les parties profondes et ouvertes de la pente proche notre zone d'étude. L'accent de ce chapitre est porté sur le rôle que peut jouer l'accumulation préférentielle de matière organique remaniée dans une station oligotrophe de bas du canyon sur la dynamique et la structure des faunes de foraminifères benthiques, via l'impact de la consommation accrue de la matière organique sur les gradients biogéochimiques au sein du sédiment.

Dans le cinquième chapitre, une révision de l'ensemble des connaissances concernant le genre *Globobulimina* est entreprise. Ce genre a été maintes fois décrit et utilisé en paléo-océanographie comme une espèce caractéristique de milieux benthiques sous-oxygénés. Cependant, *Globobulimina* constituent une composante dominante de certaines faunes actuelles de nombreux environnements bien oxygénés des marges continentales mondiales. Grâce aux données recueillies dans 7 stations de notre zone d'étude (Golfe de Gascogne), ainsi que l'utilisation d'analyses faunistiques réalisées au large de Cape Blanc (NW Afrique), il est proposé de définir plus précisément les tolérances et les exigences écologiques de ce genre et de préciser la pertinence d'utiliser ce taxon comme outil de reconstruction de paléo-environnements sous-oxygénés. L'utilisation de données génétiques, de mesures isotopiques, d'observations ultrastructurales devraient apporter de nouveaux arguments pour mieux comprendre l'écologie de ce genre.

Dans le dernier chapitre, les analyses isotopiques ($\delta^{13}C$ et $\delta^{18}O$) réalisés sur les tests de 6 espèces majeures de notre zone d'étude sont présentées. Les espèces étudiées sont

Hoegludina elegans, Cibicidoides pachydermus, Uvigerina mediterranea, Uvigerina peregrina, Melonis barleeanus et *Globobulimina* spp. ; elles ont été échantillonnées dans 5 stations de la marge aquitaine du Golfe de Gascogne (stations D, B, A, F et H). Le premier but de ce chapitre est d'apprécier les paramètres abiotiques qui influencent les signatures isotopiques des espèces étudiées le long du transect bathymétrique définis par les 5 stations. La décroissance de la température le long de la pente ainsi que la diminution du flux exporté de carbone organique pourraient avoir des rôles majeurs respectivement sur des isotopes stables de l'oxygène et du carbone de certains taxa de foraminifères. Le second aspect de ce travail consiste à apprécier l'impact de la distribution verticale des espèces de foraminifères benthiques dans le sédiment (microhabitat) sur leurs signatures isotopiques. L'effet de « microhabitat » est un argument généralement avancé pour expliquer les différences de $\delta^{13}C$ enregistrées entre les espèces vivant dans des niches de profondeurs différentes. Enfin, les mesures isotopiques effectuées à la station B pendant près de 3 ans d'échantillonnages peuvent permettre d'appréhender les variations saisonnières de signatures isotopiques en réponse notamment aux apports épisodiques de phytodétritus. L'application en paléo-océanographie des résultats sur les isotopes stables de l'oxygène et du carbone des tests des foraminifères benthiques du Golfe de Gascogne est largement discutée.

Cette thèse s'intègre donc parfaitement dans le projet OXYBENT aujourd'hui terminé (phase d'exploitation) et dans le nouveau projet en cours FORAMPROX *(FORAMinifères et PROXies)* dont l'un des buts est de répondre à la très forte demande actuelle des diverses branches de la paléo-océanographie de définir des outils efficaces et précis de reconstructions quantitatives des paléo-environnements (=proxies).

CHAPITRE 1

Faunes vivantes des foraminifères benthiques du Golfe de Gascogne : densité, composition et microhabitats.

Live benthic foraminiferal faunas
from the Bay of Biscay:
faunal density, composition, and microhabitats.

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Résumé

Dans le Golfe de Gascogne qui présente les caractéristiques d'un bassin méso-oligotrophe, la diminution avec la profondeur du flux de carbone organique exporté depuis la surface vers le fond est accompagnée par une décroissance importante des densités de foraminifères benthiques vivants. Les fluctuations d'apports de matière organique sur le fond provoquent des variations des conditions redox dans le sédiment et de l'oxygénation des eaux interstitielles, alors que l'oxygénation des eaux de fond n'est pas directement perturbée par ces apports. L'apparition d'espèces endopéliques profondes et intermédiaires a été reliée à la présence des fronts redox fondamentaux dans le sédiment ainsi que l'existence supputée de consortia bactériens associés à ces zones de gradients chimiques. La profondeur de principaux fronts redox et donc des microhabitats des espèces endopéliques profondes montre une augmentation significative avec la profondeur d'eau. Aux stations les plus profondes et les plus oligotrophes, les faunes endopéliques profondes deviennent relativement pauvres. Ainsi, le flux exporté de carbone organique apparaît comme le paramètre majeur contrôlant la densité, la composition et la distribution verticale des faunes de foraminifères benthiques sous l'interface eau-sédiment. L'oxygénation des eaux porales ne joue seulement qu'un rôle mineur. Nos résultats sont en accord avec le modèle TROX (Jorissen et al., 1995) qui décrit les microhabitats des foraminifères benthiques comme résultant du flux exporté de détritus organiques et de l'oxygénation de l'écosystème benthique. Une adaptation du modèle TROX utilisant nos données faunistiques et biogéochimiques dans le Golfe de Gascogne est présentée (Fontanie et al., 2002).

Mots-clés : Foraminifères benthiques vivants ; Flux exporté de matière organique ; Conditions redox ; Microhabitat.

Abstract

In the meso-oligotrophic Bay of Biscay, a diminishing downward organic matter flux with depth is accompanied by an important decrease of the live foraminiferal density. Although bottom water oxygenation is not directly influenced by organic matter input, the oxygenation of interstitial waters and the primary redox fronts do change in response to variations of the organic matter flux. The occurrence of deep and intermediate infaunal taxa can be linked to fundamental redox fronts and putative associated bacterial consortia. Our data are in agreement with the TROX-model, which explains the benthic foraminiferal microhabitat as a function of organic flux and benthic ecosystem oxygenation. Both the depth of the principle redox fronts and the microhabitat of deep infaunal species show important increases with depth. At the deepest oligotrophic stations, deep infaunal faunas become relatively poor. Therefore, the exported flux of organic matter appears to be the main parameter controlling the composition and the vertical distribution of benthic foraminiferal faunas below the sediment-water interface. The oxygenation of pore waters plays only a minor role. A species-level adaptation of the TROX-model is presented for the Bay of Biscay.

Keywords : Live benthic foraminifera; Exported organic matter flux; Redox conditions; Microhabitat.

Introduction

Benthic foraminifera are an important component of the meiofaunal community of deep-sea detritus feeders. In deep-sea environments, they commonly represent more than 50% of the total biomass (Gooday et al., 1992). Thanks to their extraordinary potential of adaptation, benthic foraminifera are able to survive and proliferate in a wide range of marine environments, including extreme ecosystems, such as oligotrophic abyssal plains (Tietjen, 1971; Coull et al., 1977) or hydrothermal vents (Sen Gupta and Aharon, 1994). Because of their potentially important role in deep ocean environments, they are at present studied intensively for a better understanding of their role in the benthic ecosystem and for a more precise definition of their contribution to the recycling of organic matter at the ocean floor.

There is a general consensus that the faunal composition of heterotrophic benthic foraminiferal faunas is strongly linked to the quantity and quality of the organic detritus

reaching the ocean floor, and to the oxygenation at the sediment-water interface and of the interstitial waters in the first cm of the sediment (e.g. Van der Zwaan, 1982; Altenbach and Sarnthein, 1989; Loubere et al., 1993; Fariduddin and Loubere, 1997; Jorissen et al., 1998). In this context, this paper describes the variability of live (Rose Bengal stained) benthic foraminiferal assemblages along a transect in the Bay of Biscay comprising 5 stations from 140 to 2000 m water depth (Table 1, Fig.1). Since 1997, a number of stations in this depth range have been sampled periodically in order to follow the temporal and spatial succession of the benthic foraminiferal faunas.

The Bay of Biscay is a typical temperate meso-oligotrophic environment with two annual bloom periods. The first one, in late winter or early spring, is associated with a shallowing of the mixed layer and with a strengthening of the rather shallow thermocline. Moreover, internal waves associated with strong spring neap tides cause nutrient injection into the photic zone and subsequent phytoplankton blooms at the shelf break in the northern part of the basin (Pingree et al., 1986). The second main bloom event, less marked than the first one, is commonly recorded in autumn, when the summer thermocline starts to be eroded by a deepening of mixing. The advantage of a study of benthic foraminiferal ecosystems in this mesotrophic-oligotrophic context is the fact that the oxygenation at the sediment-water interface is not seriously influenced by the seasonal variability of the organic matter input. The bottom water oxygen concentrations at the five stations are always relatively high (Table 1), and the seasonal monitoring of the oxygenation indicates that the concentrations do not vary significantly throughout the year (Anschutz et al., 1999; Hyacinthe et al., 2001). Therefore, ecosystem variability is probably caused mainly by changes in the organic flux reaching the ocean bottom. The downward organic flux varies with water depth and in response to the temporal and spatial oscillations of primary production in the surface waters. The five stations discussed in this paper were all sampled in late autumn-early winter (of the years 1997 and 1998; Table 1). The stations were selected in order to better understand the influence of the spatially variable organic matter flux reaching the ocean bottom on benthic foraminiferal faunas in an open slope setting. Our study focuses on the faunal density and composition and on foraminiferal microhabitats. The microhabitat is defined as the vertical distribution of a taxon in the first cms of the sediment, which is controlled by the composite action of all physical, chemical and biological processes (Corliss, 1985). Understanding the foraminiferal microhabitat is important, because it allows the precise trophic and oxic requirements of each species in the total live benthic foraminiferal assemblage to be known.

The main objectives of this paper are (1) to present and discuss variation of the foraminiferal density with increasing water depth and thus with calculated diminishing organic fluxes, (2) to better explain the compositional changes observed along the five stations bathymetrical/trophic transect, and (3) to explain the microhabitat changes in response to the trophic conditions at the sediment-water interface.

Study area, material and methods

The Bay of Biscay is a semi-enclosed basin at the eastern side of the North Atlantic Ocean, bathed by rather homogeneous oceanic waters belonging to the North Atlantic thermohaline and geostrophic circulation and more precisely, to the North Atlantic Drift. The Bay of Biscay is bordered by the Irish shelf in the north, the Armorican and Aquitaine shelves in the east, and by the Iberian shelf in the south. The hydrographical structure is relatively well known (Ogawa and Tauzin, 1973). The patterns of the surface waters are strongly constrained by seasonal variations of the thermocline and the mixed layer. Below the surface waters (≤150 m depth), the Northern Atlantic Central Waters (NACW) are present down to 800 m depth. Between 800 and 1200 m, a branch of Mediterranean outflow waters is present. In comparison with the surrounding water masses, these Mediterranean Waters (MW) are characterised by a high salinity (35.80-35.85, Le Floch, 1968). They have the lowest oxygen values for the Bay of Biscay (3.8 ml/l, Le Floch, 1968; 4.36 ml/l, this paper). Below the Mediterranean Waters, Intermediate Atlantic Water and Polar Atlantic Water, both belonging to Northern Atlantic Deep Waters, fill the deepest parts of the basin. Within the Bay of Biscay, exchanges between the deeper parts and the coastal waters are rather insignificant, especially in spring and summer when a dome of cold and dense water on the continental shelves limits advection of sub-surface water (Ogawa and Tauzin, 1973).

The continental slope bordering the French shelf deepens gradually, and is interrupted by two large canyons (Cap Ferret Canyon, Cap Breton Canyon, Fig.1). Vertical fluxes represent the main sedimentary component in open slope environments, whereas lateral advection may dominate sedimentary processes in the canyons (Heussner et al., 1999). The present paper concentrates on the open-slope environments, where the impact of laterally advected particles is supposed to be minimal, and where the linkage between surface water primary production, the vertical particle flux, and benthic life should be rather straightforward.

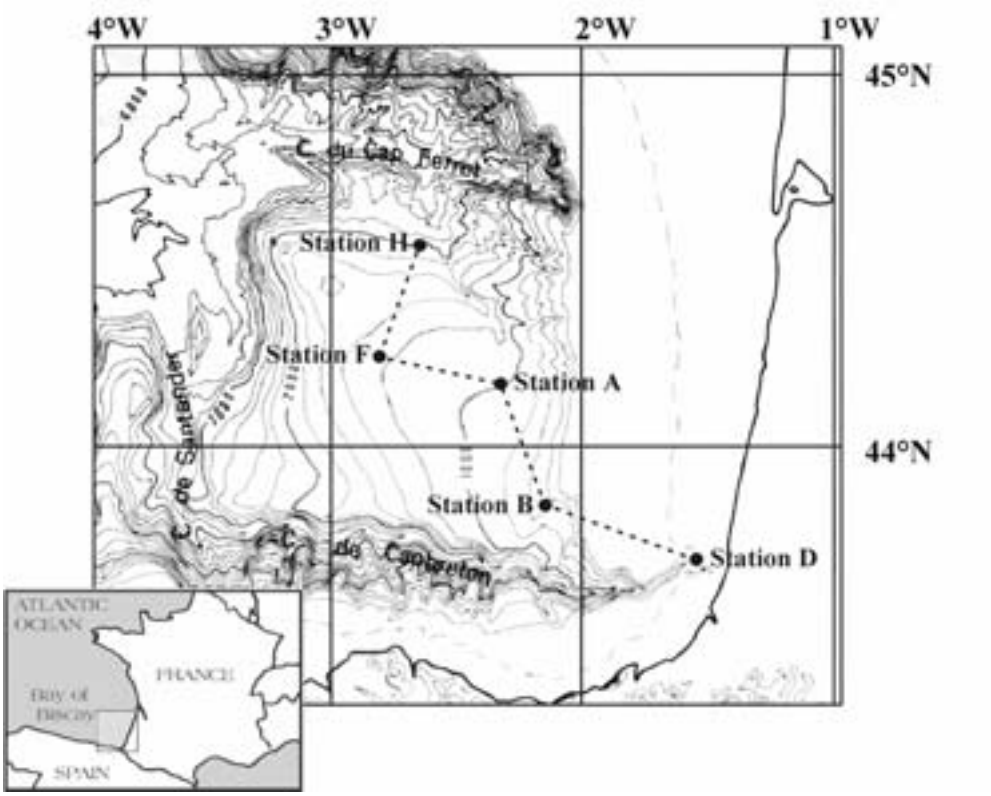

Fig. 1 Study area, bathymetry and geographical position of the five stations.

Few data are available on primary production in general or on the occurrences of bloom events in the Bay of Biscay. Tréguer et al. (1979) estimate a production between 0.4 and 1.9 g C/m^2/day for the spring bloom of 1973. Measurements of primary production in the central part of the Bay of Biscay during the autumn bloom of 1972 yielded values between 0.3 and 0.4 g C/m^2/day (Le Corre and Tréguer, 1976). These values agree with recent data obtained in the Cap Ferret region during five ECOFER cruises: from 0.7 to 1.2 g C/m^2/day in spring (May 1990 and 1991) and 0.3 g C/m^2/day in October 1990 (Laborde et al., 1999). Laborde et al. (1999) estimate total annual primary production between 145 and 170 g C/m^2/yr. Generally, phytoplankton blooms in the Bay of Biscay are composed of diatoms (mainly *Chaetoceros* spp. and *Nitzschia* spp.) and coccolithophorids (*Gephyrocapsa oceanica, Emiliania huxleyi*; Tréguer et al., 1979; Fernandez et al., 1995). Fernandez (1990), however, shows that in the Central Cantabrian Sea (southern part of the Bay of Biscay) high chlorophyll-a and primary production rates observed in March consist predominantly of microflagellates. Moreover, in the Celtic Sea, coccolithophore blooms (*Emiliania huxleyi*) may also occur during summer (Fernandez et al., 1993). Finally, Pingree et al. (1986) demonstrate a chlorophyll increase over the shelf break of the northern French shelf, due to

internal and tidal waves; these rather exceptional and short bloom events occur during neap tides in spring.

In cases where the particle flux is mainly vertical, and where we have a quantitative estimate of the surface water primary production, we can use the formula proposed by Berger and Wefer (1990), and improved by Herguera (1992), to estimate the annual organic matter flux Jz that reaches the ocean bottom at different water depths:

$$J_Z = \left(\left(2 \times \sqrt{PP}\right) \times \left(PP/z\right)\right) + \left(\left(5/\sqrt{PP}\right) \times \left(PP/\sqrt{z}\right)\right)$$

where:

PP = Primary Production, in g C/m^2/year

z = Water depth (in m)

Jz = Organic flux at a water depth of z metres, in g C/m^2/year

This formula differentiates between a labile component (first term), which is supposed to represent easily metabolisable organic detritus, and a more refractory component (second term), which decreases much more slowly with depth. We assume that benthic life will be affected mainly by the first term. When we use a mean primary production value of 150g C/m^2/year, for all stations, irrespective of water depth and distance from shore, and when we consider only the vertical transport of particles, the total exported flux at the shallowest station (D, 140 m) can be estimated at 31.4 g C/m^2/year, with a labile fraction of 26.6 g C/m^2/year. At the deepest station (H, 1993 m) the estimated total exported flux is 3.2 g C/m^2/year, with a labile component of 1.8 mg C/m^2/year. Estimated total flux values for the intermediate stations B (553 m), A (1012 m) and F (1264 m) are 9.2, 5.6 and 4.6 g C/m2/yr, respectively; whereas the estimates for the labile component are 6.6, 3.6 and 2.9 g C/m2/yr, respectively. These values suggest that the labile organic carbon flux, which should represent a readily available food source for the benthic fauna, is about 15 times higher in the shallowest station D than in the deepest station H.

The five stations D, B, A, F, and H have been selected to compose a rather ideal SE-NW transect, ranging from the outer shelf to bathyal open slope environments (Fig.1; Table 1). Station D is situated at 140 m depth, at the diffusive boundary between the surface waters and the Northern Atlantic Central Waters. According to Ogawa and Tauzin (1973), the NACW and the basal part of surface waters can be characterised by a seasonally constant temperature of 11.9° C and an invariant salinity of 35.60. CTD data recorded during

PROTAGO program (February 2003) show that water mass at 140 m depth in our study area present a temperature of about 12.5°C and a salinity of 35.50. The temperature and salinity of more superficial surface waters (0-100 m depth) are strongly influenced by the seasonality of mixing, thermocline depth, and continental runoff. The sandy mud deposits found at station D are typical of the sedimentary conditions found in outer shelf environments.

Station	Sample	Depth (m)	Date	Latitude	Longitude	Oxygenation (ml/l)	Zero O_2 boundary
D	OB1D	140	October 1997	43°41'93N	1°34'10W	4.90	8 mm
B	OB1B	553	October 1997	43°49'98N	2°23'04W	4.80	17 mm
A	OB1A	1012	October 1997	44°09'08N	2°20'27W	4.36	18 mm
F	OB2F	1264	Februar 1998	44°17'10N	2°44'95W	4.70	64 mm
H	OB5H	1993	October 1998	44°32'00N	2°37'00W	5.85	63 mm

Table 1 Water depth, sampling date, geographical position, bottom water oxygen and depth in the sediment of the zero oxygen level for the five stations used in this paper.

Station B is positioned at 553 m depth. This site represents a mid-slope environment, isolated from possible lateral input of sediment (turbidites and slumps), which could occur in this depth range in areas closer to the two main canyon systems. Station B is positioned within the NACW, which has a salinity of 35.60 and a temperature of about 11° C (Ogawa and Tauzin, 1973). The sediment consists predominantly of fine-grained silty mud.

Station A (1012 m depth) was selected for its strategic position inside the branch of Mediterranean outflow waters (MW). This water mass has a temperature of about 9.5° C and a salinity of 35.75 (Durrieu de Madron et al., 1999). Sediments at this depth are predominantly silty muds.

Station F, at 1264 m deep, is positioned in the upper layers of Northern Atlantic Deep Waters (Intermediate Atlantic Waters), commonly characterising the bottom waters of the Celtic Sea (8° C, 35.65, Ogawa and Tauzin, 1973; 8°C, 35.50, Durrieu de Madron et al., 1999). The sediments are silty muds.

Station H, at 1993 m depth, is typical for benthic environments found in the Northern Atlantic Deep Waters. Although this station is geographically rather close to the Cap Ferret Canyon, it is still an open slope environment with muddy sediments. The water temperature is about 4° C and the salinity is about 35.00 (Ogawa and Tauzin, 1973; Durrieu de Madron et al., 1999).

All cores were sampled with a classic Barnett multi-tube corer (Barnett et al., 1984). Each tube has a surface area of about 72 cm², and accordingly, all our faunal density data are

standardised for this surface area. The multi-corer allows sampling of the first dm of the sediment, the overlying bottom waters, and an undisturbed sediment-water interface. Free waters were collected immediately after core recovery for dissolved O_2 measurements by the Winkler titration method (Strickland and Parson, 1972). Profiles of pore water O_2 were obtained on board with a cathode-type mini-electrode (Revsbech and Jørgensen, 1986; Helder and Baker, 1985; Revsbech, 1983). The temperature was maintained by using an insulating device. This operation was completed in duplicate within 30 minutes after core recovery. Subsequently, the core used for O_2 profiling was sliced in thin horizontal sections (every 0.5 cm for the top 2 cm, 1 cm or 2 cm below) within 1 $^1/_2$ hours. For every level a sub-sample was immediately sealed in a pre-weighed vial and frozen under inert atmosphere (N_2) for further analyses of porosity and chemistry of the solid fraction. Another sub-sample was centrifuged under N_2 at 5000 rpm for 20 min for collection pore waters. Two aliquots of water were filtered (0.2 µm) and frozen at -25°C for nutrient analyses. In the laboratory, porosity was determined by comparison of the weights of wet and freeze-dried sediment. Interstitial water compounds were analysed by techniques adapted for small volumes (Anschutz et al., 1999; Hyacinthe et al., 2001). Nitrate and nitrite were measured by flow injection analysis (FIA) according to Anderson (1979). Sulphate was measured by a nephelometric method (Stookey, 1970).

For faunal analysis, one entire core was sliced horizontally for each station; every 0.25 cm for the first cm of sediment, every half cm between 1 and 4 cm depth, and every cm between 4 and 10 cm. Exceptionally, for station A, the core was cut into 0.5 cm slices between 1 and 4.5 cm, and, for station D, the first cm was cut into 3 slices (0-0.35 cm, 0.35-0.75 cm and 0.75-1.0 cm). Sediments were stored in 500 cm^3 bottles, which were filled with 95% ethanol containing 1g/l Rose Bengal stain. Rose Bengal staining is commonly used to identify live foraminifera (Walton, 1952). All samples were gently shaken for several minutes in order to get a homogeneous mixture. In the laboratory, they were sieved through 63 and 150 µm mesh screens, and the sieve residues were stored in 95% ethanol. Stained foraminifera belonging to the 150 µm fraction were sorted from wet samples, and stored in Chapman slides. The 63-150 µm fraction was preserved for future studies. The interpretation of staining of benthic foraminifera is rather subjective. One problem of this technique is the fact that Rose Bengal may stain the protoplasm of dead foraminifera, which may be relatively well preserved for a considerable period of time under the anoxic conditions that generally prevail deep in the sediment (Bernhard, 1988; Corliss and Emerson, 1990). As a consequence, a strict application of the staining criteria is most times easy in superficial samples, but may

become more critical in the deeper levels. In all cases, we applied our staining criteria (all chambers except the last one stained brightly pink) very strictly, and compared doubtful individuals with perfectly stained individuals of the same species found in superficial sediment layers. Non-transparent agglutinated and miliolid taxa were broken on many occasions for inspection of the interior of the test. We tried to identify most of live foraminifera at specific level. We used taxonomic references which are presented in Appendix A. Fragments of branch-like agglutinating foraminifera (such as *Hyperammina*) and *Glomospira charoides* and *Glomospira gordialis* (which, because of the orange-reddish colour of their test are very difficult to confirm as living), were not included in the quantitative analyses.

In order to describe the vertical distribution of the total faunas or individual taxa, we use the Average Living Depth (ALD, Jorissen et al., 1995), which allows a rapid description of the microhabitat patterns. The ALD is calculated with the following formula:

$$ALD_x = \sum_{i=0,x} (n_i \times D_i) / N$$

x = lower boundary of deepest sample
n_i = number of individuals in interval i
D_i = midpoint of sample interval i
N = total number of individuals for all levels

For all stations, ALD_{10} was calculated for the whole fauna as well as for individual taxa, on the basis of the numbers of stained individuals found in the successive sediment slices. Isolated individuals separated from the main population by more than 1 cm of "sterile" sediment (without live individuals of the studied taxa) were not integrated in the calculations of the ALD_{10}. We suppose that such isolated individuals had been transported downward (outside their normal microhabitat) by bioturbation, or correspond to dead organisms that have been counted erroneously. In the data sheets (Tables 2a-e), the latter individuals are indicated in brackets.

After the first classification with four main microhabitats proposed by Corliss and Chen (1988), it was argued that only species living on elevated substrates can be considered as "epifaunal" (Buzas et al., 1993). Therefore, in the soft bottom communities described in this study, we recognise only three different groups: shallow infaunal, intermediate infaunal and deep infaunal species.

Results

The total density of the live foraminiferal fauna was determined by integrating the numbers of live individuals picked in all levels from 0 to 10 cm depth. It is expressed as the number of live foraminifera found in and below a 72 cm^2 surface area (Fig.2). Concerning vertical profiles, specific foraminiferal densities were normalized for each layer to a 50 cm^3 sediment volume; we generally regrouped the four uppermost slices of each core into two 0.5 cm thick samples. The percentages of the various taxa were calculated on the basis of the non normalized densities.

Figure 2, which presents the foraminiferal densities for the five stations, shows a clear negative correlation between the foraminiferal density and water depth. The shallowest station D, with about 2000 live individuals collected, presents a maximum value, whereas stations H and F, with 179 and 122 individuals, respectively, are much poorer.

At all 5 stations, perforate foraminifera form the main component of the benthic foraminiferal faunas (75-90%; Fig.2). At station B, they compose almost 90% of the total fauna. Agglutinated taxa account for 10 to 20% of the total fauna, whereas miliolids are rare in all stations (between 0.3 and 8.2%). The latter group tends to be richer on the middle and lower slope (between 4.2 and 8.2%) than on the outer shelf and upper slope, where they are almost absent.

Species diversity is highest at station B where about 50 species are found. Station D, with 36 species, is slightly less diverse. Station A contains 48 species; at stations F and H, where agglutinated and porcellaneous taxa represent more than half of all species, 25 and 28 species are found, respectively.

Bottom waters at station D (140 m) have an oxygen concentration of 4.9 ml/l. Within the sediment, there is a rapid decrease, until anoxic conditions are reached at 0.8 cm depth (Fig.3a). The nitrate + nitrite profile shows a sharp decrease in the first mm of the sediment, suggesting that also the zone of nitrate reduction is extremely close to the sediment-water interface. Sulphate reduction is chemically detected below 5 cm depth, and corresponds to an increase of particulate sulphur and a decrease of dissolved sulphate. This is the only station where sulphate reduction is significant. Station D, which has the highest foraminiferal density

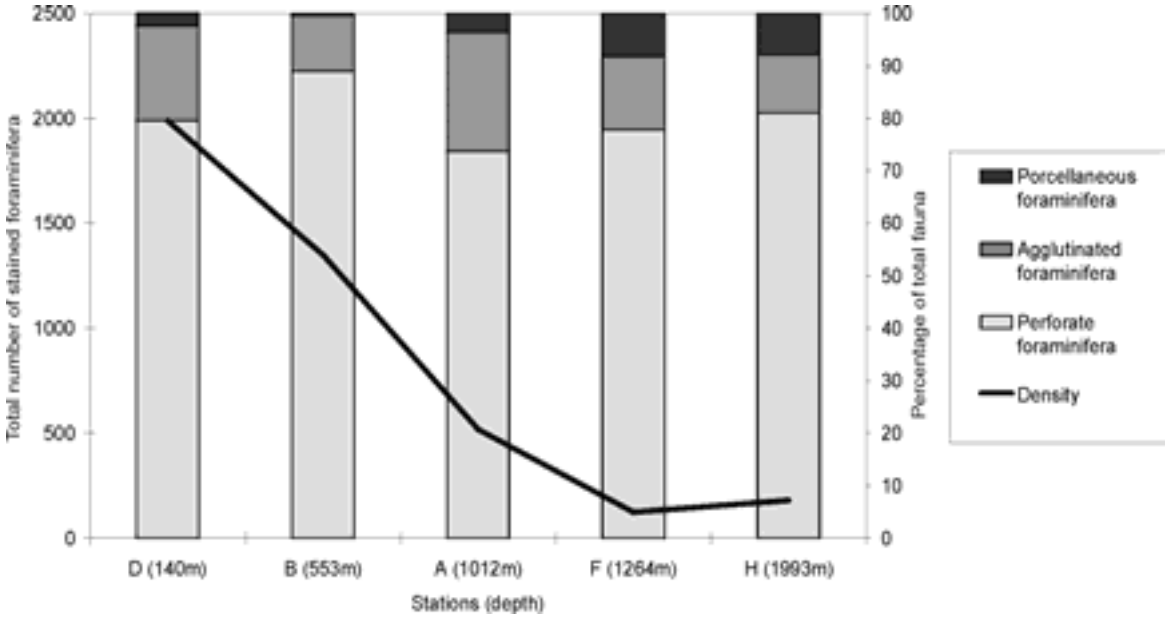

Fig. 2 Abundance of the three main foraminiferal groups, and the density of foraminiferal faunas (total number of stained foraminifera per core (720 cm^3)) along the bathymetrical transect.

of all five stations (1989 individuals/72 cm^2), presents a faunal assemblage that is strongly concentrated in the uppermost cm of the sediment (Fig.3b). The highest density is recorded in the superficial sample (0.00-0.35 cm), where a value of 1400 live individuals/50 cm^3 has been calculated. This value falls abruptly to about 350 individuals/50 cm^3 in the 0.75-1.0 cm level, where the oxygen concentration is already close to zero. About 350 live foraminifera/50 cm^3 can still be noted in the 1.0-1.5 cm level, in a completely anoxic environment. The ALD_{10} (Average Living Depth) of the total live fauna is 1.1 cm. The fauna is dominated by *Chilostomella oolina* (30.2%), *Valvulineria bradyana* (17,0%), *Clavulina cylindrica* (15.0%), *Nonion scaphum* (13.0%), *Bolivina subaenariensis* (3.1%), *Hyalinea balthica* (2.7%) and *Bulimina marginata* (2.3%) (Table 2a). *V. bradyana* (ALD_{10} = 0.4 cm), *C. cylindrica* (ALD_{10} = 0.4 cm), and *C. oolina* (ALD_{10} = 1.2 cm) are the dominant taxa in the well-oxygenated first half cm (Fig.3c). They are accompanied there by less frequent species such as *Bolivina alata, B. subaenariensis, Uvigerina peregrina* and *Rectuvigerina phlegeri*. *C. oolina* (ALD_{10} = 1.2 cm), and *N. scaphum* (ALD_{10} = 1.8 cm) dominate the faunas in the anoxic zone from 1-3 cm depth. Some rare individuals of *Bulimina aculeata* and *B. marginata* are found in the totally anoxic environments below 3 cm depth.

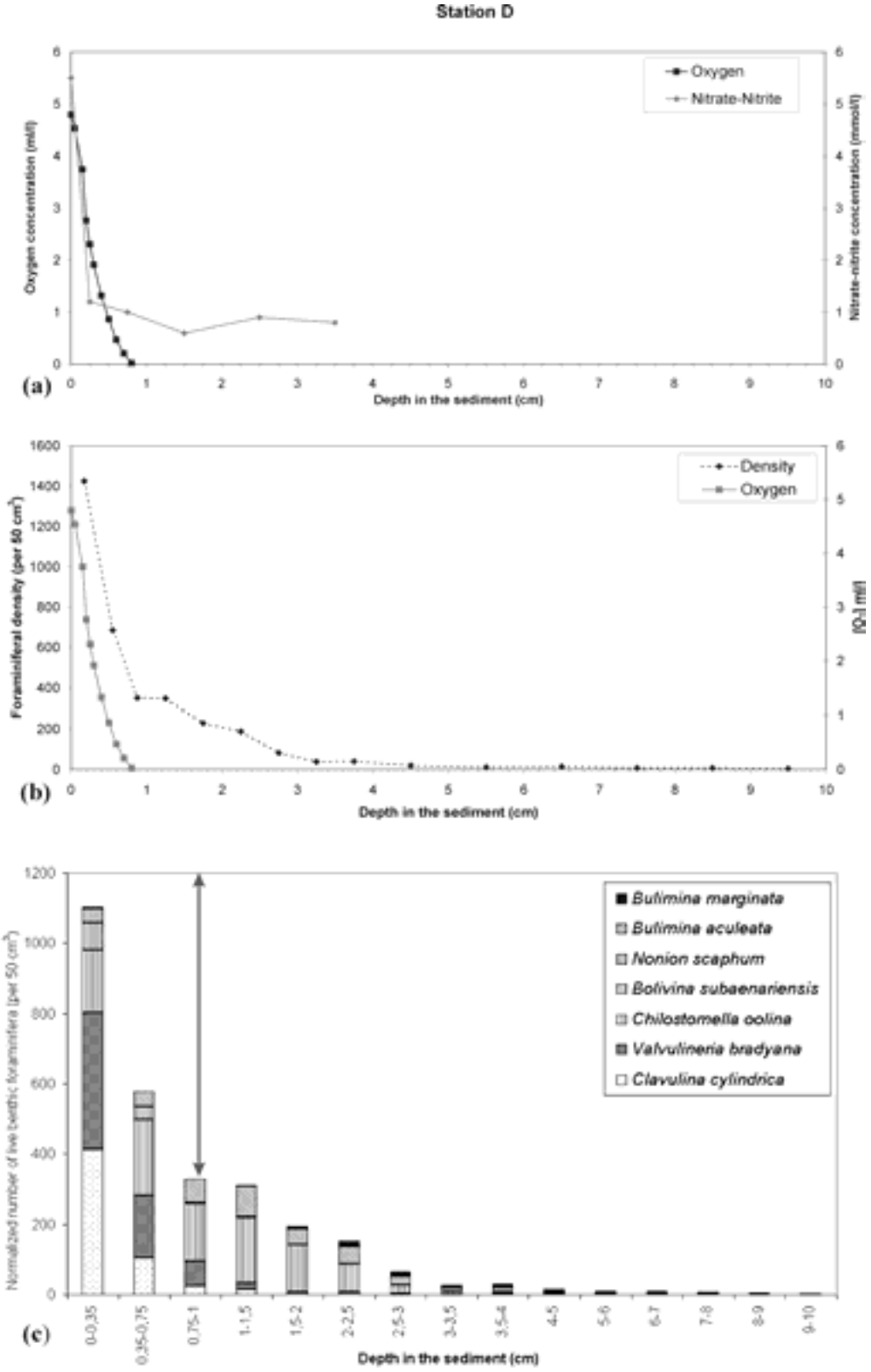

Fig. 3 Station D; 3a: Dissolved oxygen, and concentration of nitrate + nitrite; 3b: Dissolved oxygen profile and foraminiferal density (standardized for a 50 cm^3 sediment volume); 3c: Foraminiferal distribution (number of individuals found in each level, standardized for a 50 cm^3 sediment volume); double arrow represents zero oxygen boundary.

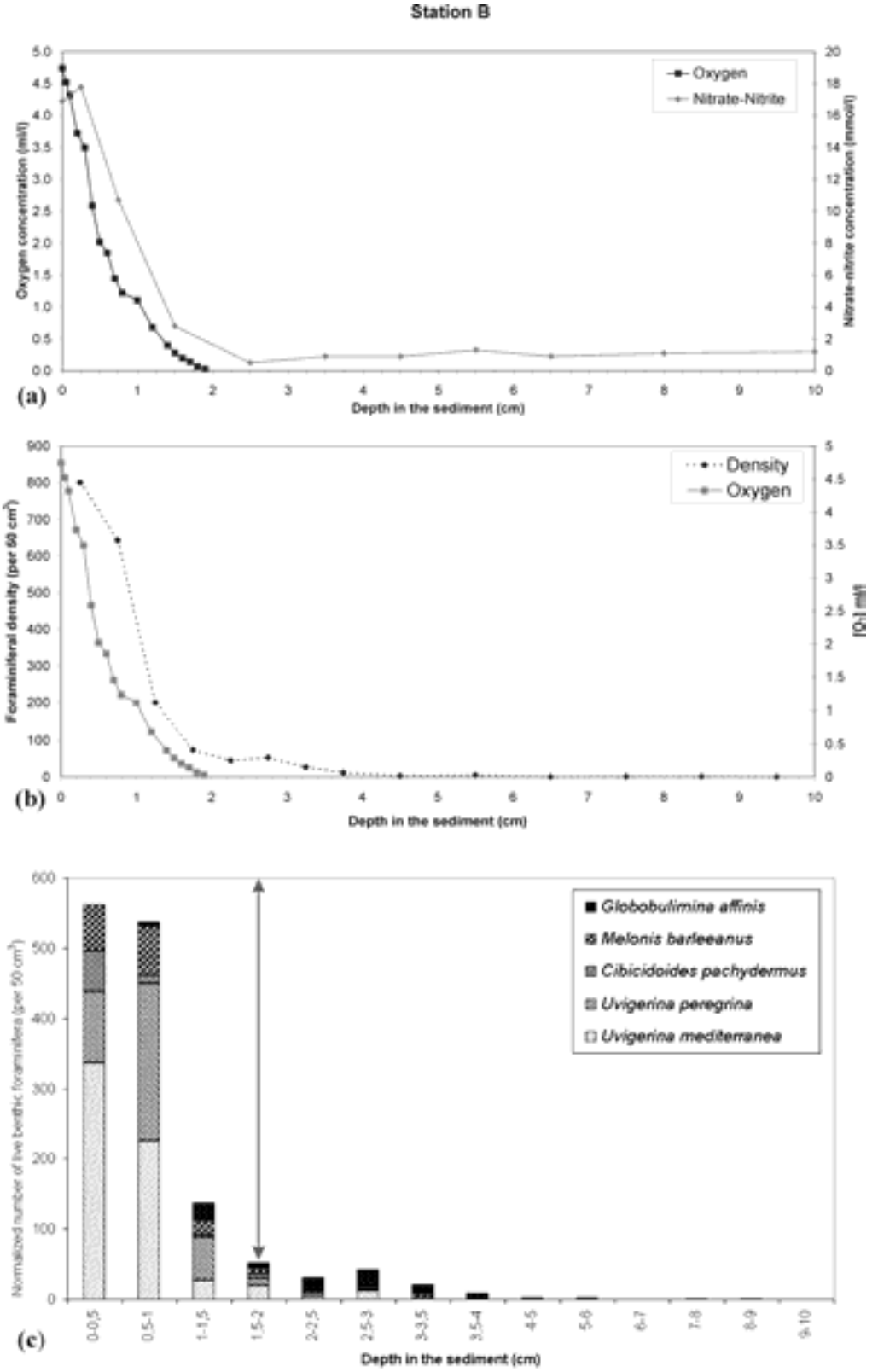

Fig. 4 Station B; 4a: Dissolved oxygen, and concentration of nitrate + nitrite; 4b: Dissolved oxygen profile and foraminiferal density (standardized for a 50 cm^3 sediment volume); 4c: Foraminiferal distribution (number of individuals found in each level, standardized for a 50 cm^3 sediment volume); double arrow represents zero oxygen boundary.

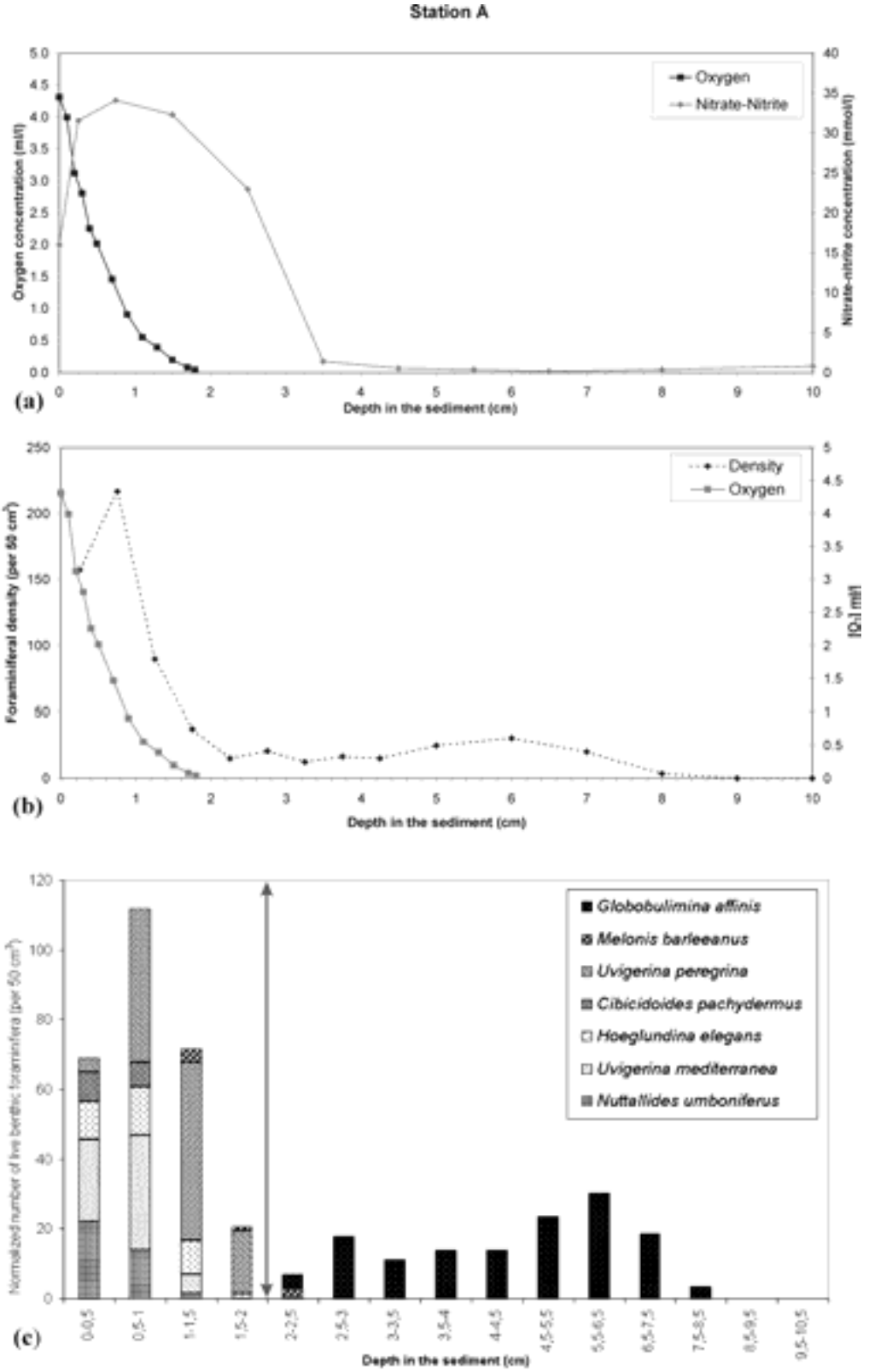

Fig. 5 Station A; 5a: Dissolved oxygen, and concentration of nitrate + nitrite; 5b: Dissolved oxygen profile and foraminiferal density (standardized for a 50 cm^3 sediment volume); 5c: Foraminiferal distribution (number of individuals found in each level, standardized for a 50 cm^3 sediment volume); double arrow represents zero oxygen boundary.

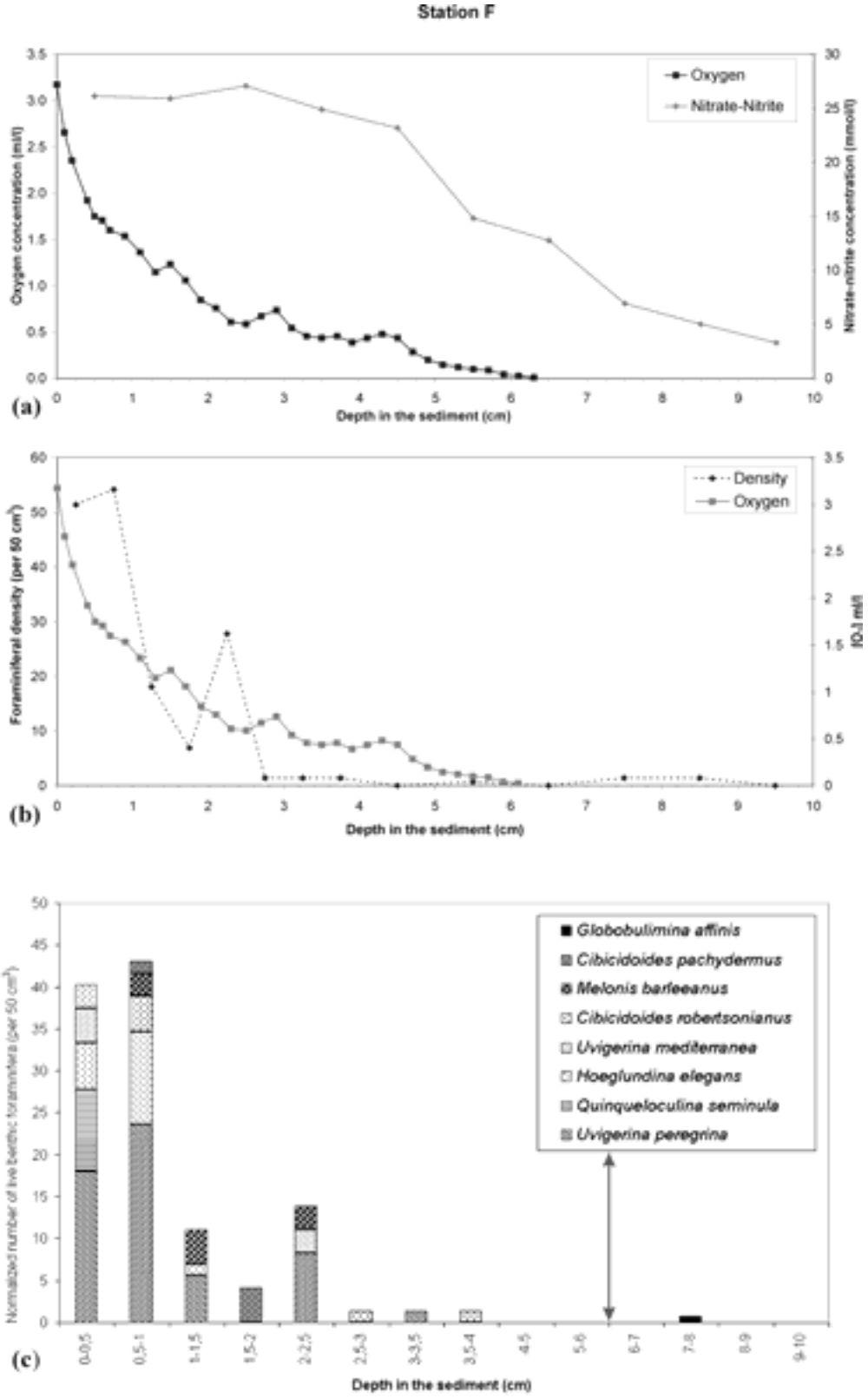

Fig. 6 Station F; 6a: Dissolved oxygen, and concentration of nitrate + nitrite; 6b: Dissolved oxygen profile and foraminiferal density (standardized for a 50 cm^3 sediment volume); 6c: Foraminiferal distribution (number of individuals found in each level, standardized for a 50 cm^3 sediment volume); double arrow represents zero oxygen boundary.

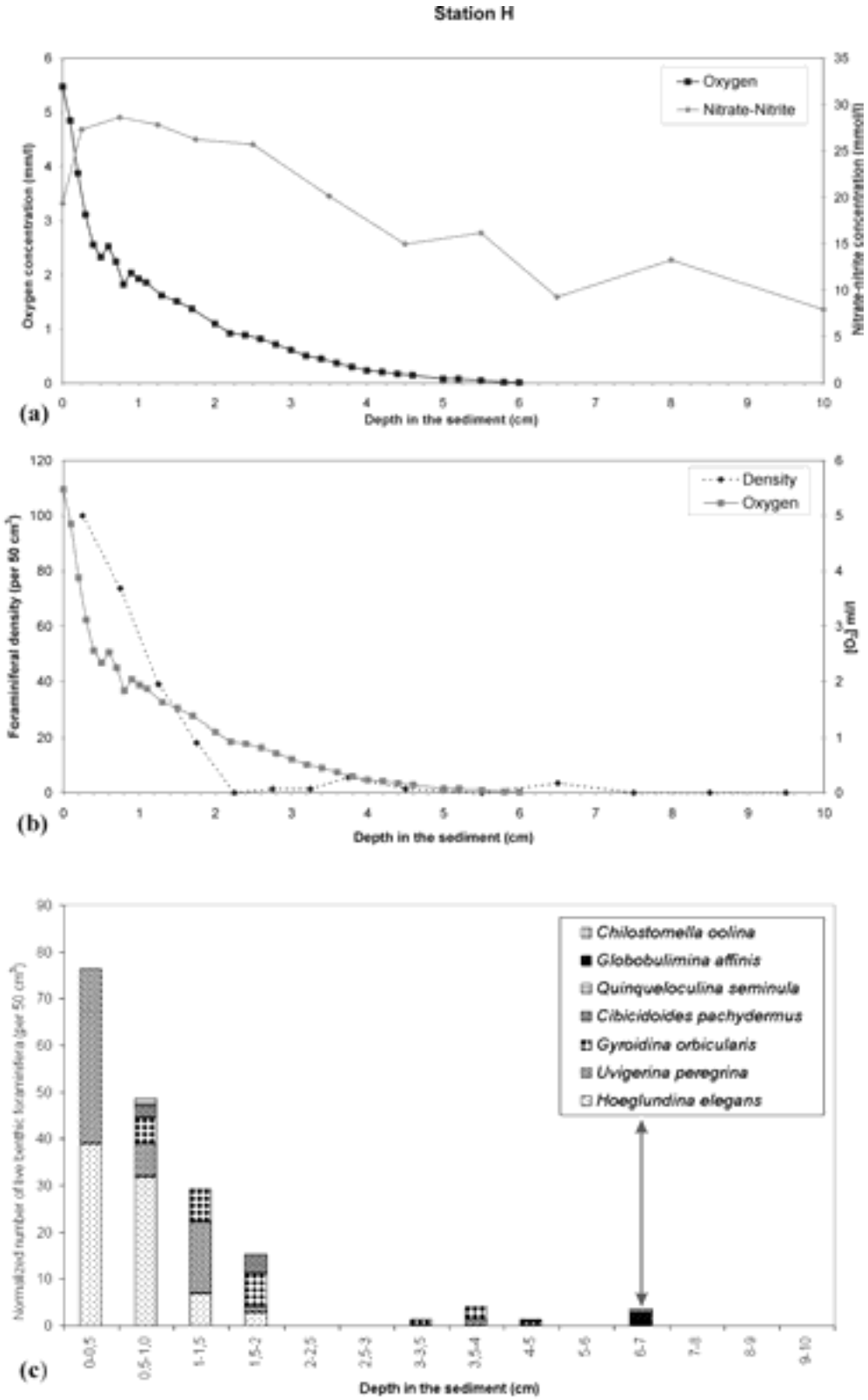

Fig. 7 Station H; 7a: Dissolved oxygen, and concentration of nitrate + nitrite; 7b: Dissolved oxygen profile and foraminiferal density (standardized for a 50 cm^3 sediment volume); 7c: Foraminiferal distribution (number of individuals found in each level, standardized for a 50 cm^3 sediment volume); double arrow represents zero oxygen boundary.

At station B (water depth 553 m), the bottom water oxygen concentration is 4.8 ml/l. The zero oxygen level is found at about 2 cm depth (Fig.4a). Well-oxygenated conditions prevail in the first half cm. A downward diffusive zone of nitrate and nitrite extends from 0.25 to 2.25 cm depth. Figure 4b shows that maximal densities (between 800 and 650 individuals/50 cm^3) are found in the top first cm. Faunal numbers drastically drop to about 40 individuals/0.5 cm level at 1.75 cm depth. The ALD_{10} of the total live fauna is 0.8 cm. The benthic foraminiferal fauna is strongly dominated by *Uvigerina mediterranea* (33.6%), *Uvigerina peregrina* (21.5%), *Melonis barleeanus* (9.0%), *Globobulimina affinis* (6.0%) and *Cibicidoides pachydermus* (4.7%) (Table 2b). *U. mediterranea* (ALD_{10} = 0.6 cm), accompanied by *C. pachydermus* (ALD_{10} = 0.6 cm), dominate the superficial sediments (Fig.4c). Slightly deeper, between 0.5 and 1.5 cm depth, *U. peregrina (*ALD_{10} = 0.8 cm) and *M. barleeanus* (ALD_{10} = 0.8 cm) show maximum frequencies. *G. affinis* (ALD_{10} = 2.4 cm) thrives preferentially in the deeper part of the core. It increases below 1.0 cm depth and becomes the only remaining dominant taxon below 2.25 and 6.5cm depth.

At station A (water depth 1012 m), the oxygen concentration is 4.36 ml/l. The zero oxygen level is found at about 2.0 cm depth, whereas a nitrate + nitrite downward diffusive zone extends from 0.75 to 3.5 cm depth (Fig.5a). Figure 5b depicts a bimodal distribution of the benthic foraminiferal fauna. A first density maximum (180 individuals/50 cm^3) is recorded around 1 cm depth, a second one (40 individuals/50 cm^3) occurs deeper in the sediment, at about 6 cm depth. The ALD_{10} of the total live fauna is 1.8 cm. *Globobulimina affinis* (26.5%), *Uvigerina peregrina* (16.4%), *Uvigerina mediterranea* (8.7%), *Nuttallides umboniferus* (5.2%), *Hoeglundina elegans* (5.0%), *Cibicidoides pachydermus* (2.1%) and *Melonis barleeanus* (1.2%) are the dominant taxa of station A (Table 2c). *N. umboniferus* (ALD_{10} = 0.4 cm), *U. mediterranea* (ALD_{10} = 0.6 cm), *C. pachydermus* (ALD_{10} = 0.3cm) and *H. elegans* (ALD_{10} = 0.8 cm) constitute a rich superficial fauna, which is present in the well-oxygenated first cm (Fig.5c). *U. peregrina* (ALD_{10} = 1.1 cm), accompanied by *M. barleeanus* (ALD_{10} = 1.7 cm), occupies slightly deeper layers and is the dominant component of the shallowest density peak. *G. affinis* (ALD_{10} = 4.7 cm) dominates the rich stained fauna below 2 cm depth.

Station D 140m																		
Depth	0-0.35	0.35-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																	
Amphicoryna scalaris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
Bolivina alata	26	10	1	0	0	0	0	0	0	0	0	0	0	0	0	37	1.9
Bolivina subaenariensis	38	21	1	1	0	0	0	0	0	0	0	0	0	0	0	61	3.1
Bulimina aculeata	1	1	0	0	2	4	2	2	2	5	3	5	4	3	0	34	1.7
Bulimina inflata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
Bulimina marginata	2	0	0	2	3	6	7	3	4	4	5	3	5	2	0	46	2.3
Cancris auriculus	6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	16	0.8
Cassidulina carinata	2	3	0	1	1	0	0	0	0	0	0	0	0	0	0	7	0.4
Chilostomella oolina	91	125	59	135	98	58	18	7	4	2	1	2	0	0	0	600	30.2
Coryphostoma sp	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.4
Dentalina sp	2	1	0	(1)	0	0	0	0	0	0	0	0	0	0	0	4	0.2
Dentalina ariena	4	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	5	0.3
Elphidium advenum	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.1
Gavelinopsis translucens	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.1
Globobulimina affinis	0	4	0	1	2	3	0	(1)	0	0	0	0	0	(1)	0	12	0.6
Hoeglundina elegans	2	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	3	0.2
Hyalinea balthica	14	8	1	6	9	4	6	1	1	0	1	1	1	0	0	53	2.7
Lenticulina peregrina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
Nonion scaphium	20	24	24	63	32	36	18	8	10	8	4	5	0	(2)	(4)	258	13.0
Nonionella turgida	0	0	0	1	0	1	0	(1)	0	0	0	0	0	0	0	3	0.2
Pseudoeponides falsobeccarii	5	1	0	4	1	3	0	0	3	1	2	3	0	1	1	25	1.3
Rectuvigerina phlegeri	16	7	1	0	2	1	0	0	(1)	(1)	0	0	0	0	0	29	1.5
Trifarina pauperata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.1
Uvigerina peregrina	27	7	0	0	(2)	(2)	0	0	0	(1)	0	0	0	0	0	39	2.0
Valvulineria bradyana	196	102	25	12	1	1	2	0	0	0	0	0	0	0	0	339	17.0
Total perforate	480	321	112	228	154	120	56	24	28	23	16	20	10	8	5	1584	79.6
Nbr species	19	17	7	14	12	12	8	6	8	8	7	8	5	5	4	25	
Porcellaneous																	
Quinqueloculina seminula	26	5	1	2	5	3	2	1	0	0	0	0	0	0	0	45	2.3
Sigmoilina sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.1
Total porcellaneous	26	5	1	2	5	4	2	1	0	0	0	0	0	0	0	46	2.3
Nbr species	1	1	1	1	1	2	1	1	0	0	0	0	0	0	0	2	
Non fossilising agglutinated																	
Clavulina cylindrica	208	60	9	11	4	4	0	0	(1)	(1)	0	0	0	0	0	298	15.0
Eggerella sp	2	1	3	4	0	(6)	0	0	0	(1)	0	0	0	0	0	18	0.9
Haplophragmoides sp.	5	2	0	1	0	0	0	0	0	0	0	0	0	0	0	8	0.4
Nouria polymorphinoides	11	3	1	1	0	0	0	0	0	0	0	0	0	0	0	16	0.8
Reophax sp	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0.3
Reophax ampullacea	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	2	0.1
Reophax scorpiurus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.1
Total agglutinated	231	68	13	18	5	10	0	0	1	2	0	0	0	0	0	349	17.5
Nbr species	10	11	7	6	4	3	0	0	0	0	0	0	0	0	0	7	
Fossilising agglutinated																	
Textularia agglutinans	0	0	0	1	0	(1)	0	0	0	0	0	0	0	0	0	2	0.1
Textularia sagittula	1	0	0	(1)	(1)	0	0	(2)	(1)	(2)	0	0	0	0	0	8	0.4
Total agglutinated	1	0	0	2	1	1	0	2	1	2	0	0	0	0	0	10	0.5
Nbr species	1	0	0	2	1	1	0	1	1	1	0	0	0	0	0	2	
Total live foraminifera	710	386	125	254	160	143	63	26	32	45	28	31	29	15	21	1989	100.0
Nbr species	30	29	15	21	17	17	9	9	8	8	7	8	5	5	4	36	

Table 2a

Tables 2a-e Benthic foraminiferal census data for stations D, B, A, F and H.

N.B. Numbers are not standardized for a sediment volume

Station B 553 m																		
	Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																			
Indet		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Amphicoryna scalaris		1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	4	0.30
Bolivina alata		0	0	1	2	2	1	0	0	0	0	0	0	0	0	0	0	6	0.44
Bolivina quadrilatera		5	2	0	0	0	0	0	0	0	(1)	0	0	0	0	0	0	8	0.59
Bulimina marginata		5	4	0	1	1	3	1	4	0	0	0	0	0	0	0	0	19	1.41
Chilostomella oolina		0	0	0	2	0	0	0	0	(1)	0	0	0	0	0	0	0	3	0.22
Cibicides lobatulus		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Cibicides wuellerstorfi		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Cibicidoides pachyderma		26	16	6	3	3	6	1	2	0	0	0	0	0	0	0	0	63	4.67
Dentalina sp.1		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Dentalina subemaciata		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Elphidium sp		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Gavelinopsis translucens		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Glandulina ovula		1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22
Globobulimina affinis		0	0	1	4	19	6	13	16	10	5	3	3	0	0	(1)	0	81	6.00
Gyroidina altiformis		7	0	2	0	0	(1)	0	0	0	0	0	0	0	0	0	0	10	0.74
Gyroidina orbicularis		1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22
Hyalinea baltica		7	2	0	0	0	0	1	1	1	0	0	0	0	0	0	0	12	0.89
Lenticulina sp.1		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Lenticulina peregrina		4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.52
Lenticulina vortex		2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22
Melonis barleeanus		14	33	27	23	14	4	1	1	3	1	0	0	0	0	0	0	121	8.97
Nuttallides umbonifera		2	2	1	0	0	0	0	0	0	0	0	(1)	0	0	0	0	6	0.44
Pseudoeponides falsobeccarii		0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.07
Robertinoides bradyi		3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22
Siphogenerina columellaris		13	7	4	1	0	2	1	1	1	0	0	0	0	0	0	0	30	2.22
Trifarina sp		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Trifarina angulosa		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15
Uvigerina elongatastriata		0	0	5	15	31	3	4	2	0	1	0	(1)	0	0	0	0	62	4.60
Uvigerina mediterranea		119	123	108	54	20	14	4	9	2	0	0	(1)	0	0	0	0	454	33.65
Uvigerina peregrina		30	43	83	78	43	7	3	2	0	0	0	0	0	(1)	0	0	290	21.50
Uvigerina proboscidea		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Total perforate		246	238	243	187	134	48	29	38	19	8	3	6	0	1	1	0	1202	89.03
Nbr species		20	12	14	13	9	11	9	9	8	4	1	4	0	1	1	0	31	
Porcellaneous																			
Cornuspira involvens		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Cruciloculina sp		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Pyrgo depressa		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Sigmoilina sp		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Total porcellaneous		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.30
Nbr species		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	
Non fossilising agglutinated																			
Ammolagena sp		1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.37
Ammoscalaria sp		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15
Clavulina cylindrica		0	0	1	6	3	0	0	0	0	0	0	0	0	0	0	0	10	0.74
Cribrostomoides subglobosus		8	5	4	0	2	1	0	0	0	0	0	0	0	0	0	0	20	1.48
Cyclammina sp 1		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.07
Cyclammina sp 2		2	3	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	6	0.44
Cyclammina sp 3		3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.52
Eggerella scabra		1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	6	0.44
Haplophragmoides bradyi		0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15
Reophax sp 1		3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22
Reophax dentaliniformis		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07
Reophax fusiformis		0	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	7	0.52
Reophax guttiferus		2	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	1.41
Reophax scorpiurus		19	2	1	1	0	1	1	0	0	0	0	0	0	0	0	0	25	1.85
Trochammina sp		0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15
Total agglutinated		39	37	17	12	6	3	2	0	0	0	0	0	0	0	0	0	116	8.60
Nbr species		8	9	9	8	3	3	2	0	0	0	0	0	0	0	0	0	15	
Fossilising agglutinated																			
Bigenerina nodosaria		5	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	9	0.67
Pseudoclavulina crustata		2	3	0	1	1	2	1	0	0	0	0	0	0	0	0	0	10	0.74
Siphotextularia affinis		4	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	9	0.67
Total agglutinated		11	6	3	1	4	2	1	0	0	0	0	0	0	0	0	0	28	2.08
Nbr species		3	3	2	1	2	1	1	0	0	0	0	0	0	0	0	0	3	
Total live foraminifera		300	281	263	200	144	53	32	38	19	8	3	6	0	1	1	0	1349	100.00
Nbr species		35	24	25	20	14	15	12	9	6	4	1	4	0	1	1	0	53	
Glomospira spp.		1	4	6	4	11	10	11	7	1	1	0	0	0	0	0	0	56	
Arborescent indet		34	30	44	61	22	12	0	0	0	0	0	0	0	0	0	0	203	

Table 2b

Tables 2a-e Benthic foraminiferal census data for stations D, B, A, F and H.

N.B. Numbers are not standardized for a sediment volume

Station A 1012 m																			
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-4.5	4.5-5.5	5.5-6.5	6.5-7.5	7.5-8.5	8.5-9.5	9.5-10.5	Total	%
Perforate																			
Indet	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Epilithe Indet.	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1.9
?Ammolmoides sp	4	0	3	0	0	1(1)	0	0	0	0	0	0	0	0	0	0	0	8	1.5
Bulimina inflata	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1.0
Bulimina marginata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.2
Cibicidoides pachyderma	4	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	2.1
Glandulina ovula	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.2
Globobulimina affinis	0	0	0	0	0	0	3	13	8	10	10	17	44	27	5	0	0	137	26.5
Gyroidina altiformis	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.6
Haeglundina elegans	4	4	4	6	7	1	0	0	0	0	0	0	0	0	0	0	0	26	5.0
Lenticulina sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Lenticulina sp.1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Lenticulina gibba	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Lenticulina peregrina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Melonis berleeanus	0	0	0	0	3	1	2	0	0	0	0	0	0	0	0	0	0	6	1.2
Nuttallides pusillus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Nuttallides umbonifernus	8	6	6	2	1	0	0	0	0	0	0	0	0	0	0	0	0	27	5.2
Rosalina sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Siphogenerina columellians	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.2
Uvigerina mediterranea	5	12	12	12	4	0	0	0	0	0	0	0	0	0	0	0	0	45	8.7
Uvigerina peregrina	2	1	10	22	37	13	0	0	0	0	0	0	0	0	0	0	0	85	16.4
Total perforate	33	30	57	42	55	18	9	13	9	12	11	18	44	27	5	0	0	381	73.7
Nbr species	11	8	11	4	7	4	3	1	2	3	2	2	1	1	1	0	0	20	
Porcellaneous																			
Biloculinella sp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Cornuspira foliacea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Cornuspira involvens	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.6
Pyrgo depressa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1.9
Pyrgo murrhina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Pyrgo subsphaerica	0	0	1	1	2	0	1	0	0	0	0	0	0	0	0	0	0	5	1.0
Pyrgoella sphaera	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.6
Quinqueloculina sp 2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Quinqueloculina seminula	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Total porcellaneous	5	1	3	3	2	3	1	0	0	0	0	0	0	0	0	0	0	18	3.5
Nbr species	4	1	3	3	1	2	1	0	0	0	0	0	0	0	0	0	0	9	
Non fossilising agglutinated																			
Agglutinated sp 11	0	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1.0
Agglutinated sp 29	0	2	2	0	0	0	1(1)	0	0	0	0	0	0	0	0	0	0	5	1.0
Agglutinated sp 45	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3	0.6
Ammobaculites agglutinans	0	5	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	10	1.9
Ammolagena clavata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Cribrostomoides subglobosus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Cyclammina sp 1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Cystammina pauciloculata	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.8
Eggerella bradyi	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Karrerella bradyi	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1.0
Lagenammina pseudodifflugiformis	0	2	12	1	0	0	0	0	0	0	0	0	0	2	0	0	0	17	3.3
Paratrochammina challengeri	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.8
Recurvoides sp	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	6	1.2
Reophax sp.6	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Reophax guttiferus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Reophax scorpiurus	15	9	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	31	6.0
Thurammina albicans	0	2	5	4	4	1	0	0	0	0	0	0	0	0	0	0	0	16	3.1
Total agglutinated	18	28	42	9	8	8	1	2	0	0	0	0	0	2	0	0	0	116	22.4
Nbr species	4	10	13	6	4	3	1	1	0	0	0	0	0	1	0	0	0	17	
Fossilising agglutinated																			
Sigmoilopsis schlumbergeri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Siphotextularia concava	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.2
Total agglutinated	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.4
Nbr species	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Total life foraminifera	57	57	103	54	65	27	11	15	9	12	11	18	44	29	5	0	0	517	100.0
Nbr species	20	17	28	13	12	9	5	2	2	3	2	2	1	2	1	0	0	48	
Arborescent indet.	3	28	76	112	267	72	2	0	0	0	0	0	0	0	0	0	0		

Table 2c

Tables 2a-e Benthic foraminiferal census data for stations D, B, A, F and H.

N.B. Numbers are not standardized for a sediment volume

Station F 1264 m																		
	Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																			
Bulimina inflata		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.8
Cibicidoides pachydermus		0	0	0	1	0	3	0	0	0	0	0	0	0	0	0	0	4	3.3
Cibicidoides robertsonianus		1	1	0	3	1	0	0	1	0	1	0	0	0	0	0	0	8	6.6
Gavelinopsis translucens		2	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	3	2.5
Glandulina ovula		0	0	1	0	0	0	0	0	0	0	0	0	0	1	2	0	4	3.3
Globobulimina affinis		0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.8
Gyroidina umbonata		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.8
Hoeglundina elegans		4	0	6	2	0	0	0	0	0	0	0	0	0	0	0	0	12	9.8
Lenticulina peregrina		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.8
Melonis barleeanus		0	0	1	1	3	0	2	0	0	0	0	0	0	0	0	0	7	5.7
Ondorsalis umbonatus		1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	2.5
Pullenia bulloides		0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.8
Robertinoides sp.		0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	2.5
Uvigerina mediterranea		2	1	0	0	0	0	(2)	0	0	0	0	0	0	0	0	0	5	4.1
Uvigerina peregrina		11	2	12	5	4	0	6	0	1	0	0	0	0	0	0	0	41	33.6
Total perforate		22	5	24	12	9	4	11	1	1	1	0	1	0	2	2	0	95	77.9
Nbr species		7	4	6	5	4	2	4	1	1	1	0	1	0	2	1	0	15	
Porcellaneous																			
Quinqueloculina sp.		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.8
Quinqueloculina seminula		3	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	5.7
Pyrgo depressa		0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	1.6
Total porcellaneous		3	5	1	0	0	0	1	0	0	0	0	0	0	0	0	0	10	8.2
Nbr species		1	2	1	0	0	0	1	0	0	0	0	0	0	0	0	0	3	
Non fossilising agglutinated																			
Ammoglobigerina sp		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.8
Ammoscalaria sp.		0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	2	1.6
Cyclammina sp.		0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	2.5
Cribrostomoides subglobosus		0	0	0	0	0	1	3	0	0	0	0	0	0	0	0	0	4	3.3
Karreriella bradyi		0	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	3	2.5
Reophax sp		0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.8
Saccammina sp.		2	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	3	2.5
Total agglutinated		2	0	2	0	4	1	8	0	0	0	0	0	0	0	0	0	17	13.9
Nbr species		1	0	1	0	2	1	5	0	0	0	0	0	0	0	0	0	7	
Total live foraminifera		27	10	27	12	13	5	20	1	1	1	0	1	0	2	2	0	122	100.0
Nbr species		9	6	8	5	6	3	10	1	1	1	0	1	0	2	1	0	25	
Arborescent indet		27	10	27	12	13	5	20	1	1	1	0	1	0	2	2	0	122	

Table 2d

Tables 2a-e Benthic foraminiferal census data for stations D, B, A, F and H.

N.B. Numbers are not standardized for a sediment volume

Station H 1993 m																	
	Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total
Perforate																		
Bulimina inflata		0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Cibicidoides pachydermus		0	0	0	2	0	3	0	0	0	0	0	0	0	0	0	0	5
Chilostomella oolina		0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1
Fissurina sp.		0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Gavelinopsis translucens		0	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	4
Globobulimina affinis		0	0	0	0	0	0	0	0	0	0	1	0	4	0	0	0	5
Gyroidina umbonata		0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1
Gyroidina orbicularis		0	0	0	4	5	5	0	0	1	2	1	0	0	0	0	0	18
Hoeglundina elegans		12	16	18	5	5	2	0	0	0	0	0	0	0	0	0	0	58
Lenticulina peregrina		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Pullenia sp		0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	3
Uvigerina peregrina		0	27	3	2	11	1	0	0	0	(1)	0	0	0	0	0	0	45
Total perforate		12	46	23	17	23	12	0	0	1	4	2	0	5	0	0	0	145
Nbr species		1	4	4	6	4	5	0	0	1	3	2	0	5	0	0	0	12
Porcellaneous																		
Biloculinella irregularis		0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1
Quinqueloculina seminula		0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1
Pyrgo depressa		0	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	3
Pyrgo subsphaerica		0	0	1	0	1	1	0	1	0	0	0	0	0	0	0	0	4
Scutuloris sp.		0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Sigmoilopsis schlumbergeri		1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Total porcellaneous		1	4	2	2	3	1	0	1	0	0	0	0	0	0	0	0	14
Nbr species		1	2	2	2	3	1	0	1	0	0	0	0	0	0	0	0	6
Non fossilising agglutinated																		
Ammoscalaria sp		2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Cribrostomoides subglobosus		0	0	2	0	2	0	0	0	0	0	0	0	0	0	0	0	4
Cyclammina sp		0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Cystammina pauciloculata		0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Haplophragmoides sp.		0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2
Karrerella bradyi		0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Reophax ampullacea		1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3
Reophax scorpiurus		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Reophax sp.		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Total agglutinated		5	4	8	1	2	0	0	0	0	0	0	0	0	0	0	0	20
Nbr species		1	3	5	1	2	1	0	0	0	0	0	0	0	0	0	0	9
Total live foraminifera		18	54	33	20	28	13	0	1	1	4	2	0	5	0	0	0	179
Nbr species		3	9	11	9	9	7	0	1	1	3	2	0	5	0	0	0	27
Arborescent indet.		0	4	4	12	6	20	4	3	0	0	1	0	0	0	0	0	54

Table 2d

Tables 2a-e Benthic foraminiferal census data for stations D, B, A, F and H.

N.B. Numbers are not standardized for a sediment volume

The oxygen concentration of the bottom waters at station F (water depth 1264 m) is 4.70 ml/l. Within the sediment, the zero oxygen level is reached at 6.3 cm depth (Fig.6a). The dissolved oxygen curve shows some minor oscillations that may be the result of microenvironments caused by burrows. A nitrate diffusive gradient extends from 4.5 to 7.5 cm depth. The benthic foraminiferal fauna (Fig.6b) is largely limited to the upper 3 cm (ALD_{10} = 1.2 cm); maximum values are found in the top first cm. *Uvigerina peregrina* (33.6%), *Hoeglundina elegans* (9.8%), *Cibicidoides robertsonianus* (6.6%), *Melonis barleeanus* (5.7%), *Quinqueloculina seminula* (5.7%), *Uvigerina mediterranea* (4.1%), and *Cibicidoides pachydermus* (3.3%) are the main taxa encountered at station F (Table 2d). Although the relatively low numbers of live individuals do not allow very precise observations of the vertical distribution, *Q. seminula* (ALD_{10} = 0.3 cm) appears to be limited to the topmost 0.5 cm, whereas *U. peregrina* (ALD_{10} = 0.9 cm), and *H. elegans* (ALD_{10} = 0.5 cm) can be found slightly deeper (Fig.6c). Just as at stations B and A, *M. barleeanus* (ALD_{10} = 1.4 cm) shows a subsurface maximum at about 1 cm depth.

At station H (water depth 1993 m), the oxygen concentration is 5.85 ml/l. The zero oxygen level is positioned at about 6 cm depth, whereas a weak nitrate + nitrite downward diffusive zone seems to be present between 2.5 and 6.5 cm depth (Fig.7a). The live fauna is almost completely limited to the uppermost 2 cm of sediment; a maximum density (about 100 individuals/50 cm^3) is found at the 0.0-0.5 cm level (Fig.7b). The ALD_{10} of the total fauna is 1.0 cm. *Hoeglundina elegans* (32.4%), *Uvigerina peregrina* (25.1%), *Gyroidina orbicularis* (10.1%), *Cibicidoides pachydermus* (2.8%), and *Globobulimina affinis* (2.8%) are the main taxa encountered at station H (Table 2d, Fig.7c). *H. elegans* (ALD_{10} = 0.6 cm) and *U. peregrina* (ALD_{10} = 0.7cm) dominate the faunas in the first half cm. *G. orbicularis* (ALD_{10} = 1.9cm) and *C. pachydermus* (ALD_{10} = 1.4 cm) appear mainly between 0.5 and 2 cm depth. Some rare individuals of *G. affinis* live in the deepest part of sediment, around the zero oxygen level at about 6 cm depth.

Discussion

Benthic ecosystem redox conditions

Bottom water oxygen concentrations for our five stations vary between 4.36 and 5.85 ml/l (Table 1). These values agree very well with the data that have been published for the

Taxa	Stations, ALD_{10} (number of specimen)					Average weighted ALD_{10}	Microhabitat
	OB1D	OB1B	OB1A	OB2F	OB5H		
Animalinoides sp.			0.3(7)			0.34	SI
Bolivina alata	0.3(37)	1.1(6)				0.41	SI
Bolivina subaenariensis	0.3(61)					0.33	SI
Bolivinita quadrilatera		0.2(7)				0.20	SI
Bulimina aculeata	4.7(34)					4.70	DI
Bulimina inflata			0.4(5)			0.37	SI
Bulimina marginata	4.2(44)	1.2(19)				3.30	DI
Cancris sp.	0.3(11)					0.35	SI
Cassidulina carinata	0.7(7)					0.71	SI
Chilostomella oolina	1.2(600)					1.20	II
Cibicidoides pachydermus		0.6(63)	0.4(11)		1.4(5)	0.62	SI
Cibicidoides robertsonianus				1.4(8)		1.40	II
Coryphostoma sp.	0.2(7)					0.23	SI
Globobulimina affinis	2.2(10)	2.4(80)	4.7(137)		6.1(5)	3.91	DI
Gyroidina altiformis		0.2(9)				0.24	SI
Gyroidina orbicularis					1.9(18)	1.90	II
Hoeglundina elegans			0.8(26)	0.5(12)	0.6(58)	0.62	SI
Hyalinea balthica	1.6(53)	1.1(12)				1.51	II
Lenticulina peregrina		0.2(7)				0.24	SI
Melonis barleeanus		0.8(121)	1.7(6)	1.4(7)		0.85	SI/II
Nonion scaphum	1.8(252)					1.81	II
Nuttallides umboniferus		0.3(5)	0.4(27)			0.42	SI
Pseudoeponides falsobeccarii	3.2(25)					3.20	DI
Rectuvigerina phlegeri	0.5(29)					0.49	SI
Siphogenerina sp.		0.6(30)				0.65	SI
Uvigerina elongatastriata		1.3(61)				1.30	II
Uvigerina mediterranea		0.6(453)	0.6(45)			0.59	SI
Uvigerina peregrina	0.4(38)	0.8(269)	1.1(85)	0.9(41)	0.7(44)	0.79	SI/II
Valvulineria bradyana	0.4(339)					0.40	SI
Pyrgo depressa			0.1(10)			0.06	SI
Pyrgo subsphaerica			1.3(5)			1.25	II
Quinqueloculina seminula	0.8(45)			0.3(7)		0.71	SI
Agglutinated sp.11			0.6(5)			0.62	SI
Ammobaculites agglutinans			0.6(10)			0.62	SI
Ammolagena sp.		0.4(5)				0.38	SI
Clavulina cylindrica	0.4(296)	1.0(10)				0.38	SI
Cribrostomoides subglobosus		0.5(20)				0.48	SI
Cyclammina sp.2		0.2(5)				0.23	SI
Cyclammina sp.3		0.3(7)				0.34	SI
Eggerella sp.	0.5(10)					0.47	SI
Eggerella scabra		0.6(6)				0.60	SI
Karreriella bradyi			0.5(7)			0.52	SI
Lagenammina pseudodifflugiformis			1.4(17)			1.36	II
Nouria polymorphinoides	0.4(16)					0.36	SI
Recurvoides sp.			1.7(6)			1.66	II
Reophax sp.	0.3(6)					0.30	SI
Reophax fusiformis		0.7(7)				0.70	SI
Reophax guttiferus		0.3(19)				0.35	SI
Reophax scorpiurus		0.3(25)	0.3(31)			0.32	SI
Thurammina albicans			0.9(16)			0.88	SI/II
Bigenerina nodosaria		0.4(9)				0.36	SI
Pseudoclavulina crustata		0.9(10)				0.93	II
Siphotextularia affinis		0.5(9)				0.51	SI
Oxygen penetration depth (cm)	0.8	1.7	1.8	6.4	6.3		

Table 3 Average Living Depth (ALD_{10}) of foraminiferal species and (between parentheses) the number of individuals on which the calculation is based. Only occurrences of ≥ 5 individuals are shown. The grey boxes represent dominant taxa with a relative proportion ≥ 5% in at least one of the stations. Microhabitat patterns are summarised as Shallow Infaunal (SI), Intermediate Infaunal (II) or Deep Infaunal taxa (DI).

various water masses in the Bay of Biscay (Ogawa and Tauzin, 1973). The minimum values encountered at station A are typical of the Mediterranean outflow waters. Measurements of bottom water oxygenation during 10 successive sampling campaigns show only minor seasonal and interannual changes for our 5 stations (Anschutz et al., 1999; Hyacinthe et al., 2001), suggesting that the oxygen concentration of the bottom waters is only very weakly influenced by the variability of the flux of organic matter to the ocean floor. The penetration of free oxygen into the sediment varies from only 8 mm at the shallow station D to more than 6 cm at the deep stations F and H (Table 1). These values strongly suggest that the oxygen gradient in the interstitial waters is only weakly dependent on bottom water oxygenation, but is strongly influenced by the rate of oxygen consumption within the sediment. This rate depends on the oxic degradation of organic matter and oxidation of upward diffusing reduced components. But the oxygen penetration depth is relatively stable through the year (Anschutz et al., 1999; Hyacinthe et al., 2001). Our flux calculations, based on primary production and water depth, suggest a labile organic carbon flux to the ocean floor that is about 14 times higher in station D (where oxygen penetration is minimal) than at station H (where oxygen penetration is maximal).

As soon as all free oxygen has been consumed for the degradation of reactive organic matter, other oxidants are used to continue the remineralisation of labile organic compounds (Froelich et al., 1979; Fenchel and Finlay, 1995). A first step of anaerobic degradation is the reduction of nitrate and nitrite in dinitrogen. This redox reaction takes place mostly below the zero oxygen level, and causes an upward diffusion of newly formed ammonia from the anoxic to oxic layers. In hypoxic sediments, ammonia is oxidised by nitrifying bacteria in nitrate and nitrite, which results in a downward diffusion of nitrate (and nitrite) from oxic to anoxic layers. At the shallowest station D, where the organic flux is maximal, the zone of nitrate reduction is probably situated in the uppermost cm of the sediment (Fig.3a). Towards the deeper, more oligotrophic stations, the zone of downward diffusion of nitrate + nitrite gradually deepens, from 0.25 - 2.25 cm at station B to 0.75 - 3.5 cm at station A, to about 2.5 - 7.5 cm at stations F and H. Sulphate reduction may be another important mechanism involved in the anaerobic degradation of organic matter; this phenomenon typical of eutrophic ecosystems was observed only in station D. Important bacterial consortia are supposed to induce these anaerobic redox reactions, which ultimately result in almost complete degradation of both labile and refractory organic matter (Hargrave, 1970; Carney, 1989). The bacterial consortia may constitute an important additional source of labile organic matter

below the oxic zone, and could trigger an important recycling of organic carbon under anaerobic conditions (Fenchel and Finlay, 1995).

Faunal characteristics

It is generally accepted that organic mater influences the composition of the foraminiferal fauna both qualitatively and quantitatively (Thiel, 1983; Berger and Diester-Haass, 1988; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Altenbach, 1988; Gooday, 1993; Jorissen et al., 1998). In our study area, the faunas of outer shelf station D contain about 15 times more stained foraminifera than those of the deeper stations F and H (Fig.2). This difference is probably induced by the increase of the vertical labile organic matter flux to the ocean floor towards shallow water. Also the number of species varies between the stations; by far the highest number (49) of taxa is found at station B. This elevated number can probably be explained by the fact that the fauna contains both outer shelf and upper slope elements. The deepest stations F and H have by far the lowest number of taxa, but this is probably at least partially due to the fact that the samples contain about 15 times fewer individuals here.

At all stations, the live faunas are strongly concentrated in the first cm of the sediment, suggesting a dependence on the flux of labile, easily consumable organic matter. Despite the strong faunal concentration in the first cm, the ALD_{10} of the total faunas (Fig.8a-b) is not uniform: between 0.8 and 1.2 cm for the relatively shallow stations D and B, as well as for the much deeper stations F and H, but about 1.8 cm for station A (1012 m). The deepening of the ALD_{10} for the total fauna at station A is mainly the result of an important increase of the ALD_{10} of the infaunal species *G. affinis,* which is the dominant taxon here (Fig.8a). Although their living depth further deepens at the deeper stations F and H, their relative proportion (and thus also their influence on the total faunal ALD_{10}) decreases strongly there. Thus, the very shallow ALD_{10} of the latter 2 stations is caused mainly by the scarcity of deep infaunal elements. When we consider the ALD_{10} of the total faunas without these two potentially deep infaunal species (Fig.8b), the result is a very stable ALD_{10} of all superficially living taxa (between 0.5 and 0.8 cm).

The shallower station D contains about 2000 individuals that are largely restricted to shallow and intermediate infaunal positions. Apparently this fauna reflects a high labile organic flux to the ocean floor. *Valvulineria bradyana* and *Clavulina cylindrica* dominate the

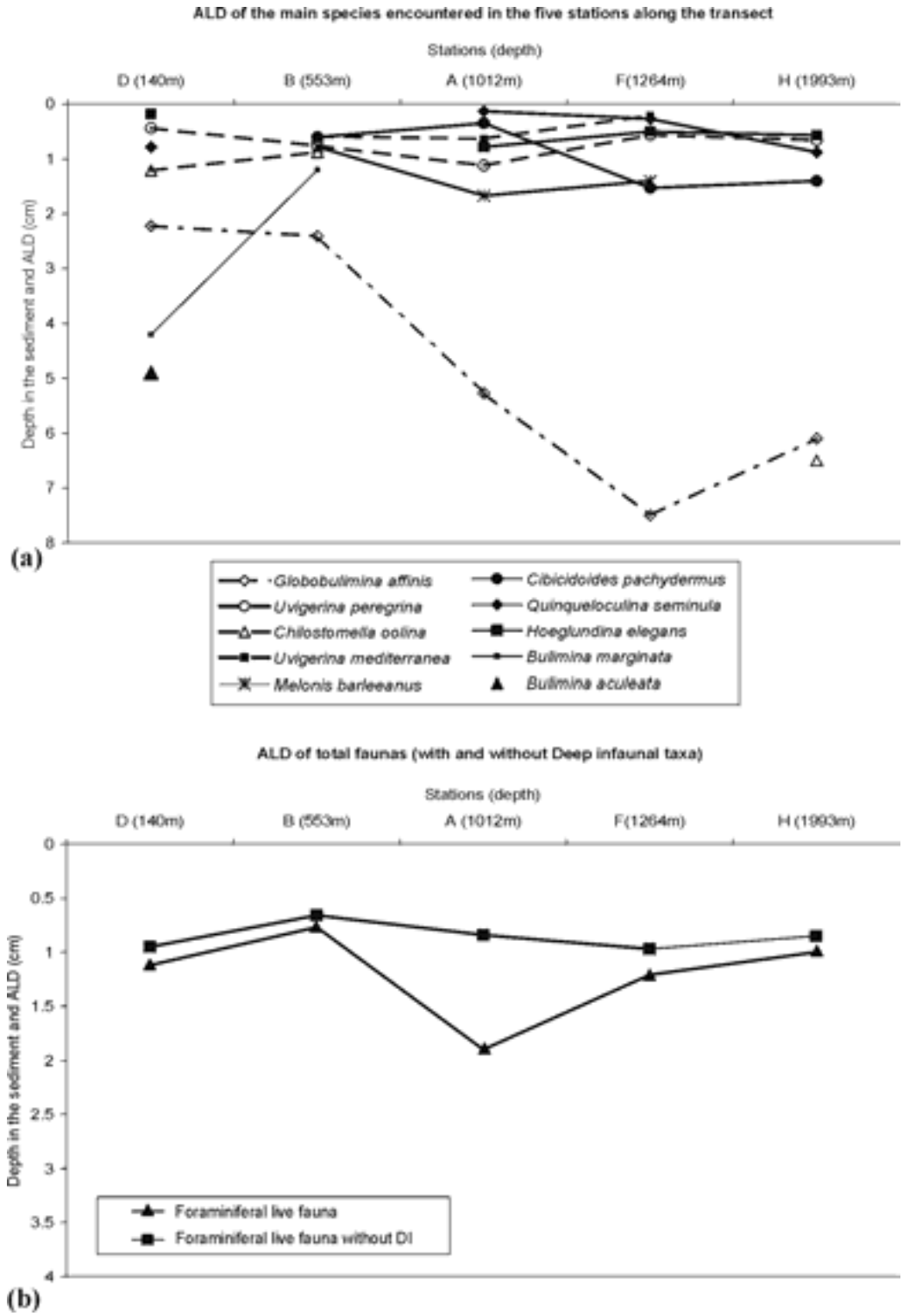

Fig. 8; 8a: ALD_{10} of the main taxa along the bathymetric transect; 8b: ALD_{10} of the total faunas (with and without deep infaunal taxa (DI)).

first half cm. They can be considered as two shallow infaunal species, tolerant of low oxygen values, which respond to a high food level at the sediment-water interface. The first species has been described in low oxygen sediments from the centre of the Adriatic Sea mud belt (Jorissen, 1987; 1988; Van der Zwaan and Jorissen, 1991). The dominant species at this station, *Chilostomella oolina,* has been described as an intermediate or deep infaunal species well adapted to suboxic conditions (Corliss, 1985; Van der Zwaan and Jorissen, 1991; Sen Gupta and Machain-Castillo, 1993; Bernhard and Sen Gupta, 1999). It settles together with *Nonion scaphum* in strongly suboxic and anoxic sediments down to 3-cm depth. In these stressed environments, these two species appear to have a competitive advantage over more superficially living taxa. They may proliferate because of the input of large quantities of organic matter into the deeper sediment layers, remineralised by anaerobic pathways, and the near-absence of less resistant competing taxa (Rathburn and Corliss, 1994). Next, an association consisting of *Bulimina aculeata*, *Bulimina marginata,* and *Pseudoeponides falsobecarii* is found deep in the sediment, under completely anoxic conditions. Several authors (e.g. Lutze and Coulbourn, 1984; Jorissen, 1987; Hermelin and Shimmield, 1990; Verhallen, 1987; Bernhard and Alve, 1996) have described *Bulimina* species as typical elements in extremely eutrophic and dysoxic settings. In view of their consistent distribution with a surface as well as a deep maximum (Jorissen, 1999a, figs.10.6d and 10.7f), and the systematic association with sea urchins in our material, we think that the deep occurrences of this association can be explained by their colonisation of macrofaunal burrows. These environments could be attractive because of the strongly increased bacterial activity in the burrow walls (e.g. Fenchel and Jørgensen, 1977).

A major faunal change takes place between stations D (140 m) and B (553 m) (Fig.9). The latter station is strongly dominated by Uvigerinids (*U. mediterranea* and *U. peregrina*). These shallow infaunal species have been described in a wide variety of eutrophic settings, needing an exported labile organic flux of at least 2.5 g C/m^2/year (e.g. Lutze and Coulbourne, 1984; Corliss, 1985; Corliss and Emerson, 1990; Corliss, 1991; De Rijk et al., 2000, Morigi et al.; 2002). They can be considered as feeding on labile organic matter in rather well oxygenated shallow infaunal microhabitats. It is important to notice that *U. peregrina* is consistently found deeper than *U. mediterranea.* This could be caused by a slightly higher tolerance for dysoxic conditions. The deeper microhabitat of *U. peregrina* would then show a slightly higher tolerance for low quality organic matter. A consequence of our observations is that the $\delta^{13}C$ of *U. peregrina* can hardly be considered as typical of bottom waters.

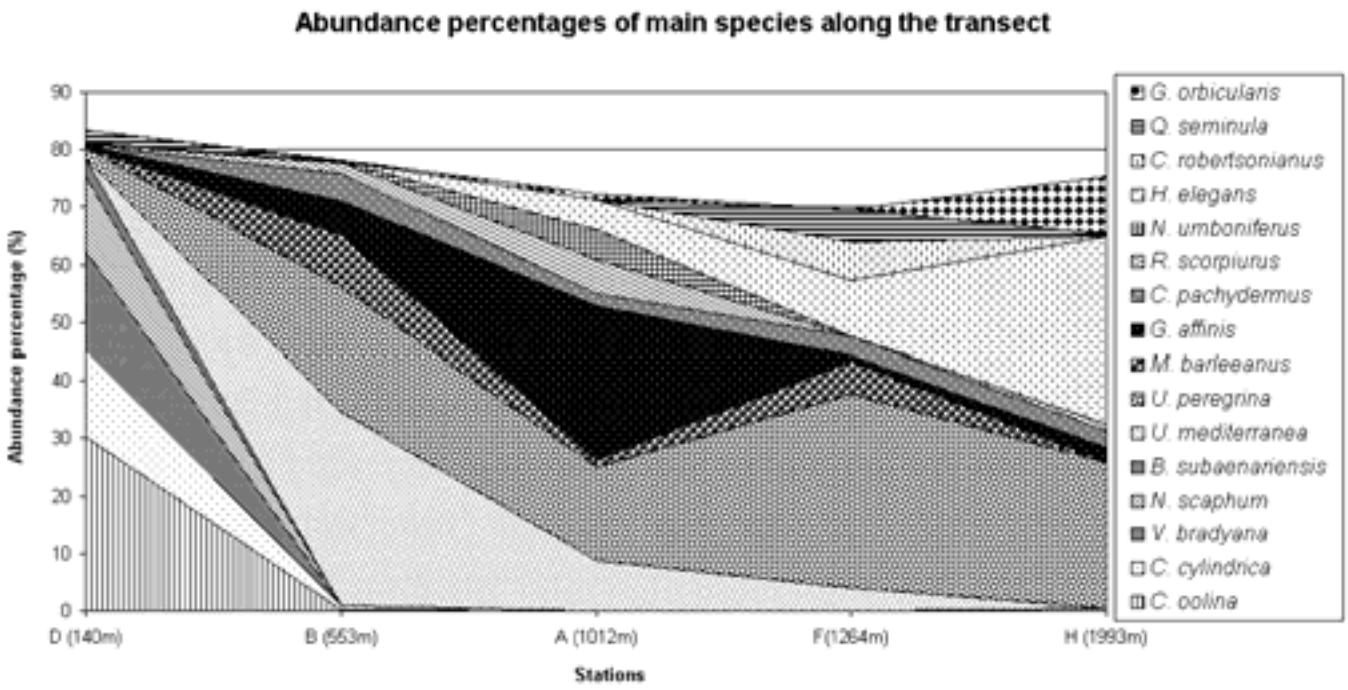

Fig. 9 Composition of the benthic live foraminiferal faunas (in % of the total fauna).

Deeper in the sediment, the infaunal niches are occupied by *M. barleeanus* and (still deeper) *G. affinis*. This combination of species has been described in numerous mesotrophic-eutrophic oceanic ecosystems (e.g. Harloff and Mackensen, 1997). Jorissen et al. (1995) observe that *M. barleeanus* occurs systematically in the lower part of the oxic zone, where nitrate production (by nitrifying bacteria) occurs, whereas *G. affinis* is consequently found in the upper part of the totally anoxic zone, where nitrate reduction occurs. Our results confirm this pattern. They suggest that both species are dependent on aerobic and anaerobic bacterial stocks degrading more or less refractory organic matter. These bacterial stocks should be concentrated directly below the major redox fronts, where maximum foraminiferal abundances have been described (*e.g.* Mullins et al., 1985; Linke and Lutze, 1993; Thomsen and Altenbach, 1993; our data). Both species would either prey directly on the bacterial stocks (Lee, 1979; Thomsen and Altenbach, 1993; Kitazato, 1994), or feed themselves with the break-off products. Our data confirm these ideas. We assume that most of the labile components will be consumed in the well-oxygenated topmost cm of the sediment, and will not arrive at the depth where *M. barleeanus* and *G. affinis* live. In the much more eutrophic station D, on the other hand, the near-absence of both species may be explained by the availability of important amounts of labile organic matter in the sub-surface dysoxic and anoxic levels, which are colonised by *C. oolina* and *N. scaphum*, species that appear to be less

able to subsist on low quality organic matter. The total dominance of *C. oolina* in the levels just below Mediterranean sapropel S1 (Jorissen et al., in prep.), which were deposited in a strongly dysoxic setting with an important labile organic matter influx, would be another argument in favour of this interpretation.

Dominant taxa found at stations A are essentially the same as those found in station B, showing that the change from North Atlantic Central Waters to Mediterranean waters has no visible impact on the benthic faunas. The almost perfect separation between the group of superficial infaunal taxa (dominated by *Nuttallides umboniferus, U. peregrina* and *U. mediterranea*) from a deep infaunal assemblages (dominated by *Globobulimina affinis*) is striking. The appearance of more oligotrophic shallow infaunal taxa such as *H. elegans, N. umboniferus* and *C. pachydermus* (compare Corliss, 1985; Corliss and Emerson, 1990; Corliss, 1991), shows the influence of the gradually decreasing organic flux towards deeper areas. Also rather oligotrophic arborescent agglutinated taxa (Jones and Charnock, 1985), which have not been included in our counting results, are very abundant at this station (575 fragments). The high quantities of *G. affinis* in the anoxic sediments from 2 to 8 cm depth can be explained in several ways. They could be (1) dead, but still staining, partially decomposed individuals, (2) live, but inactive animals with a lowered metabolism, or (3) active, facultative aerobic individuals, which dwell on an important stock of food made available by bacterial activity. The source of the originally (before bacterial conversion/partial break-off) refractory organic matter could be a former refractory organic matter input by slope failure processes.

The poor faunas (in terms of faunal density) of stations F (1264m) and H (1993m) show faunal changes characterising the further decrease of the trophic level. *U. mediterranea* and *G. affinis* show a strong relative frequency decrease, and *U. peregrina* (station F) and *H. elegans* become dominant. Furthermore, the faunas become largely restricted to the well-oxygenated top 2 cm of the sediment. The slightly deeper zone of nitrate reduction is almost devoid of benthic foraminifera. In the top of the anoxic zone, only very few individuals of *G. affinis* are found. This faunal evolution translates the trend towards oligotrophic ecosystems, where metabolisable organic matter is limited to the uppermost sediment layers. Apparently bacterial conversion of refractory organic matter in deeper, dysoxic/anoxic sediment layers is a minor process here.

Benthic foraminiferal microhabitats

The dependence of the benthic foraminiferal microhabitat on the availability of food and the oxygenation of the benthic ecosystem has been schematised in a conceptual model by Jorissen et al. (1995), as shown in Fig.10.

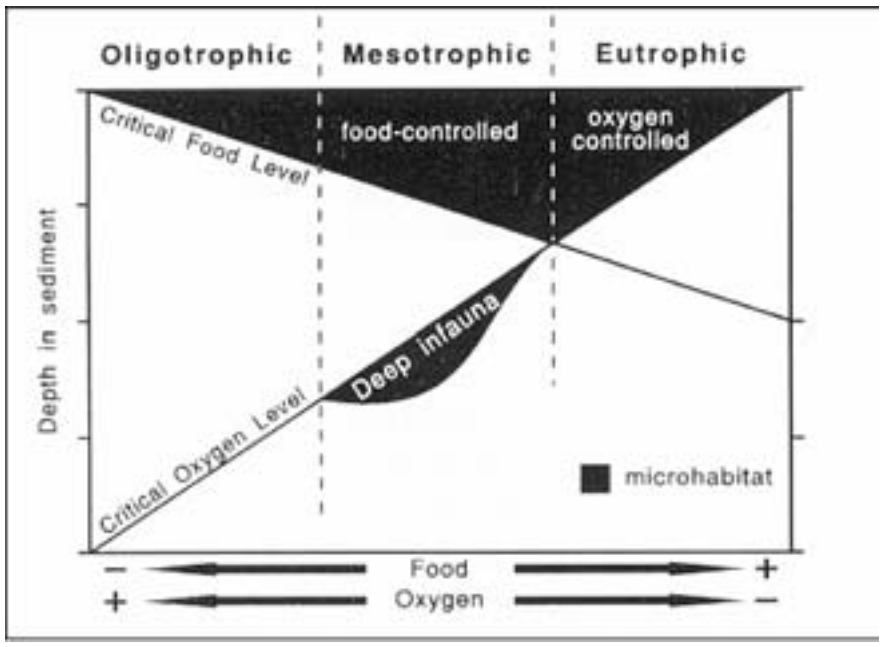

Fig. 10 TROX-model (Trophic condition and Oxygen concentration) explaining the vertical distribution of foraminifera in the top cm of the sediment (after Jorissen et al., 1995); see text for full explanation.

The so-called TROX-model explains that in very oligotrophic environments, shallow infaunal species, which are adapted to a low trophic level, will thrive close to the sediment-water interface in a well-oxygenated setting. The scarcity of organic matter introduced into the sediment (because of weak bioturbation and almost complete consumption of organic compounds in the first mms of the sediment) prevents colonisation of the deeper sediment layers by infaunal taxa. But also in much more eutrophic conditions, where the principal redox front is positioned close to the sediment surface, shallow infaunal taxa are limited to the first mm of the sediment; in this case, they have only a limited tolerance for low oxygen conditions. According to the TROX-model, faunal penetration will be maximal in mesotrophic settings, where oxygen penetration is relatively deep, and more or less labile

food particles are introduced at depth in the sediment by bioturbating macrofauna. In such mesotrophic environments, grazing on anaerobic bacterial stocks (or their break-up products) has been proposed as an explanation for the presence of rather deep-living intermediate and deep infaunal species. It is evident that the foraminiferal taxa have a dynamic behaviour, allowing them to adapt rapidly to changing conditions. Inherent to the TROX-model is the notion that the control of the foraminiferal microhabitat is dual. Whereas oxygenation is considered as the main controlling parameter in eutrophic ecosystems, food availability is supposed to control the vertical faunal distribution in more oligotrophic environments.

Our data fully confirm the main distributional trends predicted by the TROX-model. At stations D and B, which represent the eutrophic extreme in our study, the faunas are concentrated in the first 2 cm. In the "mesotrophic" station A, faunal penetration is deepest, and an important population of deep infaunal *G. affinis* is found at considerable depth in the sediment. Stations F an H, finally, represent the most oligotrophic situation in our study, and faunas are once again limited to the first centimetres of the sediment.

Despite the good fit to our data, it is evident that the TROX-model oversimplifies the foraminiferal response to the controlling environmental parameters for a number of reasons:

1) The TROX-model does not insist enough on the dependency of pore water oxygenation on the organic flux. Since the supply of metabolisable organic matter controls the oxygen consumption in the sediment and the localisation of the successive redox fronts, it is evident that the organic flux is the main parameter controlling the foraminiferal distribution in the sediment.

2) Recent studies (e.g. Alve and Bernhard, 1995; Fenchel and Finlay, 1995; Moodley et al., 1997; Jannink et al., 1998) show that anoxic conditions do not have a direct lethal effect for the majority of species. If severe dysoxia in bottom and pore waters cause the disappearance of certain taxa, this is possibly so, because reproduction is inhibited in such environments. Therefore, benthic ecosystem oxygenation appears to be a less important factor than was suggested by Jorissen et al. (1995), and in consequence, the quantity and quality of food particles appear to be by far the most important parameters.

3) The TROX-model depicts trends for the total fauna, but individual taxa may show important differences in their tolerance levels with respect to the main controlling parameters.

4) It is evident that competition between taxa for high quality food particles is an important factor causing microhabitat differences (Van der Zwaan et al., 1999). The deep microhabitat of several infaunal taxa may be caused by their low competitiveness in the more

attractive sediment surface niches (which are much richer in easily metabolisable organic matter).

5) Benthic ecosystems may know important seasonal or interannual variability. The foraminiferal faunas will respond to rapid changes in the organic flux or bottom water oxygenation by a shift of their microhabitat structure (Barmawidjaja et al., 1992; Ohga and Kitazato, 1997).

In figure 11, we show the microhabitat occupation at a species level in the range of meso-oligotrophic environments represented by our stations. Labile, particulate organic matter will be concentrated at the sediment surface. In extremely oligotrophic ecosystems such easily metabolisable material will be very scarce, or even be absent, except for rare phytodetritus deposit events (Gooday, 1993). Towards slightly less oligotrophic sites (our stations H and F), part of this material will be introduced in the top mm of the sediment. The result is the creation of a niche inhabited by very competitive, shallow infaunal taxa. In rather oligotrophic settings such faunas are dominated by *H. elegans, Q. seminula,* and *C. pachydermus*, in more mesotrophic settings (stations A, B) by *U. mediterranea, N. umboniferus* and *G. orbicularis,* and in more eutrophic environments (station D) by *C. cylindrica, V. bradyana* and *B. subaenariensis* (Fig.11). All these taxa seem to combine a preference for high quality resources (or a low tolerance for low quality food), a high competitiveness and perhaps a limited tolerance for anoxic conditions. When in eutrophic ecosystems, labile, easily metabolisable matter is introduced into anoxic parts of the sediment column (because of a shallow zero oxygen level), other, more low-oxygen resistant species, such as *C. oolina* and *N. scaphum*, will take over this superficial niche. Immediately below this surface zone with easily metabolisable organic matter, an environment is found where organic matter is less reactive (for instance in faecal pellets). *U. peregrina* seems to be one of the most tolerant species for this lower quality organic matter. In oligotrophic ecosystems, at the basal part of this zone, reactive organic matter becomes very scarce, or even absent within the sediment, and, consequently, benthic foraminifera are no longer found. Still deeper, concentrations of reactive organic matter will be associated with bacterial activity, and will logically be positioned around important redox boundaries (Lee, 1979; Mullins et al., 1985; Linke and Lutze, 1993; Kitazato, 1994; Jorissen, 1999a). One of the first of these fronts may be that of nitrifying bacteria. Between this front and the zero oxygen level, *M. barleeanus* seems to be the best-adapted taxon. The main locus of bacterial activity appears to be concentrated in the topmost part of the anoxic layer. Here, abundant benthic foraminiferal faunas dominated by *G. affinis* may be present. In the more oligotrophic environments

(stations H and F), the burial of organic compounds becomes insignificant and can no longer sustain important anaerobic bacterial stocks and associated deep infaunal foraminifera. When reading fig.11, one should, of course, realise that the limits between the various types of resources are not sharp, and consequently, large overlaps between the various taxa occur. Furthermore, ecosystems are always dynamic. The trophic level may show important short-term fluctuations, and the benthic faunas will respond accordingly. In general, more opportunistic taxa will profit from such ecosystem instability.

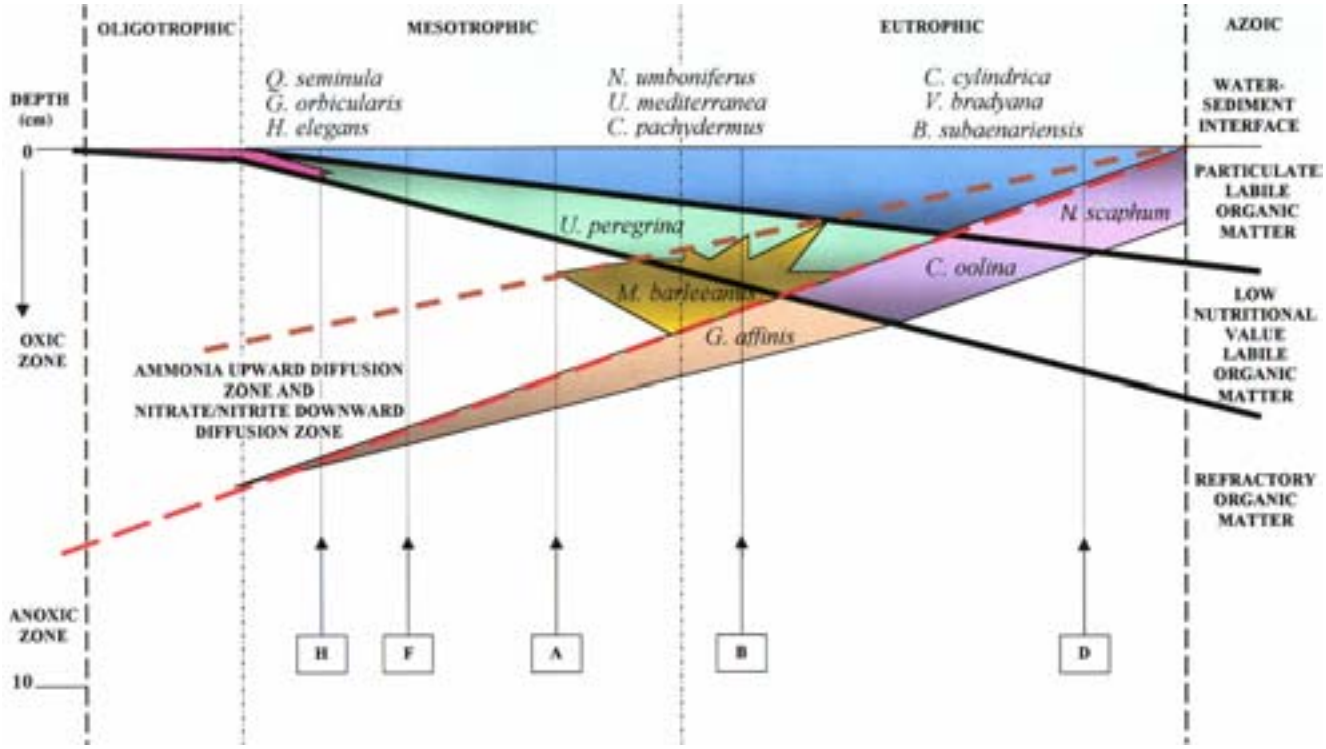

Fig.11 Microhabitat distribution and specific foraminiferal composition along the bathymetric transect in the Bay of Biscay; the approximate position of our 5 stations are indicated; see text for full explanation.

Conclusions

1. The dissolved oxygen concentration of the bottom waters is not seriously influenced by the exported organic flux. The interstitial waters, on the contrary, show a clear linkage: at the shallowest site (D), high and relatively constant organic matter inputs result in a redox front close to the sediment-water interface. At the deeper sites, the

zero oxygen level is found much deeper in the sediment, as a direct result of the decreasing organic flux.

2. The flux of organic matter to the ocean floor is the main parameter that controls the density and the composition of benthic foraminiferal faunas along the bathymetrical transect.
3. The oxygenation of the pore waters does not have a direct control on the vertical distribution of most foraminiferal taxa. Most species are able to adapt to severe dysoxia or even anoxia, provided that sufficient high quality food particles are available.
4. The TROX-model (Jorissen et al., 1995) is confirmed by the present data. Faunal penetration is indeed maximal in mesotrophic conditions, where the advantageous conditions of high-oxygen concentration and ample high quantity food availability may be found relatively deep in the sediment. However, the variability of the total faunal ALD_{10} (Average Living Depth) is mainly determined by deep infaunal taxa. Most shallow infaunal taxa show only a minor variability in their microhabitats between the various stations.
5. Certain taxa, such as *N. scaphum* and *C. oolina* appear to be typical for settings where labile organic matter is introduced into strongly dysoxic or anoxic environments. In case of an organic matter of lower quality, they are replaced by *M. barleeanus* and *G. affinis*.
6. Rather consistently, *U. peregrina* is found slightly below the most superficially living taxa, confirming that it is incorrect to consider the stable isotopic composition of its shell as representative for the bottom waters.

Acknowledgements

We thank the crews of *Côte de la Manche* for good collaboration during OXYBENT cruises. We are grateful of two anonymous reviewers for their helpful comments on the original manuscript. This work has been carried out within the framework of the french national program PROOF.

Appendices

Differentiating between *Uvigerina peregrina* and *Uvigerina mediterranea* may be difficult sometimes. This is especially the case when *U. peregrina* types loose the spinose aspect of their ornementation. A good overview of various *U. peregrina* morphotypes is given in Van der Zwaan et al. (1986), dealing with *Uvigerina* taxonomy.

In general, differences between the 2 species are as follows:

1) *U. mediterranea* has a rather bulky test, with a low length/width ratio, the opposite is true for *U. peregrina*. Adult *U. mediterranea* are much bigger than adult *U. peregrina*.

2) *U. mediterranea* has a rather large first chamber, much bigger than *U. peregrina*. Exception: microspheres of *U. mediterranea*, which may cause problems.

3) *U. mediterranea* has rather "gentle" costae, which are widely spaced, and continuous. *U. peregrina* has very sharp costae, less distance between them. The costae are very often crenulated, because from an evolutionary point of view (*U. peregrina* is very far from *U. mediterranea*); the costae have formed out of a series of spines. This difference can particularly well be seen on the basis of the test (first chamber); this is completely smooth in *U. mediterranea*, and uneven, covered with very small spines in *U. peregrina*.

4) *U. peregrina* may have spinose ornementation (the last chamber, or the surface between the costae), this can almost always be detected on the first chamber (see before); *U. mediterranea* has never such spinose ornementation.

5) Although not a 100% characteristics, the neck of *U. mediterranea* is better developed, and very often there is a prominent lip.

6) Again not a 100% characteristic: the neck of *U. mediterrnae* is very often placed in a kind of depression; the aperture of *U. peregrina* is always 100% terminal, on the highest point of the test.

Characteristic species from the outer-shelf and slope environments of the Bay of Biscay were identified by using designation and references to plates and figures in literature on Atlantic and Mediterranean foraminifera (see below).

Species	References
Ammobaculites agglutinans (d'Orbigny) 1846	Hess (1998), pl 4, Fig. 4
Ammotagena clavata (Jones and Parker), 1860	Jones (1994), pl 41 Figs. 12-16
Amphicoryna scalaris (Batsch), 1791	Jones (1994), pl 63 Figs. 28-31
Bigenerina nodosaria d'Orbigny 1826	Jones (1994), pl 44 Figs. 19-24
Biloculinella irregularis(d'Orbigny) 1839	d'Orbigny (1839), pl 8. Fig. 20 and 21
Bolivina alata (Seguenza), 1862	Schiebel (1992). pl. 1, Fig. 2
Bolivina spathulata (Williamson), 1858	Jorissen (1987), pl 1, Fig 5
Bolivina subaenariensis Cushman, 1922	Phleger et al (1953), pl. 7, Fig. 24 and 25
Bolivinita quadrilatera (Schwager), 1866	Jones (1994), pl 42 Figs. 8-12
Bulimina costata d'Orbigny, 1826	Van Leeuwen (1989), pl 8, Fig. 2 and 3
Bulimina inflata Seguenza, 1862	Van Leeuwen (1989), pl 8, Fig. 4
Bulimina marginata d'Orbigny, 1826	Hess (1998), pl 10, Fig. 7
Cancris auriculus (Fichtel & Moll), 1942	Jones (1994), pl 106. Fig. 4
Cassidulina carinata Silvestri, 1896	Phleger et al (1953), pl 9 Figs 32-37
Chilostomella oolina Schwager, 1878	Jones (1994), pl 55. Figs. 12-14
Cibicides lobatulus Walker & Jacob, 1798	Jones (1994), pl 92 Fig 10
Cibicides wuellerstorfi (Schwager). 1866	Van Leeuwen (1989), pl 10. Figs. 1-9
Cibicidoides pachydermus (Rzehac) 1886	Jones (1994), pl 94 Fig 9
Cibicidoides robertsonianus (Brady). 1881	Van Leeuwen (1989), pl 9, Figs. 1-3
Clavulina cylindrica d'Orbigny. 1952	Hofker (1932). Fig. 18 and 19
Cornuspira foliacea (Philippi), 1844	Jones (1994), pl 11. Fig 5 and 6
Cornuspira involvens (Reuss), 1950	Jones (1994), pl 11. Figs. 1-3
Cribrostomoides subglobosum (M.Sars) 1868	Jones (1994), pl 34 Figs. 8-10
Cyclammina cancellata Brady, 1879	Jones (1994), pl 37 Figs. 8-16
Cystammina pauciloculata (Brady), 1879	Jones (1994), pl 41 Fig 1
Dentalina ariena Patterson & Pettis, 1986	Jones (1994), pl 62 Figs. 27-31
Dentalina subemaciata Parr 1950	Jones (1994), pl 62. Fig 25 and 26
Eggerella bradyi (Cushman), 1911	Jones (1994), pl 47 Figs. 4-7
Eggerella scabra (Williamson), 1858	Jones (1994), pl 47. Figs. 15-17
Elphidium advenum Cushman, 1922	Phleger et al (1953) pl. 6. Fig. 15
Gavelinopsis translucens (Phleger & Parker), 1951	Schiebel (1992) pl. 4, Fig 5
Glandulina ovula d'Orbigny, 1846	Jones (1994), pl 61 Figs. 17-22
Globobulimina affinis (d'Orbigny), 1839	Phleger et al (1953) pl. 6. Fig. 32
Glomospira charoides Jones & Parker, 1860	Phleger et al (1953). pl. 5. Fig. 1
Glomospira gordialis Jones & Parker, 1860	Phleger et al (1953). pl. 5. Fig. 2
Gyroidina altiformis Stewart & Stewart, 1930	Jorissen (1987), pl 1, Fig 11
Gyroidina umbonata (Silvestri), 1898	Parker (1958), pl. 3, Fig. 19 and 20
Hanzawaia boueana (d'Orbigny) 1846	Jorissen (1987), pl. 3, Fig. 10
Haplophragmoides bradyi (Robertson), 1891	Schiebel (1992) pl. 7, Fig. 1a
Hoeglundina elegans (d'Orbigny), 1826	Phleger et al (1953) pl. 9. Fig. 24 and 25
Hyalinea baltica (Schroeter). 1783	Jones (1994), pl 112. Fig. 1 and 2
Karreriella bradyi (Cushman), 1911	Jones (1994), pl 41 Figs. 1-4
Lenticulina gibba d'Orbigny. 1839	Jones (1994), pl 69. Fig 8 and 9
Lenticulina peregrina (Schwager). 1866	Cushman and McCulloch (1950), pl 39, Fig 5
Lenticulina vortex (Fichtel and Moll), 1798	Jones (1994), pl 69, Figs 14-16
Melonis barleeanus (Williamson). 1858	Van Leeuwen (1989), pl 13. Fig 1 and 2
Nonion scaphum (Fichtel & Moll), 1798	Jones (1994), pl 109. Fig. 12
Nonionella turgida (Williamson), 1858	Jones (1994), pl 109. Figs. 17-19
Nouria polymorphinoides Heron-Allen & Earland 1914	Loeblich and Tappan (1988), pl. 123, Fig 11 and 12
Nuttallides pusillus (Parr). 1950	Phleger et al (1953). pl 9 Fig 5 and 6
Nuttallides umboniferus (Cushman), 1933	Van Leeuwen (1989), pl 15. Figs. 11-13; pl 16. Figs. 1-7
Oridorsalis umbonatus Reuss, 1851	Van Leeuwen (1989), pl 17. Figs. 1-13
Paratrochammina challengeri Bronnimann and Whittaker, 1988	Jones (1994), pl 35. Fig 10
Pseudavulina crustata Cushman. 1936	Jorissen (1987), pl. 1, Fig. 1
Pseudoeponides falsobeccarii Rouvillois 1974	Jorissen (1987), pl. 4, Fig.3a
Pullenia bulloides (d'Orbigny), 1826	Phleger et al (1953). pl. 10. Fig. 19
Pyrgo depressa (d'Orbigny), 1826	Jones (1994), Pl 2, Figs 12, 16 and 17
Pyrgo murrhina (Schwager) 1866	Hess (1998), pl 9. Fig 1
Pyrgo subsphaerica d'Orbigny, 1839	Cushman (1929), pl 18, Fig 1 and 2
Pyrgoella sphaera (d'Orbigny), 1839	Jones (1994), pl 2, Fig 4
Quinqueloculina seminula (Linné), 1758	Jones (1994), pl 5, Fig. 6
Rectuvigerina phlegeri Le Calvez, 1959	Le Calvez (1959). pl. 1, Fig. 11
Reophax ampullacea Brady 1881	Jones (1994), pl 30. Fig 6
Reophax dentiliniformis Brady. 1881	Jones (1994), pl 30 Fig 21 and 22
Reophax fusiformis (Williamson) 1858	Jones (1994), pl 30. Figs. 7-11
Reophax guttiferus Brady, 1881	Jones (1994), pl 31 Fig 10-15
Reophax scorpiurus Montfort, 1808	Loeblich and Tappan (1988), pl 44. Figs. 1-3
Robertinoides bradyi (Cushman and Parker) 1936	Jones (1994), pl 50 Fig 18
Sigmoilopsis schlumbergeri Silvestri, 1904	Jones (1994), pl 8, Figs. 1-4
Siphogenerina columellaris (Brady), 1881	Jones (1994), pl 75. Figs. 15-17
Siphotextularia affinis Fornasini, 1883	Kohl (1985). pl. 2. Fig. 5
Siphotextularia concava (Karrer) 1868	Jones (1994), pl 42, Figs 13-14
Textularia agglutinans d'Orbigny 1839	Jones (1994). pl. 43, Figs 1-3
Textularia sagittula Defrance, 1824	Jorissen (1987). pl 3 Fig 12
Thurammina albicans Brady, 1879	Jones (1994). pl.37, Figs. 2-7
Trifarina angulosa (Williamson), 1858	Jones (1994). pl. 74, Fig 17 and 18
Trifarina pauperata (Heron-Allen & Earland), 1932	Timm (1992), pl 6. Fig. 4
Uvigerina elongatastriata (Colom), 1952	Van der Zwaan et al (1986), pl 6, Figs 1-8
Uvigerina mediterranea Hofker, 1932	Van der Zwaan et al (1986) pl. 5, Figs. 1-7
Uvigerina peregrina Cushman. 1923	Van der Zwaan et al (1986). pl. 1, Figs.1-6
Uvigerina proboscidea Schawger, 1866	Van der Zwaan et al (1986). pl. 12, Figs 1-4
Valvulineria bradyana (Fornasini), 1900	Jorissen (1987). pl 4 Fig 1 and 2

CHAPITRE 2

Variabilité saisonnière et inter-annuelle des faunes de foraminifères benthiques à 550 mètres de profondeur dans le Golfe de Gascogne.

Seasonal and interannual variability of benthic foraminiferal faunas at 550 m depth in the Bay of Biscay.

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Résumé

Une station à 550 mètres de profondeur dans le Golfe de Gascogne a été échantillonnée 10 fois entre octobre 1997 et avril 2000 dans le but d'étudier la variabilité temporelle et spatiale des faunes de foraminifères benthiques vivants des fractions 63-150 µm et >150 µm. Des duplicata de carottes obtenus pour 5 campagnes permettent de faire la différence entre la variabilité spatiale et la variabilité temporelle des communautés de foraminifères benthiques. Nos données faunistiques sont comparées avec la production primaire des eaux de surface au travers d'une étude d'images satellites SeaWIFS. Dans notre zone d'étude, le régime de production primaire est marqué par un bloom de printemps long et par un bloom d'automne dont nous supputons l'existence. Ces blooms, périodes de concentration élevées de chlorophylle-a dans les eaux de surface, sont suivis, après un délai de 4-6 semaines, par une forte augmentation des effectifs d'espèces de foraminifères benthiques les plus opportunistes. Bien que le « patchiness » spatial des faunes soit substantiel, particulièrement dans la fraction 63-150 µm, la variabilité temporelle apparaît plus importante. D'une façon plus surprenante, aucun changement de l'oxygénation des eaux de fond et des eaux interstitielles ou des conditions redox dans le sédiment n'est enregistré. Les espèces de petite taille telles qu'*Epistominella exigua*, *Reophax guttiferus*, *Bolivina spathulata*, *Cassidulina carinata* et *Nuttallides pusillus* semblent répondre en premier aux apports de phytodétritus organiques labiles par des événements reproductifs marqués. Leur distribution spatiale fortement variable pourrait être liée à l'hétérogénéité spatiale des dépôts de matière organique. *Uvigerina peregrina* et *Uvigerina mediterranea,* les espèces de grande taille les plus opportunistes, dominent largement la fraction >150 µm durant les périodes eutrophes (blooms de printemps et d'automne). Ils apparaissent comme des espèces endopéliques peu profondes. *Melonis barleeanus* et *Globobulimina affinis*, taxa endopéliques intermédiaires et profonds, semblent dépendre beaucoup moins des apports épisodiques de détritus organiques, même si des légères augmentations de densité sont enregistrées dans la fraction >150 µm durant les périodes eutrophes. Un modèle conceptuel est proposé pour expliquer les délais existant entre les réponses de différentes populations remarquables de foraminifères benthiques aux périodes de bloom phytoplanctonique.

Mots-clés : Foraminifère benthique ; Microhabitat ; Saisonnalité ; Patchiness ; Opportunisme ; Bloom phytoplanctonique ; Flux organique.

Abstract

Live benthic foraminiferal faunas were sampled 10 times between October 1997 and April 2000 at a 550 m depth open-slope station in the Bay of Biscay. Duplicate cores for 5 samplings allow distinguishing between spatial and temporal variability of the foraminiferal faunas. Although spatial patchiness of the foraminiferal faunas is substantial, especially in the 63-150 μm fraction, the temporal variability appears to be larger. The foraminiferal patterns are compared with surface water primary production as assessed by the study of available SeaWIFS satellite images. In the study area, the primary production regime is marked by a pulselike and prolonged spring bloom and possibly a short fall bloom. Such periods of elevated chlorophyll-a concentration are followed, after a delay of about 4-6 weeks, by a strong frequency increase of the most opportunistic taxa of benthic foraminifera. Surprisingly, no change of bottom and interstitial water oxygenation and of redox conditions within the sediment is recorded. The small taxa *Epistominella exigua*, *Reophax guttiferus*, *Bolivina spathulata*, *Cassidulina carinata* and *Nuttallides pusillus* appear to respond first to a labile organic matter input, by a reproductive event marked by a strong patchy spatial distribution hypothetically resulting of the spatial heterogeneity of organic matter deposits. *Uvigerina peregrina* and *Uvigerina mediterranea,* the most opportunistic larger taxa, strongly dominate the >150 μm fraction during eutrophic periods (spring and fall blooms). Intermediate and deep infaunal taxa seem to depend less on fresh organic matter input, even if a small frequency increases are recorded in the >150 μm fraction during the most productive periods; *Globobulimina affinis* and *Melonis barleeanus* show reproductive events in rather shallow sediment layers in the more oligotrophic periods of the year. A conceptual model explains the increasing delay in the response to important phytoplankton bloom periods for the successive benthic ecosystem compartments.

Keywords: Benthic foraminifera; Microhabitat; Seasonality; Patchiness; Opportunism; Bloom; Organic flux.

Introduction

Mid latitude primary production regimes are marked by a seasonal and interannual alternation of algal blooms and low productivity periods (Pfannkuche and Thiel, 1987;

Parsons and Lalli, 1988; Berger et Wefer, 1990). This intermittence and seasonality of the surface water primary production is responsible for important fluctuations of the exported organic matter flux (Billett et al., 1983; Pfannkuche and Thiel, 1987; Berger and Wefer, 1990; Lohrenz et al., 1992). Since the biomass of deep-sea foraminifera is closely related to the flux of organic carbon to the seafloor (Altenbach, 1985, 1988; Altenbach and Sarnthein, 1989; Herguera and Berger, 1991; Jorissen et al., 1998; Loubere and Fariduddin, 1999a; De Rijk et al., 2000; Fontanier et al., 2002; Morigi et al., 2001), the interannual and seasonal primary production oscillations could thus result in important short term variability of the standing stocks and composition of the foraminiferal faunas. Several observations of highly opportunistic behaviour of foraminiferal taxa illustrate the capability of this group of organisms to rapidly adapt to changing trophic conditions (Gooday, 1988, 1993; Gooday and Lambshead, 1989; Barmawidjaja et al., 1992; Silva et al., 1996; Ohga and Kitazato, 1997; Jannink et al., 1998; Kitazato et al., 2000). Even in some abyssal environments (e.g. Porcupine Seabight) intermittence of food input appears to be a determinant factor, causing instantaneous and patchy bursts of benthic foraminiferal faunas that colonise freshly deposited phytodetritus (Gooday, 1988; 1993; Lambshead and Gooday, 1990; Turley et al., 1993). A similar reproductive response to artificial food input has recently been shown in laboratory experiments (Heinz et al., 2001, 2002).

Although the impact of phytodetritus deposits on foraminiferal faunas has been clearly shown, many important questions about deep-sea foraminiferal ecology remain partially unanswered:

1) What are the delays between primary production in the euphotic zone, the resulting exported organic matter input at the sediment-water interface and the response of the foraminiferal faunas in terms of density, composition and microhabitat?
2) What are the requirements of the various foraminiferal species in terms of quality and quantity of exported organic compounds?
3) How important is foraminiferal patchiness in the upper sediment layers; is this patchiness related to the micro-distribution of organic matter?
4) Is the vertical distribution of foraminiferal species in the sediment modified by organic matter input?
5) Is the foraminiferal response to food input restricted to the sediment surface, or is there a faunal response at depth in the sediment as well?

Whereas most opportunistic taxa rely on fresh phytodetritus, other, less critical taxa may feed on more altered organic substances, such as zooplankton faecal pellets or organic

matter in a more or less advanced state of decay. It has been speculated that some taxa may also feed either on bacteria involved in the aerobic or anaerobic degradation of more refractory organic compounds, or on their breakdown products (Lee, 1979; Thomsen and Altenbach, 1993; Kitazato, 1994; Jorissen et al., 1995).

A previous foraminiferal study along a five station bathymetric transect in the Bay of Biscay substantiated the determining role of exported organic matter flux on foraminiferal density, composition, and microhabitat (Fontanier et al., 2002). The foraminiferal density reflects the exported organic matter flux, and shows a clear decrease from 150 to 2000 metres depth. Foraminiferal microhabitats, which appear to be linked to principal redox fronts, deepen from the outer continental shelf to the lower slope stations. In the deepest, most oligotrophic stations, infaunal taxa tend to disappear. Finally, Fontanier et al. (2002) propose a species specific adaptation of the TROX microhabitat model of Jorissen et al. (1995). In the present paper, we study the temporal variability of live benthic foraminiferal faunas (63-150µm, >150µm) at a single upper bathyal station (550 m depth) from an open slope environment in the Bay of Biscay (Fig. 1), which is supposed to be under the influence of a typical temperate, mid latitude seasonal primary production regime. For this purpose, thirteen sampling cruises took place from October 1997 to April 2000. On-line data archives of the Joint Research Centre (SeaWIFS data) allow estimates of surface water chlorophyll-a for the duration of the study period. For all studied cores, geochemical analyses have been performed in order to determine redox conditions in the upper sediment layer. The main objectives of this study are to determine whether the foraminiferal faunas respond to the seasonal and interannual fluctuations of the exported organic matter flux. More precisely, we will concentrate on the seasonal changes of density, composition and vertical distribution of foraminiferal faunas, and their possible relationship with the qualitative and quantitative seasonal variations of the exported organic matter flux.

Study area

Hydrographical setting

The Bay of Biscay is a semi-enclosed basin where water mass circulation is disconnected from the general North Atlantic Drift. The current velocity of the various water masses is generally weak (less than 10 cm s^{-1}, Tréguer et al., 1979), and the waters which

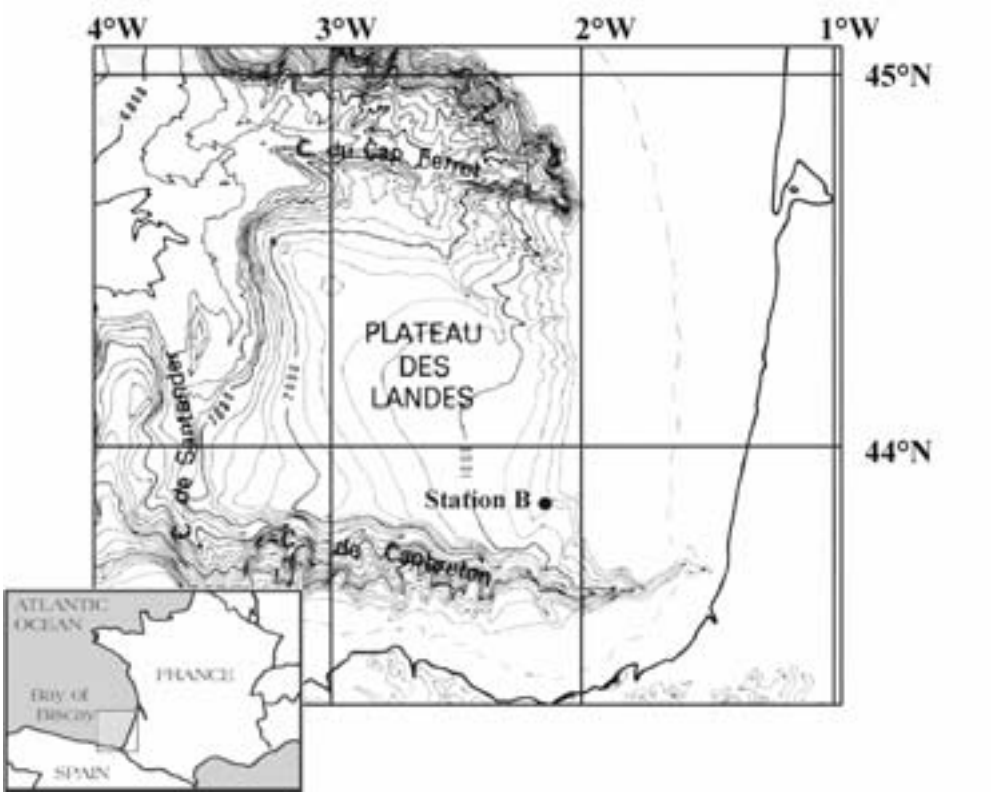


Fig. 1 Study area, bathymetry and geographical position of station B.

enter from the north, along the Irish shelf-break, leave the area near Cape Finisterre only after two years. The surface waters patterns are strongly dependent on the seasonal variations of the thermocline and mixed layer (Tréguer et al., 1979), and the surface currents (velocity and directions) are widely influenced by local wind regimes (Boucher, 1985). Hydrological patterns of water masses in the southeast part of the Bay of Biscay (our study area) are presented in a previous paper (Fontanier et al., 2002).

The continental slope bordering the French shelf deepens gradually, and is interrupted by two large canyons (Cap-Ferret Canyon, Capbreton Canyon). Vertical fluxes represent the main sedimentary component in open slope environments, whereas lateral advection may dominate sedimentary processes in the canyons (Heussner et al., 1999). The present paper concentrates on a 550 m deep open-slope station, where the impact of laterally advected particles is supposed to be minimal, and where the linkage between surface water primary production, the vertical particle flux, and benthic life should be rather straightforward. Our station B is positioned within the Northern Atlantic Central Waters (NACW), which has a salinity of 35.60 and a temperature of about 11° C (Ogawa and Tauzin, 1973). The sediment consists predominantly of fine-grained silty mud.

Primary production patterns in the north-eastern Atlantic

In temperate latitudes, the alternation between mixing and stratification of the water column, and the daily input of sunlight appear to be the main factors controlling the seasonal dynamics of phytoplankton (e.g. Harris, 1986; Berger and Wefer, 1990). The moderately strong seasonality found in the Bay of Biscay is characterized by an annual sinusoidal primary production curve, dominated by opportunistic species, with a succession of phytoplankton to zooplankton. The consequences of this temporal variability are seasonal occurrences of zooplankton grazers and predators, a fluctuating exportation of organic debris, and, possibly, seasonal changes in the growth rate of benthic organisms (Bruland et al., 1989; Jumars et al., 1989).

The Bay of Biscay is characterized by phytoplankton blooms occurring in spring, summer and autumn (Tréguer et al, 1979; Froidefond et al., 1996; Laborde et al., 1999). Spring blooms are considered as the highest chlorophyll-a concentration events throughout the year. The phytoplankton assemblages are mainly composed of diatoms and coccolithophorids (Tréguer et al., 1979; Fernandez et al., 1995). Wroblewski (1989) suggests a general duration of about two weeks for the spring bloom. Fernandez (1990), who studies the Central Cantabrian Sea (southern part of the Bay of Biscay), observes high chlorophyll-a and primary production rates in March, predominantly due to microflagellates. In a more recent study Laborde et al. (1999) describe a high productivity period, which lasts for about two months. In view of the earlier literature, it seems obvious that this relatively long period is the result of a close succession of several individual bloom events, involving different phytoplankton groups.

Minor upwelling events occur during early summer, in relation to NNW coast-parallel winds and to riverine discharge (Froidefond et al., 1996). Large coccolithophorids blooms are the result; they have been observed on the shelf-break of the Bay of Biscay by satellite imagery as well as by in situ measurements (Holligan et al., 1983; Fernandez et al., 1993; Beaufort and Heussner, 1999). Because this system has probably a very strong interannual variability, it is difficult to determine an average primary production value. Nevertheless, total primary production estimates based on satellite imagery (Antoine et al., 1996) suggest a slight increase in early summer.

In autumn, cooling of the surface waters is generally effective without causing the total disappearance of water column stratification and of the nutricline. Nevertheless, Tréguer et al. (1979) have recorded a chlorophyll-a increase in October, which they describe as an

autumn bloom. In this period, primary production is rather patchy on a basin scale, and strongly influenced by the hydrological structures. Lohrenz et al. (1992) speculate that primary production increases are generally caused by wind-induced mixing, resulting in nutrient injection from subsurface waters into the nutrient-depleted surface waters. Recently, Sellmer et al. (1998) showed an autumn bloom at the BIOTRANS site (47°N/20°W), occurring around the nutricline, at about 30 to 50 m depth, mainly composed of autotrophic dinoflagellates, with smaller amount of diatoms.

Very few quantitative data are available on primary production in general, and more specifically, on the individual bloom events occurring in the study area. Tréguer et al. (1979) estimate a primary production between 0.4 and 1.9 g C/m^2/day for the spring bloom of 1973. Primary production measurements during autumn 1972 indicate a bloom with values of 0.3 - 0.4 g C/m^2/day (Le Corre and Tréguer, 1976). This range of values agrees with recent data obtained in the Cap-Ferret region during five ECOFER cruises: 0.7 - 1.2 g C/m^2/day in spring (May 1990 and 1991) and 0.3 g C/m^2/day in autumn (October 1990; Laborde et al., 1999). Total annual primary production has been estimated between 145 and 170 gC/m^2/yr (Laborde et al., 1999).

Material and Methods

In order to complete the rather scarce information about seasonal and interannual changes of phytoplankton biomass in the surface waters from the Bay of Biscay, we used on-line data archives of the Joint Research Center (European Commission) to estimate chlorophyll-a concentrations (SeaWIFS data) in the study area for the duration of our sampling period (October 1997 to April 2000; Fig. 2). Unfortunately, weather conditions strongly affect the availability of images. Especially during autumn and winter, satellite monitoring is only rarely possible, because of the dense cloud cover.

In order to obtain a good overview of the temporal variability of the benthic foraminiferal assemblages, thirteen sampling cruises were organized between October 1997 and April 2000. For meteorological reasons, sampling was impossible during 3 cruises, and consequently, station B (43°49'98 N, 2°23'04 W, water depth 550 m, Fig. 1) was sampled 10 times (Table 1). Cores were sampled with a Barnett multi-tube corer (Barnett et al., 1984), which allows sampling of first decimetres of the sediment, the overlying bottom waters, and an undisturbed sediment-water interface. Free waters were collected immediately after core

Cores Station B	Date	O_2 concentration (µmol/l)	Oxygen penetration depth (mm)	Whitish filamenteous and/or amorphous phytodetrital aggregates	Radiolarians
OB1B/OB1B^{bis}	10/26/1997	217	17	++/-	--/--
OB2B/OB2B^{bis}	1/30/1998	216	24	+	--
OB3B	6/7/1998	212	19	-/+	--/--
OB4B	7/23/1998	208	18	+	--
OB5B	10/17/1998	205	21	-	--
OB6B	12/8/1998	212	20	-	--
OB7B	1/23/1999	220	26	+	--
OB8B/OB8B^{bis}	4/19/1999	207	20	-/-	-/+
OB9B/OB9B^{bis}	6/24/1999	215	21	+/++	+/+
OB10B/OB10B^{bis}	4/25/2000	221	23	++/++	-/-

Table 1 Sampling dates, bottom water oxygen concentration, depth in the sediment of the zero oxygen level and semi-quantitative analysis performed on the sedimentary residual parts of the first quarter of sediment for 15 cores at station B for the 10 sampling cruises; Phytoplankton and zooplankton components were observed and described according to the following classes: ++ abundant, + common, - rare, -- absent.

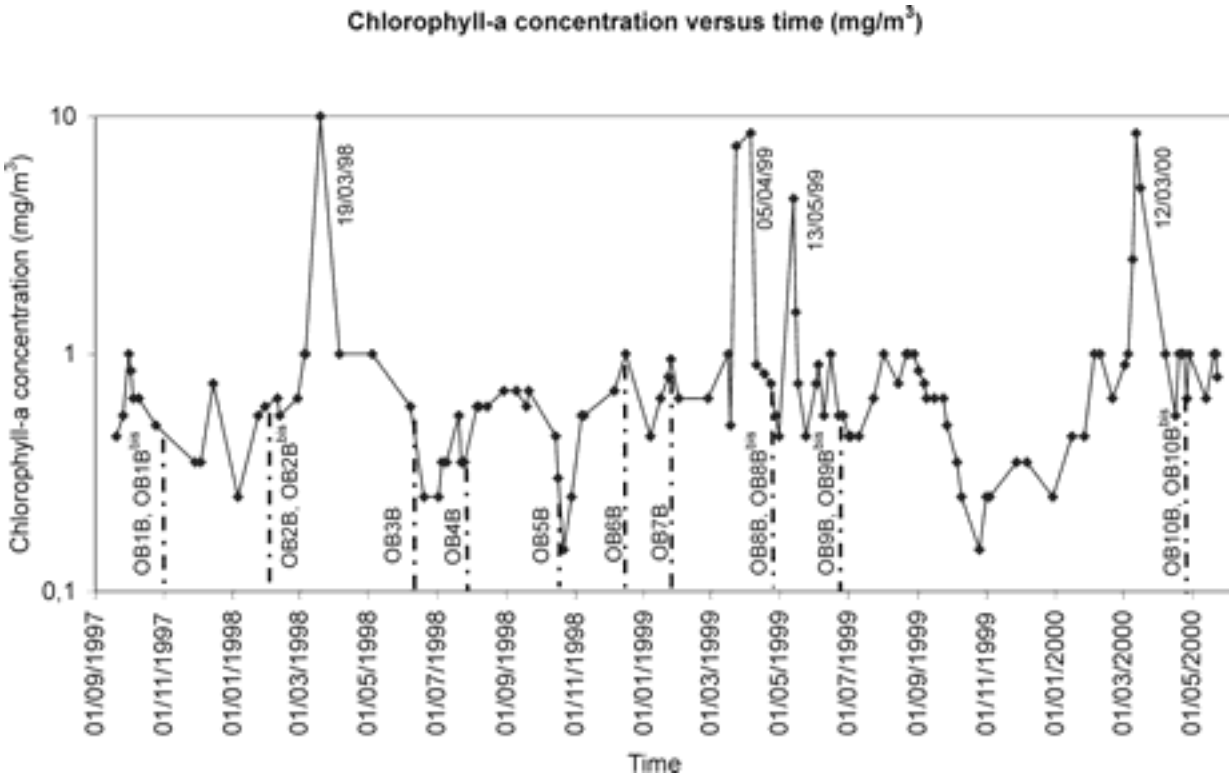


Fig. 2 Chlorophyll-a concentrations in the surface waters in our study area between October 1997 and April 2000 (estimates based on SEAWIFS images). Vertical dot-dash lines indicate when the sampling cruises took place.

recovery for dissolved O_2 measurements by the Winkler titration method (Strickland and Parsons, 1972). Profiles of pore water O_2 were obtained on board with a cathode-type mini-electrode (Revsbech and Jørgensen, 1986; Helder and Bakker, 1985; Revsbech, 1983). The temperature was maintained stable with an insulating device. This operation was completed in duplicate within 30 minutes after core recovery. Subsequently, the core used for O_2 profiling was sliced into thin horizontal sections (every 0.5 cm for the top 2 cm, 1 or 2 cm below) within 1 hour and 30 minutes. For every level a sub-sample was centrifuged under N_2 at 5000 rpm for 20 min in order to collect pore waters. Two aliquots of water were filtered (0.2 µm) and frozen at -25°C for nutrient analyses. Interstitial water compounds were analyzed by techniques adapted for small volumes of samples (Anschutz et al., 1999; Hyacinthe et al., 2001). Nitrate and nitrite were measured by flow injection analysis (FIA) according to Anderson (1979).

For faunal analysis, one entire 72 cm^2 core was sliced horizontally for each station, usually every 0.25 cm for the first cm of sediment, every half cm between 1 and 4 cm depth, and every cm between 4 and 10 cm. For evaluating the amplitude of spatial heterogeneity, all available duplicate samples were analyzed as well. This concerns samples $OB1B^{bis}$ (the top 2 cm of a second core, partially sampled in 0.5 cm intervals), $OB2B^{bis}$ (top 5 cm sampled in 2.5 cm intervals), $OB8B^{bis}$ (sampled down to 5 cm according to the standard sampling protocol), $OB9B^{bis}$ and $OB10B^{bis}$ (both completely sampled). Except for OB10 (two consecutive multi-corer deployments), each duplicates pair was recovered from the same multi-corer deployment. Since in all cores more than 95% of the fauna is found in the top 5 cm, $OB2B^{bis}$, $OB8B^{bis}$ and $OB9B^{bis}$ can be considered as fully reliable duplicates. Census data of core OB1B (>150 µm fraction) have already been presented in Fontanier et al. (2002).

We follow the same sediments storage and preparation as presented in Fontanier et al. (2002). Foraminifera belonging to the >150 µm fraction were studied along the 10 cm long cores. Because of its extremely time-consuming character, we limited our study of the 63-150µm fraction to the first half cm of the sediment. In cases where the sediment surface is oblique, the volume of the top half cm layer may be slightly variable, and therefore, absolute density values for the superficial samples are less reliable. During picking, semi-quantitative analyses were performed on the residual parts of both fractions to evaluate some remarkable sedimentary components (phytodetritus and zooplankton compounds; Table 1).

The Rose Bengal staining technique (Walton, 1952; Bernhard, 1988) is routinely used to recognize foraminifera that were alive at the time of sampling. A problem of this method is that Rose Bengal may also stain the dead foraminiferal protoplasm, which may be partially

preserved below the zero oxygen level within the sediment for a considerable period of time after the death of the organism (Bernhard, 1988; Corliss and Emerson, 1990). As a consequence, we use the same strict staining criteria as those detailed in Fontanier et al. (2002). Non-transparent agglutinated and miliolid taxa were broken in order to inspect the test interior. Fragments of the very fragile arborescent agglutinating foraminiferal fragments (such as *Hyperammina* spp., and *Glomospira* spp.) were not included in the quantitative analyses, because the orange-reddish color of their test makes it particularly difficult to appreciate whether the organism was alive or dead at the time of sampling.

Our taxonomical framework is given in Appendix A. All foraminiferal census data are listed in Appendices B and C. The total density of the live foraminiferal fauna total density has been determined by summing up the number of individuals for all levels between 0 to 10 cm depth for the >150 µm fraction, but only for the 0-0.5 cm interval for the 63-150 µm fraction. The total density per core is expressed as number of individuals found at and below a 72 cm² sediment surface. In all graphs depicting the vertical distribution of the foraminifera in the >150 µm fraction (Figs. 5a-m), the faunal densities have been standardised for a 50 cm^3 sediment volume.

The average living depth (ALD_x, Jorissen et al., 1995) seems the best way to describe the overall vertical distribution of the total foraminifera fauna or of individual taxa, and to get a general idea about the microhabitat patterns. After a first classification with four main microhabitats proposed by Corliss and Chen (1988), it has been argued that only species living on elevated substrates can be considered as “epifaunal” (Buzas et al., 1993). Therefore, in the soft bottom communities described in this study, we recognise only three different microhabitat categories: shallow infaunal, intermediate infaunal and deep infaunal taxa. The ALD_x is calculated with the following formula:

$$ALD_x = \sum_{i=0,x} (n_i \times D_i) / N$$

where x = lower boundary of deepest sample, n_i = number of specimen in interval i, D_i = midpoint of sample interval i, and N = total number of individuals for all levels.

For all stations, ALD_{10} was calculated for the whole fauna, as well as for individual taxa, on the basis of the numbers of stained individuals found in the successive sediment slices. Isolated individuals separated from the main population by more than 1 cm of "sterile" sediment (without live individuals of the studied taxon) were not integrated in the

calculations of the ALD_{10}. In Appendix B, those individuals are present between brackets. We suppose that such isolated individuals have been transported downward (outside their normal microhabitat) by bioturbation, or correspond to dead organisms that have been counted erroneously**.** Overall, weighed ALD_{10} values were calculated for each taxon by integrating the results obtained in the 13 cores:

$$\overline{ALD_{10}} = \sum_{i=1,n}^{n} (ALD_{10}^{i} \times n_i) / \sum_{i=1,n}^{n} n_i$$

where n = number total of cores, ALD_{10}^{i} = Average Living depth for the ten first cms of the core I, and n_i = number of specimen in the core i.

In order to evaluate the differences between duplicate and temporally distinct samples, a non-standardised principal component analysis (Davis, 1986) was applied for both size fractions, using the percentages of all taxa with an occurrence of more than 5% in at least one sample.

Results

Chlorophyll-a concentrations from October 1997 to April 2000

In the Bay of Biscay, the spring bloom chlorophyll-a increase is the most prominent seasonal event of the year (Fig. 2). This gradual or pulse-like increase of chlorophyll-a concentration generally starts with a first pulse at the end of winter, in the second part of March (Fig. 2), which affects the whole Bay of Biscay. A second pulse appears in the second half of April, and lasts through the first weeks of May. This second pulse has a more restricted geographical distribution, and at our sampling station, we observed it only in spring 1999.

In summer, the offshore waters of the Bay of Biscay exhibit rather low chlorophyll-a concentrations (0.1-0.5 mg/m^3); higher values are present over the shelf and shelf break. However, we can imagine that phytoplankton biomass associated with a putative Deep chlorophyll maximum is not represented in satellite images.

In autumn, the scarcity of satellite images allows far reliable estimates of chlorophyll-a concentrations. This period is characterised by low surface water phytoplankton biomass for

the whole Bay of Biscay. Chlorophyll-a concentrations are minimal in late autumn and early winter.

At our station B, the variability of the chlorophyll-a concentrations in the overlying surface waters is in close agreement with the basin-wide patterns inferred before. In late autumn and in the winter, chlorophyll-a concentrations are low (<0.7 mg/m^3). They precede high and abrupt chlorophyll-a increases (up to 10 mg/$m^{3)}$, which can be noticed every year in late winter (March 1998, 1999 and 2000). Only in 1999 is a second chlorophyll-a increase observed, on the 13th of May. The summer is characterised by intermediate chlorophyll-a concentrations (about 1 mg/m^3). In early autumn (October), the chlorophyll-a concentrations are comparable to those in summer. Minimal surface water chlorophyll-a values, of about 0.2 mg/m^3, are reached in October; surface waters remain oligotrophic (0.2 – 0.5 mg/m^3) until January.

Sedimentary organic deposits

Semi-quantitative observations of the sieve residues of the first half centimetre reveal that cores sampled in October 1997, in June 1999 and in April 2000 (OB1B, OB9B^{bis}, OB10B and OB10B^{bis}, respectively) contain high amounts of whitish amorphous aggregates composed of diatoms and of radiolarians (Table 1). These organic aggregates were observed after sieving of the samples, and therefore, benthic eventual foraminiferal faunas living within the organic aggregates could not be substantiated.

Oxygen concentration and redox conditions of interstitial waters

Bottom water oxygen concentrations (Table 1, Fig. 3a) vary from 205 to 221 µmol/l. The zero oxygen boundary varies from 17 mm depth (0B1B, October 1997) to 26 mm depth (OB7B, January 1999). In all cases, there is a steep decrease of oxygen concentration in the first half cm of the sediment. The nitrate and nitrite concentrations (Fig. 3b) have maximum values (of about 20 µmol/l) in the first half cm, and show a rapid decrease to background values at about 2.5 cm depth.

Faunal density and number of taxa

In the >150 µm fraction, foraminiferal densities vary from 245 to 1346 individuals per core (Fig. 4). Maxima of 1346 and 845 individuals are found in October 1997 (OB1B) and April 2000 (OB10B) respectively.

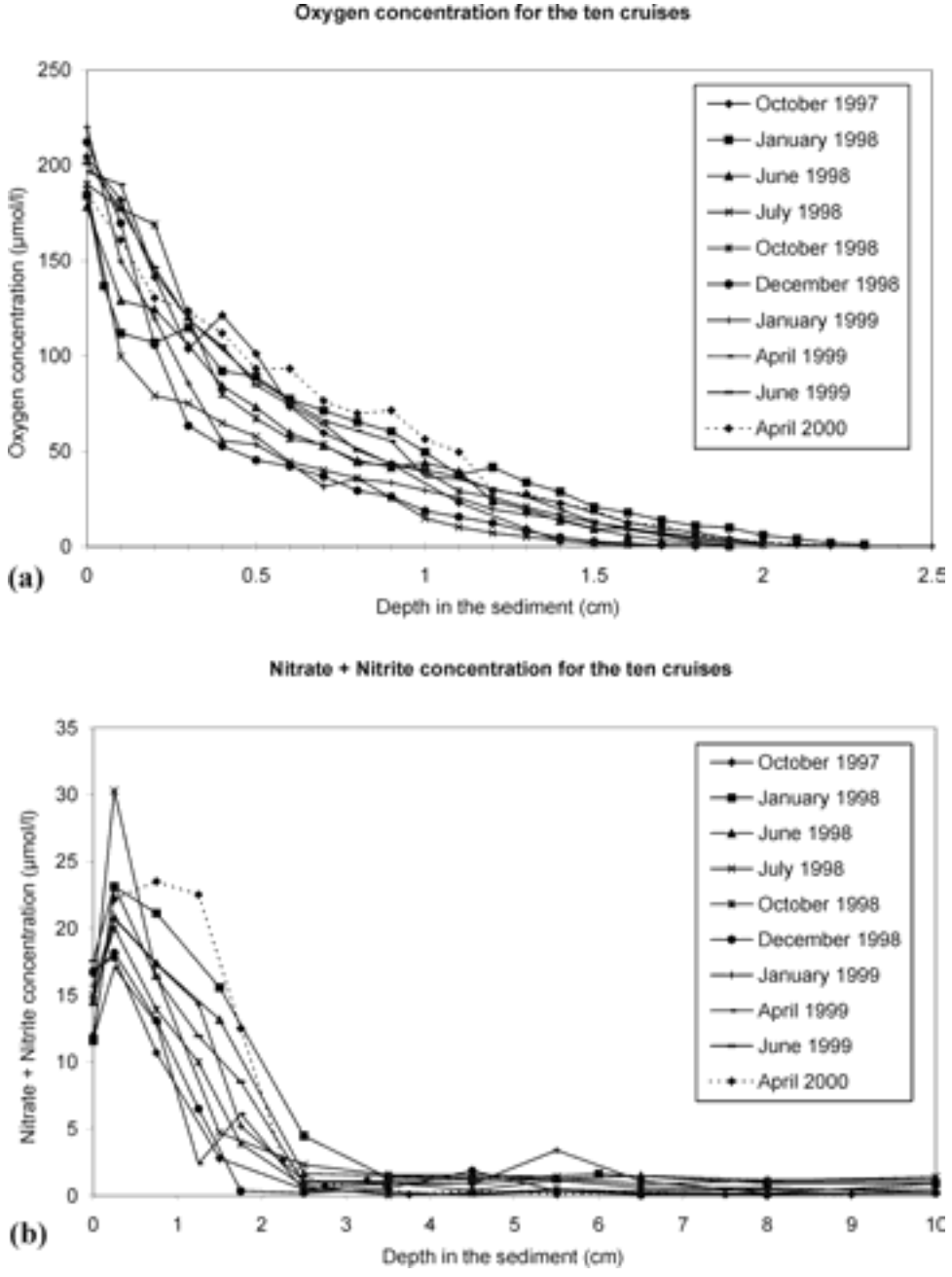


Fig. 3; 3a Dissolved oxygen concentrations in the sediment for the ten cruises; 3b Nitrate + nitrite concentrations in the sediment for the ten cruises.

Minimum values are recorded in July 1998 (OB4B, 281 individuals), October 1998 (OB5B, 322 individuals) and April 1999 (245 and 465 individuals in two replicate cores). For the 63-150 µm fraction, foraminiferal densities (only for the topmost 0.5 cm) vary from about 40 to

2195 individuals (Fig. 4). Maxima of 1505 and 2195 individuals are found in October 1997 (OB1B) and in April 2000 (OB10B^{bis}); minimum values are found in December 1998 (OB6B, 37 individuals) and in October 1998 (OB5B, 73 specimens). Part of this variability, however, may be due to the variable sample size of the first 0.5 cm in the case of oblique sediment surfaces.

In the >150 µm fraction, perforate foraminifera form the main faunal component (60% to 90% of the fauna). Non fossilising agglutinated taxa account for 10 to 30 %, whereas fossilising agglutinated taxa (maximum 10%) and miliolids (maximum 3.5%) are rare in all cores. Also in the 63-150 µm fraction, the perforate group is largely dominant (50-95%), but non fossilising agglutinated individuals can represent up to 48% of the total fauna (in April 1999, OB8B). Miliolids and fossilising agglutinated foraminifera account for less than 5% of the foraminiferal faunas.

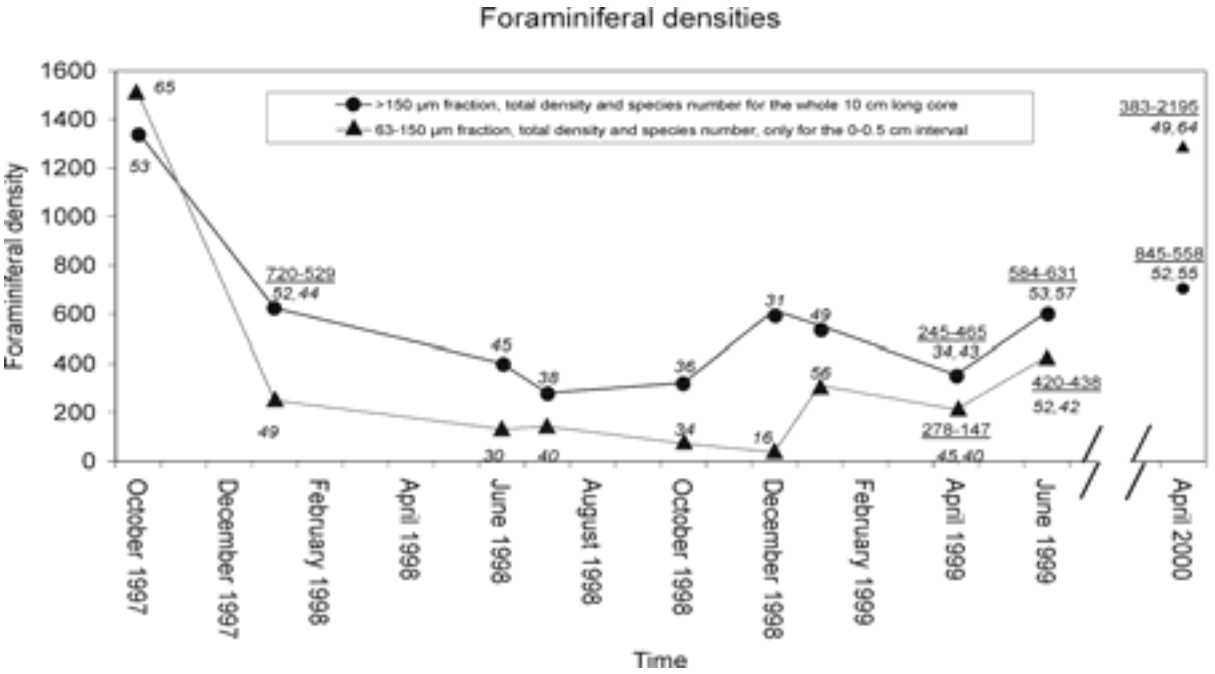


Fig. 4 Foraminiferal density for both size fractions during the ten cruises. The foraminiferal density for the >150 µm fraction is calculated as the total number of live individuals per core of 72 cm^2. The foraminiferal density for the 63-150 µm fraction is calculated as the total number of live foraminifera in the first half cm of the core. When duplicate cores are available, an average value is plotted, and the values of the individual cores are given (underlined numbers). For all cores, the number of species is given in italics. When duplicate cores are available, the values of the individual cores are also presented (couple of numbers in italics).

The number of taxa in the >150 µm fraction varies from 31 (December 1998, OB6B) to 57 (June 1999, OB9B^{bis}), without a clear relation to faunal density. In the 63-150 µm fraction, where only the topmost 0.5 cm was studied, the number of taxa varies from 16 (December 1998, OB6B) to 65 (October 1997, OB1B); there is a clear positive correlation with the faunal density here.

Faunal composition and microhabitat

1) >150µm fraction

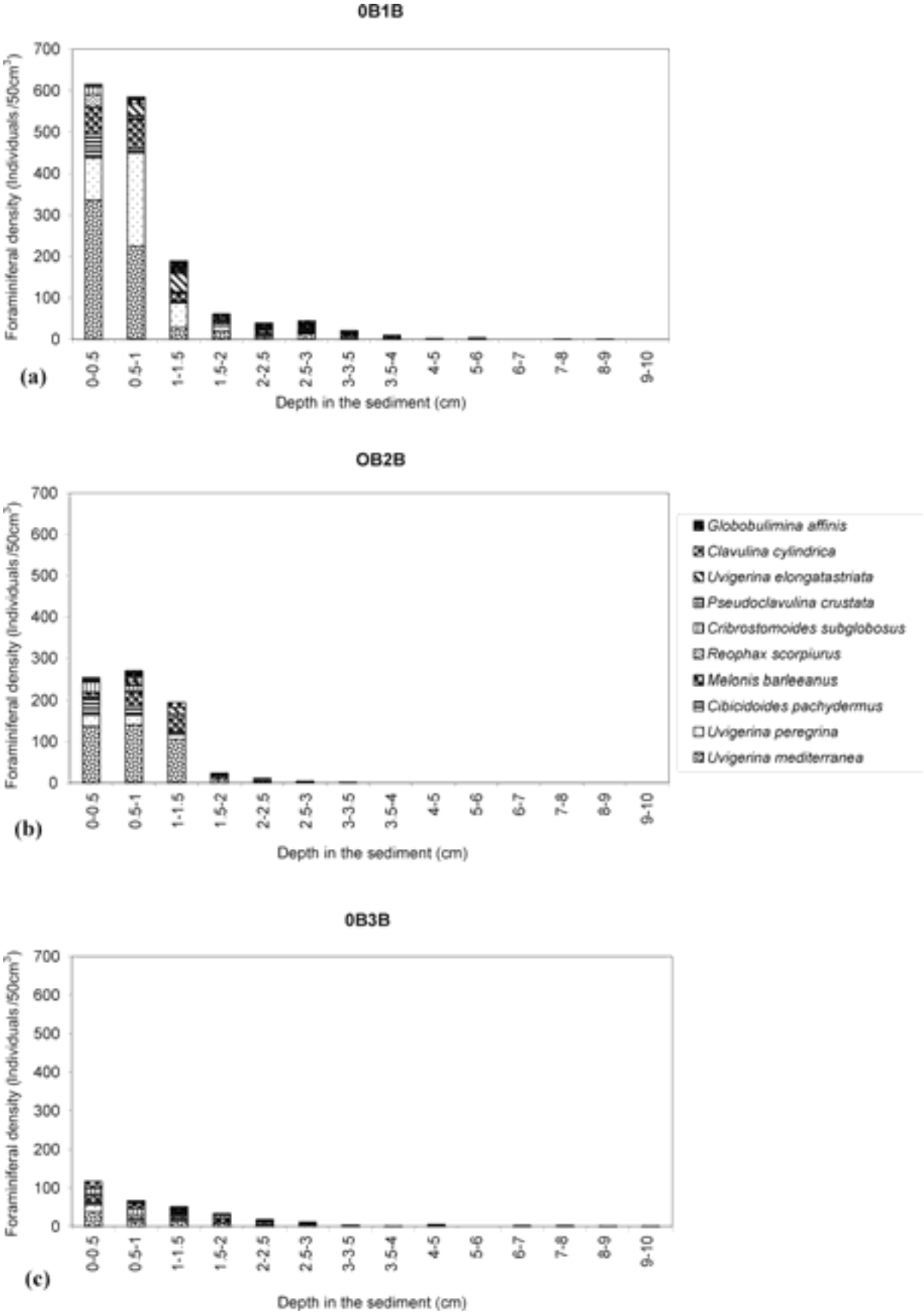
For most of the cores, the foraminiferal fauna is strongly concentrated in the oxygenated sediment top layers (Figs. 5a-m). The highest density is normally found in the first half cm. Maximum values were observed in October 1997 (OB1B; ~800 specimens/50 cm^3) and April 2000 (OB10B; ~500 specimens/50 cm^3). In most cores, the faunal density drops rapidly in the second cm, where dysoxic conditions prevail. Only low-density foraminiferal faunas are found in the generally anoxic sediments below 2 cm depth. The cores taken in December 1998 (OB6B) and April 1999 (OB8B^{bis}), which contain fair amounts of live individuals below the zero oxygen level, form notable exceptions. Consequently, for most of the cores, the ALD_{10} of the total fauna is about 1 cm. Maximum ALD_{10} values are found in December 1998 (OB6B; 2.0 cm) and April 1999 (OB8B^{bis}; 1.6 cm). The shallowest microhabitat depth was observed in July 1998 (ALD_{10} = 0.6 cm).

Uvigerina mediterranea dominates the faunas in every core (Appendix B); its relative abundance fluctuates from 17.8 to 39.9%, with maximum percentages observed in January 1998 (OB2B) and June 1999 (OB9B^{bis}). Minimum values are found in July 1998 (OB4B) and April 1999 (OB8B^{bis}). *Melonis barleeanus* is the second most abundant species; in most samples it counts for about 10% of the total fauna (4.1-16.7%). *Uvigerina peregrina* has a much more variable percentage. It is very frequent in October 1997 (OB1B and OB1B^{bis}), when its percentage reaches 21%. In many other samples, the species is rather infrequent (2-5%). *Globobulimina affinis* is well represented in most cores, with relative abundances of about 5%. The highest percentage (12-15%) is found in April 1999 (OB8B and OB8B^{bis}). *Uvigerina elongatastriata* and *Reophax scorpiurus* account each for about 5% of the faunas. Some other taxa show relatively low background values (1-3%), but can occasionally occur with high percentages. *Cibicidoides pachydermus* shows a 7.2% maximum in January 1998 (OB2B), whereas *Clavulina cylindrica* is well represented (7.7%) in June 1998 (OB3B).

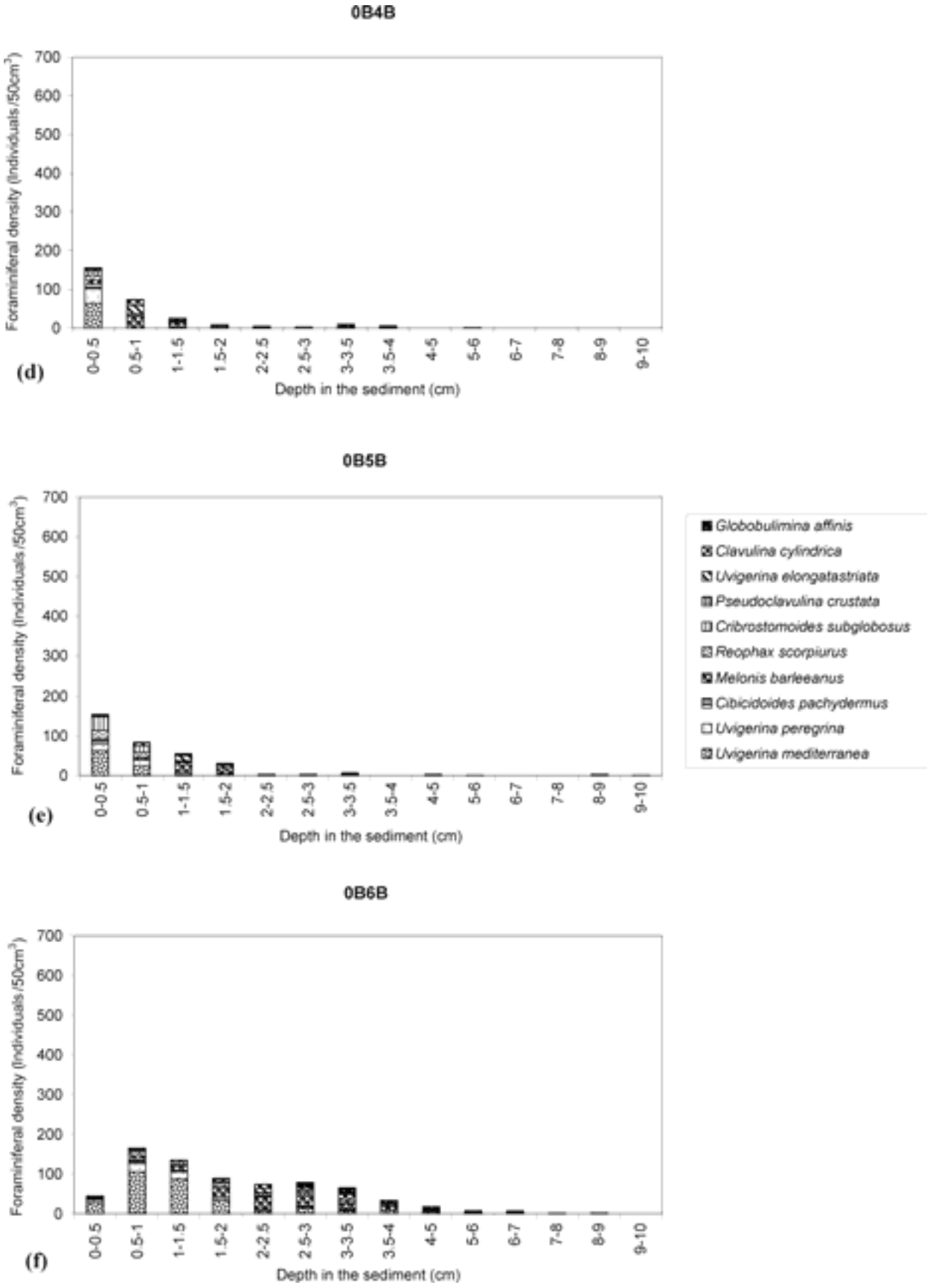
Cribrostomoides subglobosus shows peak values (9-12%) in June 1998 (OB3B), October 1998 (OB5B), and April and June 1999 (OB8B^{bis} and OB9B^{bis}). *Pseudoclavulina crustata* shows one single peak occurrence (9%), in April 1999 (OB8B).

The microhabitat of the majority of the taxa is very shallow (Table 2). The overall, weighed, values are lowest for *C. pachydermus* (ALD_{10} = 0.54 cm), *P. crustata* (ALD_{10} = 0.71 cm), *R. scorpiurus* (ALD_{10} = 0.75 cm), *U. mediterranea* (ALD_{10} = 0.77 cm), *U. peregrina* (ALD_{10} = 0.78 cm) and *C. subglobosus* (ALD_{10} = 0.82 cm); these species are largely restricted to the shallow infaunal microhabitats in the first cm of the sediment (Figs. 5a-m). Their ALD_{10} shows very little variability between the 13 cores (Table 2), with the exception of core OB6B, where the microhabitat of all taxa is significantly deeper than normal. The anomalously low numbers in the first 0.5 cm level at this station (in the 63-150 µm as well as in the >150 µm fraction) suggest that, because of a strongly oblique sediment surface, only a minor part of the 72 cm^2 surface was sampled. This sampling artefact effects the calculation of the microhabitat, and the density value in the 63-150 µm fraction, but not the total density values (down to 10 cm) in the >150 µm fraction.

M. barleeanus (overall weighed ALD_{10} = 1.30 cm), *U. elongatastriata* (overall weighed ALD_{10} = 1.47 cm) and *C. cylindrica* (overall weighed ALD_{10} = 1.46 cm) show a rather constant intermediate infaunal microhabitat, with the exception of core OB6B, where all occurrences are deeper. *G. affinis* (overall weighed ALD_{10} = 2.84 cm) occupies a deep infaunal microhabitat, in dysoxic or sometimes totally anoxic sediment layers.



Figs. 5a-m Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for 14 available cores.



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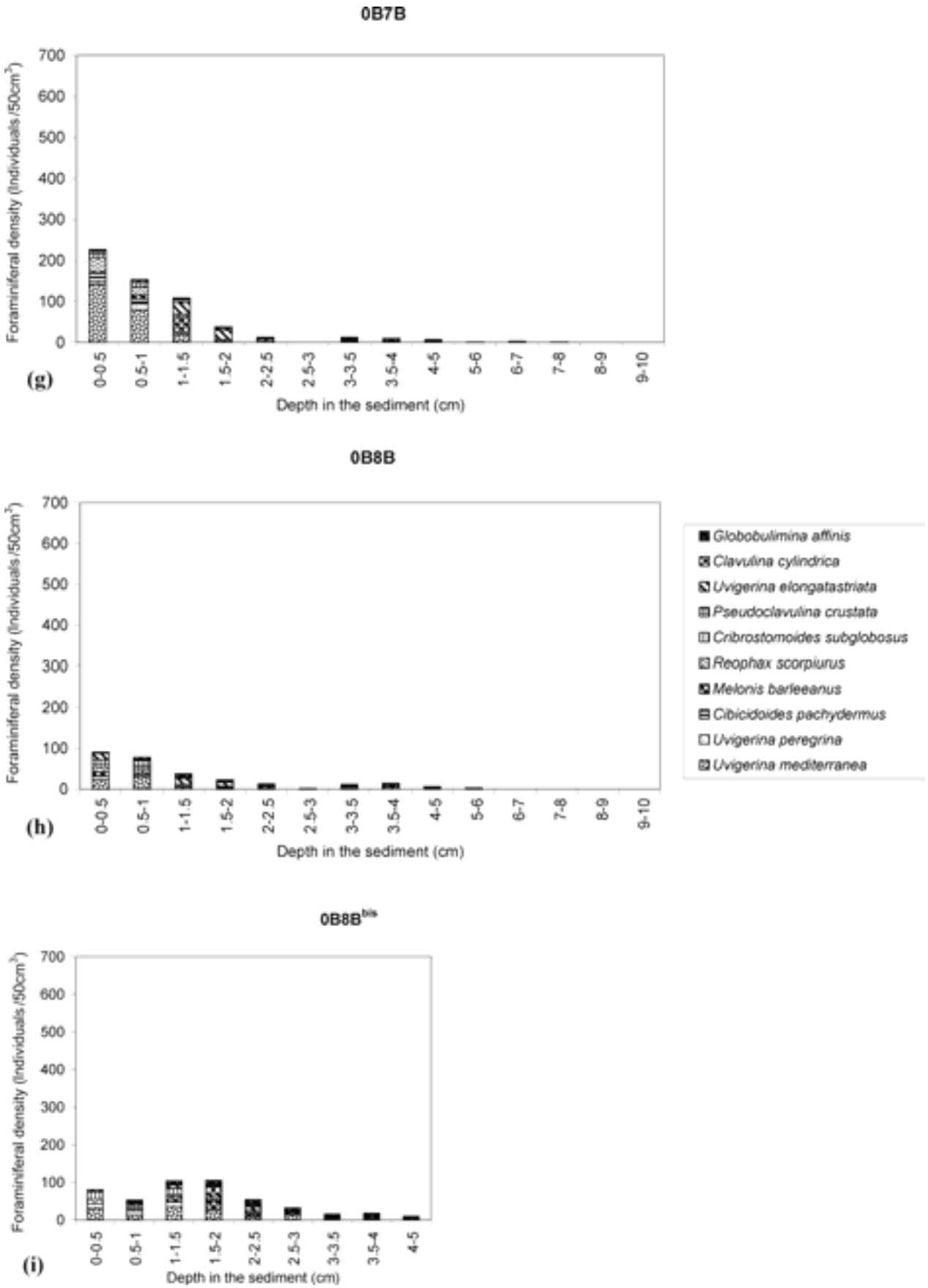

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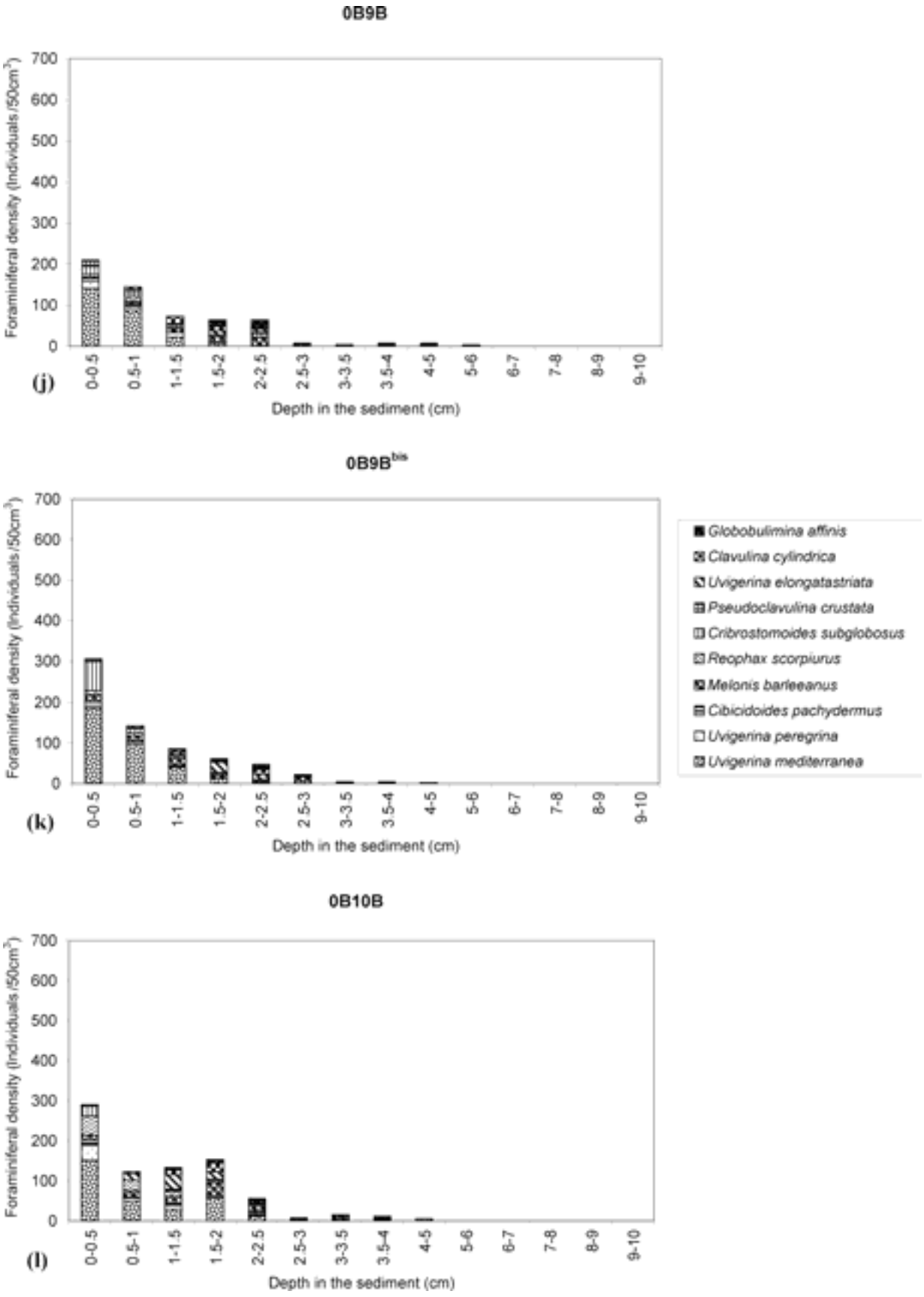
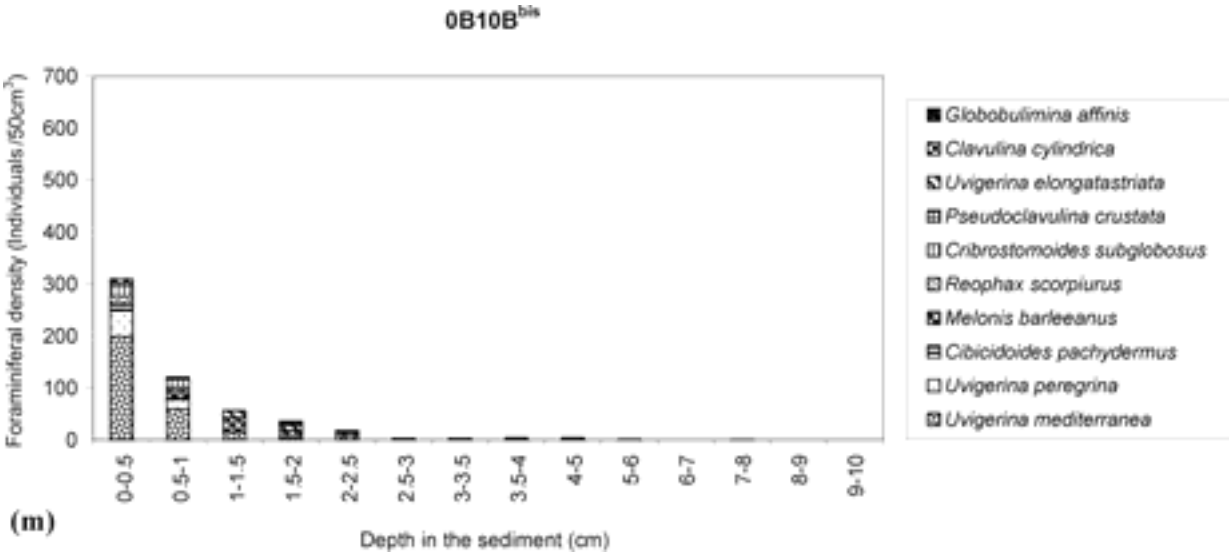


Figs. 5a-m Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for 14 available cores.



Figs. 5a-m Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for 14 available cores.

Taxa	Cores, ALD_{10}												Average weighted ALD_{10}	Microhabitat
	C01B	C02B	C03B	C04B	C05B	C06B	C07B	C08B	C08B^{rep}	C09B	C09B^{rep}	C10B	C10B^{rep}	
Amphicoryna scalaris											0.7 (6)	0.3 (9)		0.49	SI
Bolivina alata	1.1 (6)	0.9 (7)			1.5 (8)	2.7 (7)	1.7 (20)		2.0 (8)			1.6 (18)	2.0 (8)	1.68	II
Bolivinita quadrilatera	0.2 (7)											0.4 (6)		0.31	SI
Bulimina marginata	1.2 (19)	2.7 (18)	2.8 (9)			1.8 (5)			0.9 (9)	0.4 (9)		1.0 (8)	0.2 (5)	1.54	II
Chrostomella oolina									3.2 (19)	4.2 (12)		2.4 (31)	3.5 (18)	3.09	DI
Obscitos wuellerstorfi		0.6 (6)												0.63	SI
Obscitoidea pachyderminus	0.6 (63)	0.5 (52)	0.5 (11)	0.1 (8)	0.2 (15)	1.5 (14)	0.4 (23)			0.5 (11)	0.4 (11)	0.6 (16)	0.3 (10)	0.54	SI
Cibicidoides ungerianus				0.1 (5)			0.3 (8)				0.8 (5)	1.2 (7)	0.8 (8)	0.63	SI
Globobulimina affinis	2.4 (80)	0.9 (19)	2.5 (30)	2.3 (17)	3.1 (13)	4.1 (55)	3.8 (38)	2.9 (31)	2.7 (71)	3.1 (51)	2.5 (24)	2.5 (41)	3.2 (26)	2.84	DI
Gyroidina altiformis	0.2 (9)													0.24	SI
Hyalinea balthica	0.8 (12)	0.8 (7)					0.3 (14)			0.4 (10)	0.3 (6)	0.6 (7)		0.54	SI
Lenticulina peregrina	0.2 (7)													0.23	SI
Melonis barleeanus	0.8 (125)	1.1 (89)	1.1 (40)	0.9 (43)	1.4 (34)	2.3 (103)	1.2 (45)	0.5 (10)	1.7 (35)	1.7 (41)	1.2 (52)	1.3 (61)	1.2 (41)	1.30	II
Nuttallides umbonifera	0.3 (5)									0.8 (5)				0.56	SI
Pullenia quinqueloba		1.1 (9)			1.3 (6)									1.16	II
Siphogenerina columellaris	0.6 (30)	0.5 (17)		0.2 (11)	0.6 (6)	1.3 (9)	0.4 (12)			0.6 (8)	0.5 (14)	0.6 (22)	0.4 (14)	0.60	SI
Uvigerina elongatastriata	1.3 (61)	1.4 (26)	1.8 (11)	0.7 (20)	1.2 (25)	2.5 (21)	1.5 (42)	1.1 (32)	1.7 (22)	1.7 (15)	1.7 (37)	1.4 (58)	1.8 (25)	1.47	II
Uvigerina mediterranea	0.6 (433)	0.7 (287)	1.4 (88)	0.4 (50)	0.5 (52)	1.6 (225)	0.5 (177)	1.2 (52)	1.3 (90)	0.6 (199)	0.6 (251)	0.8 (216)	0.4 (208)	0.77	SI
Uvigerina peregrina	0.8 (289)	0.6 (44)	1.2 (36)	0.5 (31)	0.6 (26)	1.4 (45)	0.7 (19)	1.1 (13)	1.3 (33)	0.7 (27)	0.8 (11)	0.6 (48)	0.4 (50)	0.78	SI
Corruspira involvens		0.8 (5)		0.4 (8)										0.59	SI
Agglut. sp.A											0.3 (8)			0.28	SI
Adercotryma glomerata							0.1 (7)			1.0 (9)				0.63	SI
Ammosigerina sp.	0.4 (5)													0.38	SI
Ammosolenia sp.									1.0 (17)				0.3 (10)	0.71	SI
Cribrostomoides subglobosus	1.0 (10)	1.0 (17)	0.9 (31)	0.9 (14)	1.2 (6)	2.6 (32)	1.3 (13)	0.9 (6)	1.7 (35)	1.4 (27)	2 (16)	1.6 (35)	0.2 (5)	1.46	II
Cribrostomoides subglobosus	0.5 (20)	0.5 (30)	1.1 (43)	0.5 (13)	0.9 (41)	2.0 (26)	0.2 (7)	1.2 (14)	1.2 (41)	0.9 (26)	0.4 (61)	0.5 (23)	0.4 (27)	0.82	SI
Cyclammina sp.1													0.3 (5)	0.28	SI
Cyclammina sp.2	0.2 (5)	1.0 (6)			2.5 (8)		0.3 (5)			0.4 (6)				1.01	II
Cyclammina sp.3	0.3 (7)	0.4 (14)										0.3 (7)		0.37	SI
Eggerella scabra	0.6 (6)	0.6 (15)	1.1 (6)	0.5 (12)	1.0 (11)	0.6 (6)				0.5 (6)	0.5 (10)	0.9 (11)	0.3 (7)	0.71	SI
Hapalophragmoides bradyi								0.9 (5)		0.9 (6)		0.6 (6)		0.82	SI
Recphax sp.1												0.2 (7)		0.16	SI
Recphax fusiformis	0.7 (7)									0.7 (6)				0.71	SI
Recphax gullmus	0.3 (19)	0.9 (14)										0.3 (14)		0.50	SI
Recphax scorpiurus	0.3 (25)		1.1 (14)	0.2 (9)	0.4 (25)	1.2 (20)	0.5 (41)	1.0 (22)	0.8 (18)	0.6 (14)	0.9 (21)	1 (24)	0.5 (15)	0.75	SI
Rhabdammina cornuta												0.4 (9)		0.39	SI
Saccammina spp.							0.6 (8)		1.9 (5)	0.8 (21)		0.9 (19)		0.91	SI
Technitella melo												0.6 (8)		0.59	SI
Bigenerina nodosaria	0.4 (9)					0.9 (5)	0.5 (8)				0.5 (8)	0.3 (27)	0.4 (8)	0.43	SI
Pseudoclavulina crustata	0.9 (10)						0.5 (14)	0.7 (22)		0.9 (24)	0.5 (5)		0.3 (5)	0.71	SI
Spiroplectinata annectens	0.5 (9)													0.51	SI
Oxygen penetration depth (cm)	1.7	2.4	1.9	1.8	2.1	2.0	2.6	2.3	2.0	2.1	2.1	2.3	2.3		

Table 2 Average living depth (ALD_{10}) of foraminiferal species and (in parentheses) the number of individuals on which the calculation is based. Only occurrences of ≥ 5 individuals are shown. The grey boxes represent dominant taxa with a relative proportion ≥ 5% at least one of the stations. Microhabitat patterns are summarised as shallow infaunal (SI), intermediate infaunal (II) or deep infaunal taxa (DI).

2) 63-150 µm fraction

The densities of the main taxa in the topmost 0.5 cm of the fifteen cores are shown in Fig. 6 and Appendix C.

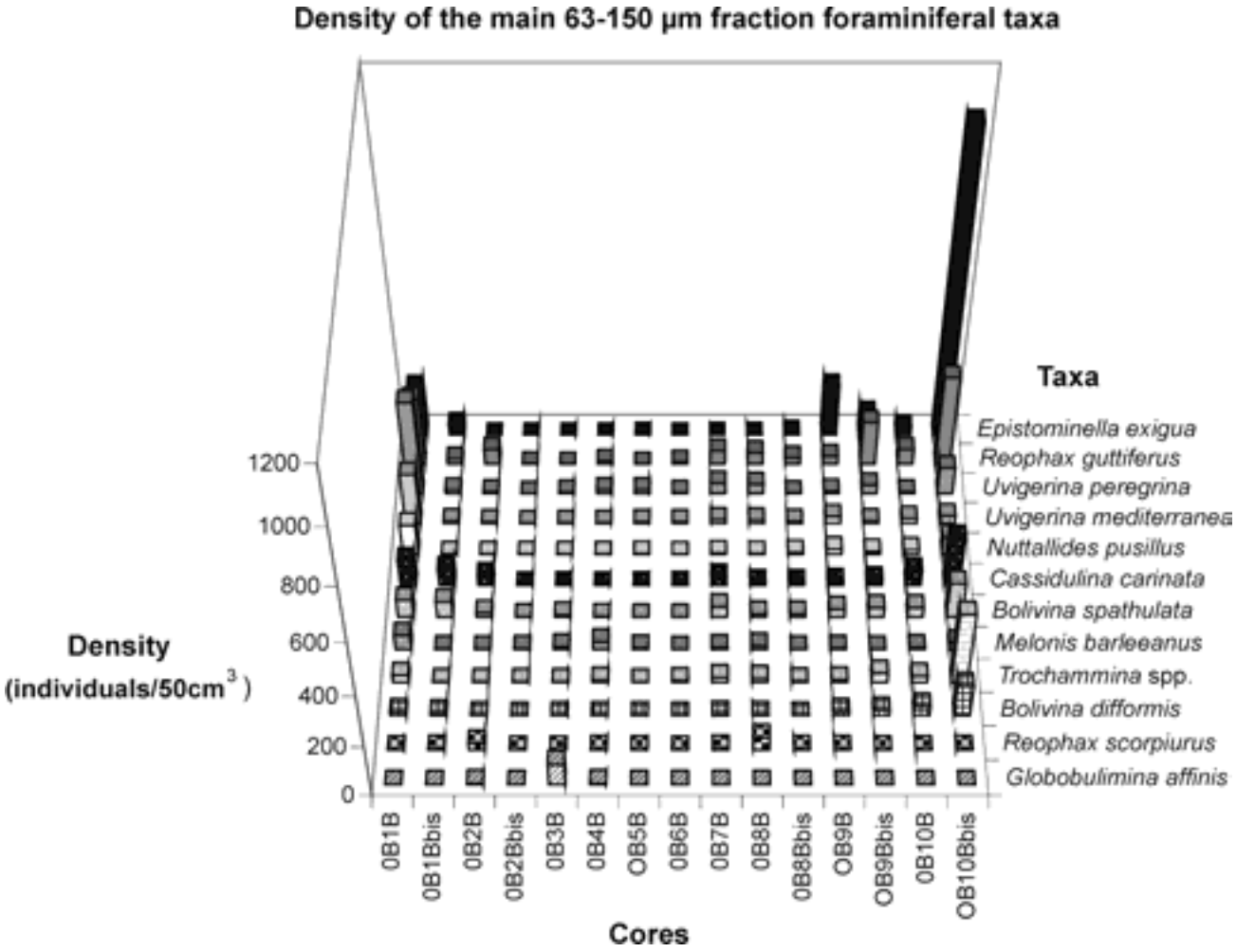


Fig. 6 Foraminiferal density of the main foraminiferal taxa in the 63-150 µm fraction for the 15 cores. Densities are standardised to a 50 cm^3 sediment volume.

Because of the extreme variability of foraminiferal density, which may be partially due to a varying sampling volume (see Methods section), the faunal variability may be better represented by percentage data, which are presented in Appendix C. The faunas in this small size fraction are much more variable than those in the >150µm fraction. *Reophax guttiferus* is a frequent taxon in many cores; it accounts for about 27% in June 2000 (OB9B^{bis}), and for 10-15% in October 1997 (OB1B), January 1998 (OB2B), December 1998 (OB6B), January 1999

(OB7B), April 1999 (OB8B and OB8B^{bis}) (OB9B) and April 2000 (OB10B and OB10B^{bis}). *Epistominella exigua* occurs with spectacular peak abundances in April 2000 (OB10Bbis – 35.6%), June 1999 (OB9B -- 32.5%; OB9B^{bis} -- 14%) and October 1997 (9% in both OB1B and OB1B^{bis}). *U. peregrina* occurs with about 15% abundance in October 1997 and October 1998 (OB1B and OB5B), whereas *C. carinata* exhibits values from 10-15% in October 1997 (OB1B^{bis}), April 2000 (OB10B), January 1998 (OB2B) and December 1998 (OB6B). *Globobulimina affinis* shows a spectacular peak occurrence in June 1998 (OB3B -- 45%), whereas *Melonis barleeanus* is frequent in July 1998 (OB4B -- 15%). Many other species, such as *Bolivina spathulata, Gyroidina umbonata, Nonionella* spp.*, Siphogenerina columellaris, Uvigerina mediterranea, Reophax scorpiurus,* and *Trochammina* spp. show shifts from near-absence to values of about 10%, highlighting the extreme variability of the 63-150 μm fraction.

Discussion and Conclusions

Organic matter deposits

The presence of organic aggregates at the sediment water-interface appears to follow phytoplankton bloom events taking place several weeks before the cruises (Table 1, Fig. 2). This is especially the case for OB10 (6 weeks after the first 2000 spring bloom) OB9 (6 weeks after the second 1999 spring bloom) and 0B1 (4 weeks after a 1997 autumn chlorophyll-a maximum). We suppose that the organic aggregates represent the remains of phytoplankton deposits following these surface water bloom periods.

Spatial heterogeneity of the benthic ecosystem at station B

Most of studies dealing with temporal variability of benthic foraminiferal faunas taxa (e.g. Gooday, 1988; Gooday and Lambshead, 1989; Thiel et al., 1990; Gooday and Turley, 1990; Kitazato and Ohga, 1995; Silva et al., 1996; Kitazato et al., 2000) avoid the fundamental question what part of the observed differences is due to spatial variability (patchiness) and what part is really due to temporal variability, resulting from the intermittence of export production. Barmawidjaja et al. (1992) moderate their conclusions about seasonal changes of foraminiferal faunas from the Northern Adriatic Sea by underlining the possible importance of a patchiness effect and insist on the necessity to study replicate

cores. Thiel et al. (1990) suggest that current activity and microtopography may induce a patchy distribution of phytodetritus at the sea floor. Organic deposits create a mosaic of ephemeral organic rich patches on the ocean floor, which maintain sea floor heterogeneity, and contribute to the high diversity of deep sea benthic communities (Grassle and Morse-Porteous, 1987; Grassle, 1989; Snelgrove et al., 1994; 1996). Hohenegger et al. (1993) demonstrate that foraminiferal faunas have patchy distributions which are interpreted as being food controlled. In a study using duplicate cores, in recently enriched sediments, Silva et al. (1996) show that spatial faunal variability (patchiness) exists but does not obscure studies on the temporal and seasonal changes of the foraminiferal faunas, which are much more prominent.

In order to distinguish between spatial and temporal variability in our cores we performed a non-standardised principal component analysis (Davis, 1986) on the basis of the percentage data of all taxa which appear with at least 5% in one of the cores. For the >150µm fraction, this multivariate analysis is based on 15 samples (10 samples and 5 duplicates) and 10 taxa, and yields two significant axes, explaining 68% of the total variability. The eigenvalues for these two axes and the species loadings on the axes are given in Table 3a. The positive side of axis 1 is highly dominated by *Uvigerina mediterranea* (0.90), whereas *Globobulimina affinis, Reophax scorpiurus, Uvigerina elongatastriata, Cribrostomoides subglobosus,* and *Clavulina cylindrica* all load negatively on the first axis. The positive side of the second axis is strongly dominated by *Uvigerina peregrina* (0.92), while *U. mediterranea, G. affinis* and *C. subglobosus* load negatively. Fig. 7 shows the position of the 15 cores in the axial plot. The first axis allows separation of all rather poor samples (total density less than 500 individuals, PCA1 ≤16.0) from all relatively rich samples (total density > 500 specimens, PCA1 >18.0), suggesting that the first axis is related to ecosystem enrichment due to phytodetritus deposits, a phenomenon which is always accompanied by an increase of the percentage of *U. mediterranea*. The second axis tends to separate cores OB1B and OB1B^{bis}, which are both strongly enriched in *U. peregrina*, from all other cores with high scores on axis 1. This suggests that there are two possible responses to ecosystem enrichment; in most cases *U. mediterranea* shows the clearest response, but in October 1997 the large increase of *U. peregrina* is the most obvious phenomenon accompanying the faunal density increase. These two possible responses, translated by a different position on axis 2, could be explained by a different quality of the organic matter between the spring and autumn blooms. All five pairs of duplicate cores are fairly close to each other. Although individual cores of these duplicate couples may have a higher similarity to other cores (e.g. core OB9B is much

closer to OB7B than to OB9B^{bis}), showing the presence of significant spatial variability, the distances between extreme samples are much bigger than the maximum distance between duplicate couples. This suggests that for the >150µm fraction, temporal variability is more important than spatial variability.

The 63-150µm data (for the topmost 0.5 cm of the sediment) were subjected to a similar analysis, this time with 22 taxa. Because of extreme variability of the data set, with many different taxa having occasional peak occurrences, this second principal component analyses yields no less than five significant axes, explaining 86.8% of the total variability (Table 3b). In order to evaluate differences between samples, we calculated distances between all samples in the 5 dimensional space defined by the significant axes (Table 3c). This table confirms that differences between duplicate samples (11-30 units) are larger in the 63-150 than in the >150 µm fraction (2-12 units), but that maximum temporal differences (59 units) are still about two times higher than maximum spatial differences.

These multidimensional analyses suggest that small-scale patchiness exists, and can not be completely ruled out, as a parameter explaining differences between the cores taken at different times. In the >150µm fraction, spatial variability seems to be smaller than in the 63-150µm fraction, and, consequently, temporal variation should be more prominent in this larger size fraction. An important question is why duplicate samples are more different in the 63-150µm than in the >150µm fraction. It is very probable that the high degree of patchiness is related to micro-relief and current activity, which cause a patchy distribution of organic matter on the ocean floor. In case of abundant input of organic detritus, phytodetritus aggregates will concentrate in depressions on the sea floor. This may explain important small-scale spatial variability in terms of concentration of phytodetrital compounds between duplicate samples (see for example the difference between OB1B and OB1B^{bis}). Small opportunistic taxa, such as *Epistominella exigua*, may have a faster response than larger (>150 µm) taxa, and will be first in colonising freshly deposited phytoplankton floccules (Gooday and Turley, 1990). This can be seen in October 1997 (OB1B and OB1B^{bis}), in June 1999 (OB9B and OB9B^{bis}) and in April 2000 (OB10B^{bis}), when organic aggregates are observed in the sieve residues, and when *E. exigua* reaches high densities (Table 1, Fig. 6). This taxon could feed on fresh microalgae and reproduce rapidly after phytodetritus deposits following the important surface water bloom periods preceding our sampling (Fig. 2).

(a)

>150 µm fraction	PCA1	PCA2
Eigenvalues column	67.8	37.3
Percent of trace	44.3	24.4
Cumulative percent of trace	44.3	68.7
Taxa		
Cibicidoides pachydermus	0.11	0.12
Globobulimina affinis	-0.28	-0.16
Melonis barleeanus	0.03	0.09
Uvigerina elongatastriata	-0.16	-0.11
Uvigerina mediterranea	0.90	-0.19
Uvigerina peregrina	0.04	0.92
Clavulina cylindrica	-0.14	-0.12
Cribrostomoides subglobosus	-0.16	-0.15
Reophax scorpiurus	-0.17	-0.07
Pseudoclavulina crustata	-0.09	-0.06

(b)

63-150 µm fraction	PCA1	PCA2	PCA3	PCA4	PCA5
Eigenvalues column	172.4	123.9	51.3	36.4	23.6
Percent of trace	36.7	26.4	10.9	7.8	5.0
Cumulative percent of trace	36.7	63.1	74.1	81.8	86.8
Taxa					
Bolivina sp.1	0.00	-0.04	0.09	0.06	0.05
Bolivina spathulata	-0.04	0.04	0.16	0.40	0.10
Bolivina difformis	-0.06	0.06	0.04	0.05	-0.06
Bulimina marginata	-0.03	-0.05	0.08	-0.06	-0.02
Cassidulina carinata	-0.06	-0.12	0.21	0.38	0.17
Ceratobulimina sp.	0.03	0.00	-0.03	0.02	0.04
Epistominella exigua	-0.57	0.76	-0.10	-0.08	-0.04
Globobulimina affinis	0.75	0.53	0.29	-0.18	0.03
Gyroidina umbonata	-0.02	-0.04	-0.12	-0.20	0.27
Melonis barleeanus	0.14	-0.05	-0.38	0.04	-0.50
Nonionella spp.	0.09	0.00	-0.13	0.10	-0.22
Nuttalides pusillus	-0.04	0.03	-0.06	-0.07	0.05
Pullenia spp.	-0.02	0.02	-0.13	-0.05	0.04
Siphogenerina columellaris	0.08	-0.09	-0.09	0.05	-0.52
Uvigerina mediterranea	-0.01	-0.12	-0.10	-0.18	0.11
Uvigerina peregrina	0.02	-0.17	-0.32	-0.55	0.25
Haplophragmoides sp.	0.00	-0.03	0.09	0.09	0.17
Psammosphaera fusca	-0.01	-0.07	0.01	0.18	-0.06
Reophax guttiferus	-0.24	-0.19	0.68	-0.42	-0.28
Reophax scorpiurus	0.01	-0.11	0.04	0.02	0.17
Reophax sp.1	-0.02	-0.09	0.09	0.07	0.10
Trochammina spp.	-0.09	-0.01	0.13	-0.17	-0.31

(c)

63-150 µm	OB1B^{bis}	OB2B	OB2B^{bis}	OB3B	OB4B	OB5B	OB6B	OB7B	OB8B	OB8B^{bis}	OB9B	OB9B^{bis}	OB10B	OB10B^{bis}
OB1B	**22.4**	20.2	19.2	50.1	21.2	13.6	14.2	14.1	10.9	15.2	28.0	19.8	17.4	31.1
OB1B^{bis}		16.1	15.1	49.4	27.2	24.6	24.5	16.0	18.6	11.1	26.3	26.7	11.9	31.1
OB2B			**17.6**	49.2	25.9	26.4	12.4	7.9	11.8	8.0	36.0	21.1	10.7	38.3
OB2B^{bis}				47.1	12.7	20.6	20.9	12.1	14.7	13.7	31.6	27.8	11.0	34.9
OB3B					46.6	48.8	52.1	48.2	48.1	48.4	56.2	55.1	48.5	59.3
OB4B						21.1	23.7	16.8	19.1	23.1	38.1	32.5	20.8	40.5
OB5B							23.3	20.1	15.7	22.2	33.7	32.9	24.4	39.3
OB6B								9.8	9.3	13.8	37.5	18.2	16.1	39.0
OB7B									5.7	6.8	33.3	20.7	8.5	35.9
OB8B										**11.4**	32.7	22.3	23.5	37.8
OB8B^{bis}											28.4	18.2	5.5	31.2
OB9B												**27.6**	27.9	8.9
OB9B^{bis}													18.6	25.7
OB10B														**29.9**

Tables 3a-c Results of non standardised principal component analyses based on the percentages of the main foraminiferal taxa in the >150 and 63-150 µm fraction (percentage ≥ 5%). Table 3a. Eigenvalues and species loadings of the two significant axes for the >150 µm fraction. Table 3b. Same, for the 63-150 µm fraction. Table 3c. The normative distance between cores in the 5-dimensional space (normative distance between the five pairs of replicate cores are given in bold letters).

Furthermore, different small opportunistic taxa may colonise different organic-rich patches, increasing local patchiness. Still another possible explanation for the much higher variability of the 63-150 µm fraction could be that reproductive response to phytodetritus inputs of larger taxa would first be noticed by the presence of juveniles in the small size fraction. This is clearly the case in October 1997, when juvenile *U. peregrina* peak in the 63-150 µm fraction, and in June 1998, when *G. affinis* exhibits a similar reproductive event. Apparently, the response of the >150µm fraction is delayed, and increased numbers of the larger opportunistic taxa are found only after the impact of organic input has already been homogenised for a large surface area. Except for cores OB10B and OB10B^{bis}, which were collected in two different multi-tube corer deployments, spatial patchiness recorded for each other couple of duplicate samples suggests strong spatial variability of foraminiferal faunas on a scale of less than a metre. Faunal differences between cores OB10B and OB10B^{bis} reflect a larger scale (several hundred metres) foraminiferal variability.

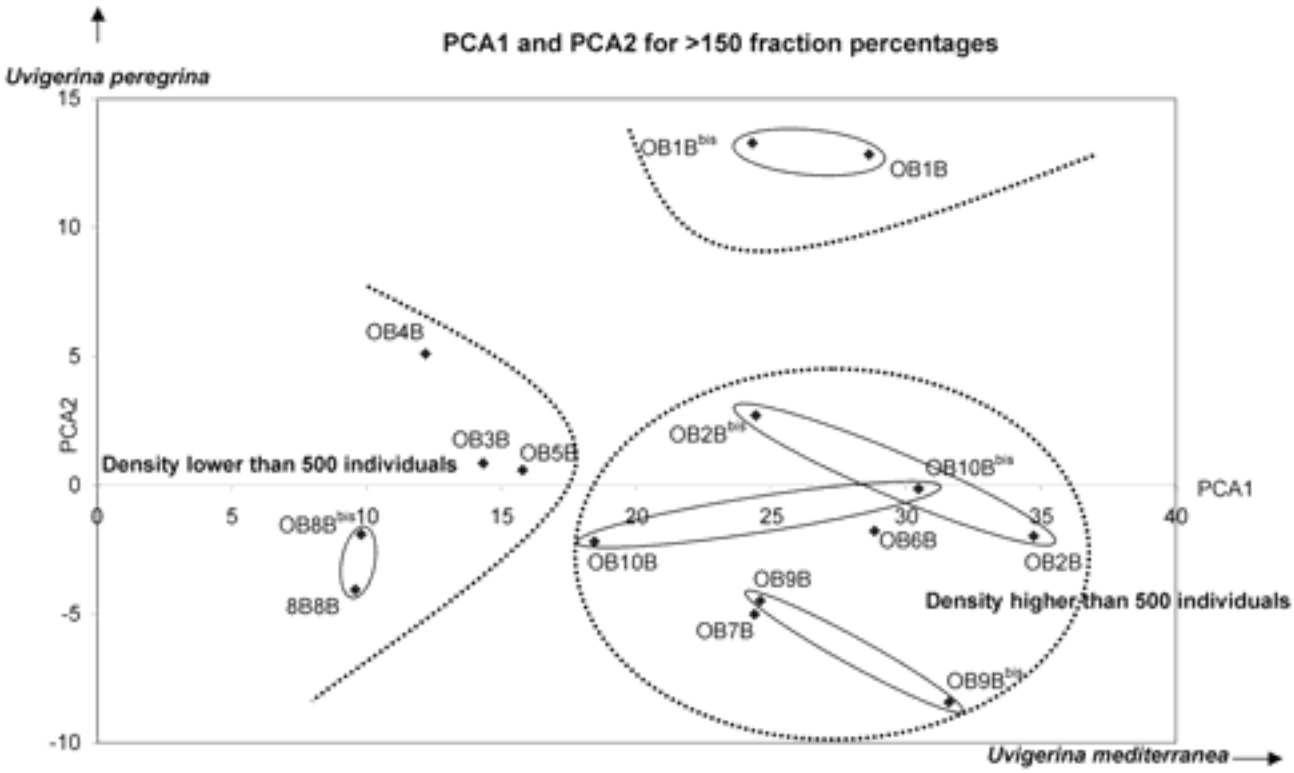


Fig. 7 Plot of the 15 cores in the 2-D space defined by the two main axes of the non standardised principal component analysis (PCA1, PCA2), and three distinct faunal assemblages (indicated by the dotted lines).

Our results suggest that at least part of the foraminiferal patchiness is due to a spatially heterogeneous distribution of organic matter aggregates at the sediment-water interface. Just as heterotrophic bacterial consortia, which can respond quickly to patchy organic matter deposits (Turley et al., 1988; Thiel et al., 1990), some foraminiferal taxa can also take rapid advantage of freshly deposited organic patches. According to Gooday and Turley (1990), the patchy distribution of the organic material deposited after bloom events play a major role in structuring deep-sea benthic ecosystems.

Temporal variability of bottom and pore water chemical characteristics

Our data show a relative constancy in the chemistry of the bottom and interstitial waters. Bottom water oxygen concentrations are almost invariable throughout the investigated years; values range from 205 to 221 µmol/l. The vertical profiles of dissolved oxygen and nitrate in the uppermost sediment are rather similar for the 1997-2000 period (Fig. 3a-b). Deeper in the sediment bacterial consortia are able to reduce nitrate in anoxic environments in order to decompose the available organic compounds (Froelich et al., 1979; Fenchel and Finlay, 1995). The ammonia that is created during the mineralization of organic nitrogen migrates upward to oxygenated layers, where it is transformed back into nitrate and nitrite by nitrifying bacterial consortia (Anschutz et al., 1999). Nitrate and nitrite diffuse downward to the anoxic layer, thus creating a gradient that overlies the oxygen zero boundary. In our cores, the downward nitrate-nitrite gradients always occur in the 0.25 to 2.5 cm depth range (Fig. 3b). The depth and amplitude variability is rather limited. No clear sulphate reduction zone was detected at station B; i.e. we detected no decrease with depth of sulphate and no significant increase of sulphide (Anschutz, 2002, pers. com.). Apparently, in this deep open-slope environment, the exported organic matter fluxes are not high enough to sustain a sharp sulphate gradient in the sampled cores. However, sulphate reduction may be a discrete phenomenon in the anoxic part of the core.

It seems that the seasonal variability of the exported organic matter flux is not high enough to induce significant fluctuations of the early diagenetic processes in the upper sediment. Apparently, we are far away from the variable conditions prevailing in the lower part of oxygen minimum zone areas (Jannink et al., 1998) or in some oligotrophic basins where sudden organic matter deposits may severely modify redox patterns at and below the sediment water interface (Kitazato and Ohga, 1995; Kitazato et al., 2000; Duijnstee et al., 2001). At our station B, the phytodetritus deposits following main bloom periods (October

1997, June 1999 and April 2000; Table 1) have at most a minor impact on the redox conditions within the sediment and at the sediment-water interface. This is probably because of the overall eutrophic conditions reigning at our site. Fresh organic matter deposits, which are strongly concentrated at the sediment surface, are preferentially used as food by bacteria (Turley et al., 1988; Thiel et al., 1990; Donavaro et al., 2000), but also by meiofaunal foraminifera, which as a whole appear to be an opportunistic group of organisms. This explains why most foraminiferal taxa are concentrated in the first cm and why the highest foraminiferal densities are most times recorded in the first half cm. The restriction of ^{234}Th (half life time 24.1 days) activity to the uppermost 1.5 cm, and the vertical aspect of the ^{210}Pb profile in the upper cm, strongly suggest that macrofaunal bioturbation is largely limited to the topmost part of the sediment (Jouanneau, 2001, pers. comm.). This rather shallow bioturbation zone will cause an absence of labile components deeper in the sediment. There, a constant, much slower flux of more refractory organic matter sustains a rather invariable succession of redox zones, where stable dysaerobic and anaerobic bacterial pools develop, which may form a food source for some highly specialised deeper dwelling taxa. Thus, the microhabitat of many foraminiferal taxa appears to be controlled largely by their trophic requirements (Jorissen et al., 1995).

Temporal variability of foraminiferal faunas at station B

E. exigua shows the most important frequency variations in our successive samples. Whereas this taxon is almost absent for most of the winter and summer months, it exhibits strong density increases after the spring and autumn phytoplankton bloom periods; density peaks are recorded in October 1997, in June 1999 and April 2000 (Fig. 6). These strong absolute and relative density variations show a highly opportunistic behaviour, and suggest that this species feeds on fresh organic phytodetritus. These results confirm similar observations in other deep-sea environments (Gooday, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Gooday, 1993; Loubere, 1998; Jannink et al., 1998). Boltovskoy and Lena (1969) show that in eutrophic shallow water environments, *Epistominella* has a very short reproductive cycle (about one month), and reproduces throughout the year. We think that the intermittent occurrences of *E. exigua* at our station B are a direct response to phytodetritus deposits of a rather ephemeral nature. The species responds to the freshly deposited organic matter by a reproductive event, which is especially clear during the spring

bloom of the year 2000 (see OB10B^{bis} data). Such a reproductive response has also been shown after food addition in culture experiments (Heinz et al., 2001; 2002).

Other small taxa, which are largely restricted to the 63-150 µm fraction, such as *R. guttiferus*, *N. pusillus, C. carinata,* and *B. spathulata*, show a similar density variability, albeit to a lesser degree. The peak periods are essentially the same as those for *E. exigua*, but the weaker response of these taxa suggests a slightly less opportunistic behaviour (Fig. 6).

Trochammina spp. and *Bolivina difformis,* which are also limited to the 63-150 µm fraction, show only a strong density increase after the spring bloom of 2000 (Fig. 6). This differential response suggests that not only the quantity, but also the quality, of the organic matter input could be a controlling factor. The quality of the organic matter may vary in function of the different phytoplankton groups responsible for the surface water bloom conditions.

In the >150 µm fraction, the shallow infaunal species *U. mediterranea* and *U. peregrina* show by far the largest frequency variations and can thus be considered as most opportunistic (Figs. 5a-m). *U. peregrina* shows a major peak (in both size fractions) after the putative 1997 autumn bloom. Apparently it is the most opportunistic species occurring in the >150 µm fraction. *U. mediterranea* is responsible for most of the density variations of the total foraminiferal fauna in this larger size fraction, and shows a relative, as well as absolute, frequency increase in all eutrophic periods. The different behaviour of the two *Uvigerina* species suggests slightly different trophic requirements, where *U. peregrina* and other taxa (e.g. *N. pusillus*), which exclusively show a density increase in the October 1997 sample, may prefer a diet based on microflagellates remains, which are especially abundant in the autumn bloom (Sellmer et al., 1998). Species that peak only after the spring bloom, such as *Trochammina* spp. and *B. difformis,* could prefer to feed on diatoms, coccolithophores, or other microalgae typical of spring blooms (Tréguer et al., 1979; Bender et al., 1992; Fernandez et al., 1995). Finally, *U. mediterranea*, and other species occurring both in autumn and spring, may be less critical with respect to food quality.

Uvigerina mediterranea and *Uvigerina peregrina* have been described in a wide range of mesotrophic to eutrophic settings (e.g. Lutze, 1980; Lutze and Coulbourne, 1984; Corliss, 1985; Corliss et Emerson, 1990; Corliss, 1991; Jannink et al., 1998; Schmiedl et al., 2000; Morigi et al., 2001). According to De Rijk et al. (2000), they would need an exported labile organic flux of at least 2.5g C/m²/year. The observations made by Fontanier et al. (2002) at OB1B, where *U. peregrina* is found slightly deeper than *U. mediterranea*, suggesting a higher tolerance to slightly more degraded organic matter, are not confirmed during the other

sampling periods, where the microhabitat of both species is very similar. However, in all other samples, *U. peregrina* is much poorer than in OB1B, and the present data may not be representative for its optimum conditions.

The infaunal niches deeper in the sediment are permanently occupied by *M. barleeanus, U. elongatastriata* and, still deeper, *G. affinis*. A deeper infauna dominated by *M. barleeanus* and *G. affini*s has been described in numerous mesotrophic-eutrophic oceanic ecosystems (e.g. Corliss, 1985; Harloff and Mackensen, 1997; Jorissen et al., 1995; 1998; Schmiedl et al., 2000). Jorissen (1999a) and Fontanier et al. (2002) observe that *M. barleeanus* occurs systematically in the lower part of the oxic zone whereas *G. affinis* is consequently found in the upper part of the totally anoxic zone. Our present results fully confirm this pattern, suggesting that deeper infaunal species may be dependent on anaerobic bacterial stocks degrading more or less refractory organic matter. They could either directly prey on the bacterial stocks (Lee, 1979; Kitazato, 1994), or feed on the organic matter breakdown products (Caralp, 1989; Alve, 1990; Bernhard, 1992; Jorissen, 1999a). Although we do not think that *G. affinis* and *M. barleeanus* feed directly on fresh organic matter (concentrated in the upper first cm of the sediment), they do show a significant frequency increase (in the >150 µm fraction) in some of the most productive months (October 1997, December 1998; Figs. 5a-m). A very similar increase of the population density was observed by Heinz et al. (2001) in a culture experiment. This suggests that increased surficial biological activity is rapidly transmitted towards deeper sediment layers, perhaps by an increase of bioturbation and accompanying bacterial activity.

In a previous study, Barmawidjaja et al. (1992) suggested that some infaunal taxa (e.g. *Eggerella scabra, Morulaeplecta bullosa, Textularia agglutinans*) could reproduce close to the sediment-water interface with a time lag with respect to more opportunistic epifaunal taxa. More recently, Kitazato et al. (2000) speculated that deep infaunal taxa (*Chilostomella ovoidea* and *Globobulimina affinis*) are able to profit from fresh organic matter supplies after spring blooms, by moving to the sediment-water interface in order to feed on fresh organic matter and to reproduce at the end of the spring bloom. At our site, *G. affinis* shows a clear reproductive event in June 1998, when an abundant fauna consisting exclusively of juvenile specimens is found in the first half cm (Fig. 6). We think that this reproductive event is a delayed response to the 1998 spring bloom, which took place only when all other species have fallen back to background level (Figs. 5a-m and Fig. 6). This taxon does obviously not reproduce at the same time as the more opportunistic shallow infaunal taxa (e.g. *E. exigua*), which are more adapted to profiting quickly from labile phytodetritus input. The *G. affinis*

reproductive event could be triggered by increased bacterial activity due to the delayed input (by bioturbation) of large amounts of less labile material in dysoxic microenvironments, once the more labile components have been consumed by more opportunistic taxa. Such a reproductive behaviour would also characterize intermediate infaunal taxa. An increase in the density of *M. barleeanus* in July 1998 (in both size fractions), accompanied by a shoaling of its microhabitat, could represent a similar reproductive event at one of the least productive moment of our 3-year study. In the eutrophic context of the Bay of Biscay, this migrational and reproductive behaviour is apparently independent of changes of redox gradients but is triggered by changes in the trophic level (presence of bacterial pools; quantity and quality of organic remains).

Stepwise benthic ecosystem response to phytodetritus input

The results of our study show that it is not easy to detect a straightforward relationship between phytoplankton bloom and benthic foraminiferal faunal characteristics. In case of the important spring phytoplankton blooms of 1999 and 2000 and the putative autumn bloom of 1997, a significant response of the foraminiferal fauna was only noticed about 6 weeks after surface water chlorophyll maxima. Figure 8 graphically represents our ideas about the time delays between the surface water phytoplankton bloom and the responses in the benthic ecosystem. A first important delay will exist between the time of maximum chlorophyll-a concentrations and phytodetritus deposits at the ocean floor. This delay is caused by the longevity of the phytoplankton assemblages, the time involved in the formation of organic aggregates, and the time for physical transport to the ocean floor. We do not have a precise idea about the first two parameters (Lampitt, 1985); transport to 550 metres depth will take about one week (McCave, 1975**;** Lampitt, 1985**;** Deuser, 1986). Many publications suggest that the first response in the benthic environment will be by heterotrophic bacteria (Fenchel and JØrgensen, 1977; Lochte et Turley, 1988; Jumars et al., 1989; Rowe, 1991; Della Groce et al., 1996; Danovaro et al, 2000a, b). Meiofaunal organisms, such as ostracods, nematode, and annelids, are thought to be secondary deposit feeders, which will have a delayed response. Larger meiofauna and macrofauna are extremely scarce at our 550 m station (Sorbe, 2001, pers. com.). The first foraminiferal response to phytodetritus supply, about 4-6 weeks after maximum surface water chlorophyll-a values, can be seen in the most opportunistic, small surface dwelling taxa like *E. exigua* and *R. guttiferus.* This delay may be shorter, but the temporal resolution of our study does not allow us to precisely determine the exact timing of

the response of the foraminiferal opportunistic taxa. However, this estimate corresponds very well with the observations of Heinz et al. (2002), who describe a clear increase of the foraminiferal density about three weeks after food addition in a laboratory experiment. Slightly less opportunistic taxa such as *B. spathulata, C. carinata, N. pusillus, U. peregrina* and *U. mediterranea* could respond somewhat later. In the first phase of benthic foraminiferal response, the degree of patchiness appears to be very high, probably due to the spatial heterogeneity of phytodetritus deposits at the sea floor. Because of the rather superficial depth of bioturbation, the transmission of benthic ecosystem enrichment towards deeper sediment layers is a slow process. This explains why a reproductive event of intermediate and deep infaunal taxa is only noticed 2-3 months after maximum chlorophyll-a values (e.g. *G. affinis* in June 1998, and *M. barleeanus* in July 1998).

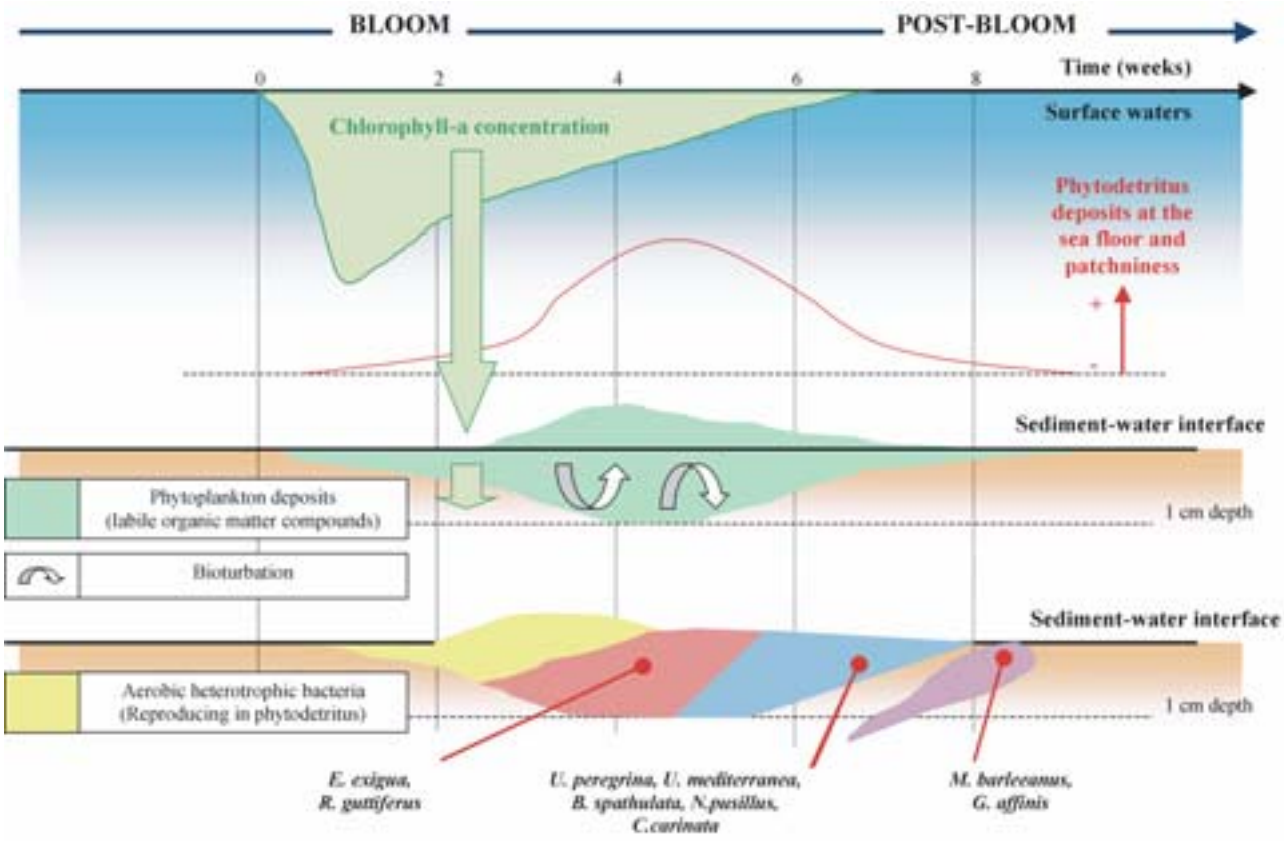


Fig. 8 Pelagic-benthic coupling and stepwise benthic ecosystem response to phytodetritus input. See text for further explanation.

Acknowledgements

We would like to thank the French national program PROOF (INSU-CNRS) for sponsoring the OXYBENT program. We have special and kind thoughts for the crews and the captains of the Côte de la Manche, our scientific ship during all campaigns. We would like to thank the Space Applications Institute/Marine Environment Unit (SAI/ME) from the Joint Research Center (European Commission) (JRC/EC) and more precisely N. Hoepffner and G. Zibordi, for the easy access to the on-line archives of chlorophyll-a concentration (SeaWIFS data). We are grateful for the SeaWIFS project (NASA/ GSFC DAAC), which provides very useful satellite images. We also thank Cecilia Laprida, Sandra Langenzaal, Gerhard Schmiedl, Pierre Carbonel and Jean-Claude Sorbe for the very interesting and helpful discussions we had about macro- and meiofaunal ecology in the Bay of Biscay and elsewhere. We have particular thanks for Ralf Schiebel and Luis Lampert for insights and pieces of advice about phytoplankton changes in the northeastern Atlantic Ocean. We are grateful to Jean-Marie Jouanneau for providing us access to his data on radioactive elements in our cores. We thank Jean-Jacques Pichon for his help in identifying the observed phytodetritus components. We highly appreciate the very constructive criticism of two anonymous reviewers.

Appendix A

Species of benthic foraminifera recognised at station B from the Bay of Biscay, with references to plates and figures in the literature on Atlantic and Mediterranean foraminifera.

Appendix B

Census data for benthic foraminifera in the >150 µm size fractions for all 15 cores.
N.B. Numbers are not standardized for sediment volume.

Appendix C

Census data for benthic foraminifera in the 63-150 µm size fractions for all 15 cores.
N.B. Numbers are not standardized for sediment volume

Appendix A

Species	References
Adercotryma glomerata (Brady), 1878	Jones (1994), pl. 34, Figs. 15-18
Ammoscalaria pseudospiralis (Williamson) 1958	Jones (1994), pl. 33, Figs. 1-4
Amphicoryna scalaris (Batsch) 1791	Jones (1994), pl. 63, Figs. 28-31
Astacolus crepidulus (Fichtel & Moll), 1798	Jones (1994), pl. 67, Fig. 20; pl. 68 Fig. 1 and 2
Bigenerina nodosaria d'Orbigny 1826	Jones (1994), pl. 44, Figs. 19-24
Bilocularella irregularis(d'Orbigny) 1839	d'Orbigny (1839), pl. 6, Fig. 20 and 21
Bolivina alata (Sequenza) 1862	Schiebel (1992) pl. 1, Fig. 2
Bolivina difformis (Williamson) 1958	Cushman (1937) pl. 15 Fig. 5 and 6
Bolivina spathulata (Williamson) 1858	Jorissen (1987) pl. 1 Fig. 5
Bolivina striatula (Cushman) 1922	Cushman (1937) pl. 18 Fig. 30 and 31
Bolivina subaenariensis Cushman 1922	Phleger et a. (1953) pl. 7 Fig. 24 anc 25
Bolivina variabilis (Williamson) 1858	Cushman (1937) pl. 16 Figs. 6-12-14
Bolivinita quadrilatera (Schwager) 1866	Jones (1994), pl. 42 Figs. 8-12
Bulimina aculeata d'Orbigny 1826	Jones (1994) pl.51 Figs. 7-9
Bulimina costata d'Orbigny 1826	Van Leeuwen (1989) pl. 8 Fig. 2 and 3
Bulimina inflata Seguenza 1862	Van Leeuwen (1989), pl. 8 Fig. 4
Cancris auriculus (Fichtel & Moll) 1942	Jones (1994), pl. 106 Fig. 4
Cassidulina carinata Silvestri, 1896	Phleger et a. (1953) pl. 9 Figs. 32-37
Cassidulina crassa d'Orbigny 1839	Jones (1994), pl. 54 Fig. 4 anc 5
Chilostomella ovoma Schwager 1878	Jones (1994), pl. 55, Figs. 12-14
Cibicides lobatulus Walker & Jacob, 1798	Jones (1994), pl. 92, Fig. 10
Cibicides wuellerstorfi (Schwager) 1866	Van Leeuwen (1989) pl. 10 Figs. 1-9
Cibicidoides pachyderma (Rzehac), 1886	Jones (1994), pl. 94, Fig. 9
Cibicidoides robertsonianus (Brady) 1881	Van Leeuwen (1989), pl. 9, Figs. 1-3
Cibicidoides ungerianus d'Orbigny, 1846	Jones (1994), pl. 94, Fig. 9
Clavulina cylindrica d'Orbigny 1952	Hofker (1932), Fig. 18 and 19
Cornuspira involvens (Reuss), 1850	Jones (1994), pl. 11 Figs. 1-3
Cribrostomoides subglobosus (Cushman), 1910	Jones (1994), pl. 34, Figs. 8-10
Cyclammina cancellata Brady 1879	Jones (1994), pl. 37, Figs. 8-16
Cystammina pauciloculata (Brady), 1879	Jones (1994), pl. 41, Fig. 1
Dentalina advena (Cushman), 1923	Jones (1994), pl. 63, Fig. 1
Dentalina arena Patterson & Pettis 1966	Jones (1994), pl. 62, Figs. 27-31
Dentalina bradyensis (Dervieux), 1894	Jones (1994), pl. 62, Fig. 19 and 20
Dentalina subemaciata Parr 1950	Jones (1994), pl. 62, Fig. 25 and 26
Eggerella scabra (Williamson), 1858	Jones (1994), pl. 47, Figs. 15-17
Elphidium advenum Cushman 1922	Phleger et a. (1953) pl. 6 Fig. 15
Epistommella exigua (Brady), 1884	Schiebel (1992) pl.5 Fig.9
Gavelinopsis translucens (Phleger & Parker) 1951	Schiebel (1992) pl. 4, Fig. 5
Glandulina ovula d'Orbigny 1846	Jones (1994), pl. 61 Figs. 17-22
Globobulimina affinis (d'Orbigny) 1839	Phleger et a. (1953) pl. 6 Fig. 32
Globocassidulina subglobosa (Brady), 1881	Jones (1994), pl. 54 Fig.17
Gyroidina altiformis Stewart & Stewart 1930	Jorissen (1987) pl. 1 Fig. 11
Gyroidina umbonata (Silvestri) 1898	Parker (1958) pl. 3 Fig. 19 and 20
Hanzawaia boueana (d'Orbigny) 1846	Jorissen (1987) pl. 3 Fig. 10
Hoeglundina elegans (d'Orbigny) 1826	Phleger et a. (1953) pl. 9 Fig. 24 and 25
Hyalinea balthica (Schroeter) 1783	Jones (1994), pl. 112 Fig. 1 and 2
Karreriella bradyi (Cushman) 1911	Jones (1994), pl. 41, Figs. 1-4
Lagena multilatera M'Culloch, 1977	Jones (1994), pl. 58, Figs 2-3, 7-8, 22-24
Lenticulina peregrina (Schwager) 1866	Cushman and McCulloch (1950) pl. 39, Fig. 5
Lenticulina vortex (Fichtel and Moll) 1798	Jones (1994) pl.69 Figs. 14-16
Marginulina obesa (Cushman) 1923	Jones (1994), pl. 65, Fig. 5 anc 6
Melonis barleeanus (Williamson) 1858	Van Leeuwen (1989) pl. 13 Fig. 1 and 2
Nonion scapham (Fichte & Moll) 1798	Jones (1994), pl. 109 Fig. 12
Nonionella turgida (Williamson) 1858	Jones (1994) pl. 109 Figs. 17-19
Nouria polymorphinoides Heron-Allen & Earlanc 1914	Loeblich and Tappan (1988) pl. 123, Fig. 11 and 12
Nuttallides pusilus (Parr) 1950	Phleger et a. (1953) pl. 9 Fig. 5 and 6
Nuttallides umboniferus (Cushman) 1933	Van Leeuwen (1989) pl. 15 Figs. 11-13 p. 16 Figs. 1-7
Ondorsalis umbonatus Reuss 1851	Van Leeuwen (1989) pl. 17 Figs. 1-13
Psammosphaera fusca Schulze 1875	Jones (1994), Pl. 18 Fig. 1-6
Pseudatavulina crustata Cushman, 1936	Jorissen (1987) pl. 1 Fig. 1
Pseudoeponides falsobeccari Rouvillois 1974	Jorissen (1987) pl. 4, Fig 3a
Pullenia bulloides (d'Orbigny) 1826	Phleger et a. (1953) pl. 10 Fig. 19
Pullenia quinqueloba (Reuss), 1851	Jones (1994), Pl. 84 Fig. 14 and 15
Pyrgo depressa (d'Orbigny), 1826	Jones (1994), Pl. 2, Figs. 12, 16 and 17
Pyrgo subsphaerica d'Orbigny, 1839	Cushman (1929), pl. 18 Fig 1 and 2
Pyrgoella sphaera (d'Orbigny), 1839	Jones (1994), pl. 2 Fig. 4
Quinqueloculina seminula (Linné) 1758	Jones (1994), pl. 5 Fig. 6
Rectuvigerina phlegeri Le Calvez 1959	Schiebel (1992) pl 3 Fig. 10a-d
Reophax ampullacea Brady 1881	Jones (1994), pl. 30, Fig. 6
Reophax dentaliniformis Brady, 1881	Jones (1994), pl. 30, Fig. 21 and 22
Reophax fusiformis (Williamson) 1858	Jones (1994), pl. 30, Figs. 7-10, 211
Reophax guttiferus Brady, 1881	Jones (1994), pl. 31, Fig. 10-15
Reophax scorpiurus Montfort 1808	Loeblich and Tappan (1988) pl. 44 Figs. 1-3
Reophax spiculifer (Brady) 1879	Jones (1994), pl. 31 Fig. 16 and 17
Rhabdamina cornuta (Brady) 1879	Jones (1994), pl. 22 Fig. 11 and 13
Robertinoides bradyi (Cushman and Parker), 1936	Jones (1994), pl. 50 Fig. 18
Sigmoilopsis schlumbergeri Silvestri 1904	Jones (1994), pl. 8, Figs. 1-4
Siphogenerina columellaris (Brady) 1881	Jones (1994), pl. 75 Figs. 15-17
Siphotextularia affinis Fornasini, 1893	Kohl (1985), pl. 2, Fig. 5
Siphotextularia concava (Karrer) 1868	Jones (1994), pl. 42 Figs. 13-14
Spiroloculina tenuiseptata Brady, 1884	Jones (1994), pl. 10 Fig. 5 and 6
Stainforthia concava (Hoglund), 1947	Timm (1992), pl. 5, Fig. 11
Technitella melo Norman 1878	Jones (1994), pl. 25 Fig. 7
Textularia agglutinans d'Orbigny 1839	Jones (1994), pl. 43, Figs. 1-3
Textularia conica d'Orbigny 1839	Le Calvez (1977), p. 18, Fig. 1 and 2
Textularia sagittula Defrance 1824	Jorissen (1987) pl. 3 Fig. 12
Textularia truncata Hoglund, 1947	Le Calvez (1958), pl. 1 Fig. 5
Trifarina angulosa (Williamson) 1858	Jones (1994), pl. 74 Fig. 17 and 18
Trifarina bradyi Cushman, 1923	Jones (1994), pl. 67, Figs. 1-3
Trochammina inflata (Montagu) 1808	Jones (1994), pl. 47, Fig. 4
Uvigerina elongatastriata (Colom) 1952	Van der Zwaan et a. (1986) pl. 6, Figs. 1-8
Uvigerina mediterranea Hofker 1932	Van der Zwaan et a. (1986), pl. 5, Figs. 1-7
Uvigerina peregrina Cushman 1923	Van der Zwaan et a. (1986), pl. 1, Figs. 1-6
Uvigerina proboscidea Schwager 1866	Van der Zwaan et a. (1986) pl. 12, Figs. 1-4
Valvulineria bradyana (Fornasini), 1900	Jorissen (1987) pl. 4 Fig 1 and 2

Appendix B

	OB1B																		OB1B^{bis}							
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%	0-0.25	0.25-0.5	0.5-0.75	0.75-1.0	1.0-1.5	1.5-2.0	Total	%
Perforate																										
Indet	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Amphicoryna scalaris	1	0	1	0	1	1	0	0	0	0	0	0	0	0	0	0	4	0.30	1	1	1	0	1	1	5	1.04
Bolivina alata	0	0	1	2	2	1	0	0	0	0	0	0	0	0	0	0	6	0.44								
Bolivina quadrilatera	5	2	0	0	0	0	0	0	0	(1)	0	0	0	0	0	0	8	0.59								
Bolivina striata																			0	0	0	1	0	1	2	0.42
Buliminella elegantissima	5	4	0	1	1	2	1	4	0	0	0	0	0	0	0	0	19	1.41	0	0	1	1	8	1	11	2.29
Cassidulina carinata																			0	0	0	1	0	1	2	0.42
Chilostomella ovoidea	0	0	0	2	0	0	0	0	(1)	0	0	0	0	0	0	0	3	0.22								
Cibicides lobatulus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Cibicides wuellerstorfi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Cibicidoides pachyderma	25	16	5	3	3	6	1	2	0	0	0	0	0	0	0	0	63	4.67	1	4	9	2	2	2	20	4.17
Cibicidoides ungerianus																			1	0	1	0	9	0	11	2.29
Dentalina sp 1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Dentalina subemaciata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Elphidium sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Gavelinopsis translucens	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Glandulina ovula	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22	0	0	0	0	1	0	1	0.21
Globobulimina affinis	0	0	1	4	19	6	13	16	10	5	3	3	0	0	(1)	0	81	6.00	0	0	0	0	1	10	11	2.29
Gyroidina altiformis	7	0	2	0	0	(1)	0	0	0	0	0	0	0	0	0	0	10	0.74	0	3	0	1	0	0	4	0.83
Gyroidina orbicularis	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22	0	1	0	0	0	4	5	1.04
Hanzawaia boueana																			1	0	0	0	1	0	2	0.42
Hyalinea balthica	7	2	0	0	0	0	1	1	1	0	0	0	0	0	0	0	12	0.89	1	0	1	0	0	1	3	0.63
Lenticulina sp 1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Lenticulina peregrina	4	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.52								
Lenticulina vortex	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22								
Melonis barleeanus	14	33	27	23	14	4	1	1	3	1	0	0	0	0	0	0	121	8.97	1	0	0	2	13	20	36	7.50
Nuttallides umbonifera	2	2	1	0	0	0	0	0	0	0	0	(1)	0	0	0	0	6	0.44	0	1	1	0	1	1	4	0.83
Polymorphinidae																			0	0	1	0	0	1	2	0.42
Pseudoeponides falsobeccarii	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.07								
Robertinoides bradyi	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22	0	0	0	1	0	0	1	0.21
Siphogenerina colombiana	13	7	4	1	0	2	1	1	1	0	0	0	0	0	0	0	30	2.22	0	0	0	0	1	1	2	0.42
Sphaeroidina bulloides																			0	0	1	0	0	0	1	0.21
Trifarina sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Trifarina angulosa	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15								
Uvigerina elongatostriata	0	0	5	15	31	3	4	2	0	1	0	(1)	0	0	0	0	62	4.60	1	0	0	1	1	11	14	2.92
Uvigerina mediterranea	119	123	108	54	20	14	4	9	2	0	0	(1)	0	0	0	0	454	33.65	1	5	11	19	52	51	139	28.96
Uvigerina peregrina	33	43	83	78	43	7	3	2	0	0	0	0	0	0	(1)	0	290	21.50	1	0	2	3	38	58	102	21.25
Uvigerina proboscidea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Porcellaneous																										
Cornuspira involvens	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Cruciloculina sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Pyrgo depressa	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Pyrgo subsphaerina																			5	3	1	1	3	2	15	3.13
Sigmoilopsis sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Non fossilising agglutinated																										
Indet																			0	0	2	1	0	0	3	0.63
Ammotogena sp	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.37								
Arenoscalana sp	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15	0	0	1	0	3	0	4	0.83
Clavulina cylindrica	0	0	1	6	3	0	0	0	0	0	0	0	0	0	0	0	10	0.74	0	0	0	1	3	0	4	0.83
Cribrostomoides subglobosus	8	5	4	0	2	1	0	0	0	0	0	0	0	0	0	0	20	1.48	1	6	6	4	3	1	21	4.38
Cyclammina sp 1	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.07								
Cyclammina sp 2	2	3	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	6	0.44	1	1	2	0	0	1	5	1.04
Cyclammina sp 3	3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0.52								
Eggerella scabra	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	6	0.44	0	0	0	0	0	1	1	0.21
Hyperammina bradyi	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15								
Reophax sp 1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.22								
Reophax dentaliniformis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.07								
Reophax fusiformis	0	0	5	2	0	0	0	0	0	0	0	0	0	0	0	0	7	0.52								
Reophax guttiferus	2	17	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19	1.41	0	0	0	0	1	0	1	0.21
Reophax scorpiurus	19	2	1	1	0	1	1	0	0	0	0	0	0	0	0	0	25	1.85	2	2	9	6	4	4	27	5.63
Trochammina sp	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.15	0	0	0	1	0	0	1	0.21
Fossilising agglutinated																										
Bigenerina nodosaria	5	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	9	0.67	0	0	1	2	2	1	4	0.83
Pseudoclavulina crustata	2	3	0	1	1	2	1	0	0	0	0	0	0	0	0	0	10	0.74	0	1	9	2	2	0	14	2.92
Siphotextularia affinis	4	1	2	0	2	0	0	0	0	0	0	0	0	0	0	0	9	0.67								
Textularia sagittula																			1	0	1	0	0	1	3	0.63
Total live foraminifera	300	281	263	200	144	53	32	38	19	8	3	6	0	1	1	0	1349	100.00	19	28	61	50	150	174	480	100.00
Nbr species	35	24	25	20	14	15	12	9	6	4	1	4	0	1	1	0	53		14	11	18	17	21	22	33	
Glomospira spp	1	4	5	4	11	10	11	7	1	1	0	0	0	0	0	0	56		0	0	0	1	0	1	2	
Arborescent indet	34	30	44	61	22	12	0	0	0	0	0	0	0	0	0	0	203		4	13	8	5	19	29	78	
Ostracoda																			0	0	0	2	5	1	8	

	OB2B													OB2B^{bis}			
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	**Total**	**%**	0-2.5	2.5-5	**Total**	**%**
Perforate																	
Indet.														1	0	1	0.19
Amphicoryna scalaris	0	0	0	1	0	0	0	0	0	0	0	1	0.14	2	0	2	0.38
Bolivina alata	0	1	1	2	3	0	0	0	0	0	0	7	0.97	3	0	3	0.57
Bulimina marginata	1	0	3	1	1	0	0	0	0	12	0	18	2.50	7	2	9	1.70
Cassidulina carinata	1	0	1	0	0	0	0	0	0	0	0	2	0.28				
Cassidulina crassa														0	1	1	0.19
Chilostomella ovoina	0	0	0	0	2	0	1	0	0	0	0	3	0.42	6	7	13	2.46
Cibicides lobatulus	0	0	0	0	1	0	0	0	0	0	0	1	0.14	3	0	3	0.57
Cibicides wuellerstorfi	0	1	4	1	0	0	0	0	0	0	0	6	0.83	2	0	2	0.38
Cibicidoides pachydermus	16	14	13	4	5	0	0	0	0	0	0	52	7.22	30	3	33	6.24
Dentalina bradyensis	0	0	0	0	1	0	0	0	0	0	0	1	0.14	2	0	2	0.38
Dentalina subemaciata														2	0	2	0.38
Glandulina ovula														1	0	1	0.19
Globobulimina affinis	1	3	3	8	0	3	1	0	0	0	0	19	2.64	22	17	39	7.37
Gyroidina altiformis	1	0	1	1	0	0	0	0	0	0	0	3	0.42				
Gyroidina orbicularis														1	1	2	0.38
Hoeglundina elegans														1	0	1	0.19
Hyalinea balthica	0	0	2	5	0	0	0	0	0	0	0	7	0.97	2	0	2	0.38
Lagena sp.	2	0	0	0	0	0	0	0	0	0	0	2	0.28	1	0	1	0.19
Lenticulina peregrina	1	1	0	0	1	0	0	0	0	0	0	3	0.42	3	0	3	0.57
Lenticulina vortex	2	0	0	0	(1)	0	0	0	0	0	0	3	0.42	1	0	1	0.19
Marginula obesa	1	0	1	0	0	(1)	0	0	0	0	0	3	0.42	1	0	1	0.19
Melonis barleeanus	1	8	9	14	28	5	4	0	0	0	0	69	9.58	40	2	42	7.94
Nuttallides umboniferus	1	1	0	2	0	0	0	0	0	0	0	4	0.56				
Polymorphinidae	1	0	1	0	0	(1)	0	0	0	0	0	3	0.42				
Pullenia quinqueloba	0	1	2	2	1	3	0	0	0	0	0	9	1.25	3	1	4	0.76
Robertinoides brabyi	0	0	0	1	0	0	0	0	0	0	0	1	0.14				
Rosalina sp.	1	0	0	0	1	1	0	0	0	0	0	3	0.42				
Siphogenerina columellaris	3	5	7	1	1	0	0	0	0	0	0	17	2.36	8	4	12	2.27
Trifarina angulosa	0	1	0	0	0	0	0	0	0	0	0	1	0.14				
Uvigerina elongatastriata	0	0	2	3	10	2	1	2	0	0	0	20	2.78	35	4	39	7.37
Uvigerina mediterranea	73	26	58	43	76	7	2	1	1	0	0	287	39.86	149	14	163	30.81
Uvigerina peregrina	16	3	11	6	8	0	0	0	0	0	0	44	6.11	54	3	57	10.78
Porcellaneous																	
Biloculinella sp.	0	1	0	0	0	0	0	0	0	0	0	1	0.14				
Biloculinella irregularis	0	0	1	1	0	0	0	0	0	0	0	2	0.28				
Cornuspira involvens	1	0	1	1	2	0	0	0	0	0	0	5	0.69	4	1	5	0.95
Cruciloculina sp.	0	0	1	0	0	0	0	0	0	0	0	1	0.14				
Pyrgo subsphaerica	0	1	0	0	0	0	0	0	0	0	0	1	0.14				
Pyrgoella sphaera	0	0	1	0	0	0	0	0	0	0	0	1	0.14				
Sigmoilina sp.	1	0	0	0	0	0	0	0	0	0	0	1	0.14				
Non fossilising agglutinated																	
Adercotryma glomerata														1	0	1	0.19
Ammolagena sp.	0	0	0	1	0	0	0	0	0	0	0	1	0.14				
Ammoscalaria sp.	0	0	0	0	2	0	0	0	0	0	0	2	0.28				
Ammoscalaria pseudospiralis														1	0	1	0.19
Clavulina cylindrica	1	0	4	3	9	0	0	0	0	0	0	17	2.36	11	0	11	2.08
Cribrostomoides subglobosus	9	9	2	6	4	0	0	0	0	0	0	30	4.17	6	1	7	1.32
Cyclammina sp.1														1	0	1	0.19
Cyclammina sp.2	0	0	2	1	3	0	0	0	0	0	0	6	0.83	4	0	4	0.76
Cyclammina sp.3	5	0	0	1	0	0	2	0	0	0	0	8	1.11	2	0	2	0.38
Eggerella scabra	2	2	3	2	6	0	0	0	0	0	0	15	2.08	2	0	2	0.38
Haplophragmoides bradyi	2	0	0	0	0	0	0	0	0	0	0	2	0.28				
Psammosphaera fusca														1	0	1	0.19
Reophax sp.	3	1	0	2	1	0	1	0	0	0	0	8	1.11				
Reophax sp.1														0	1	1	0.19
Reophax fusiformis														5	0	5	0.95
Reophax guttiferus	0	3	3	2	6	0	0	0	0	0	0	14	1.94	3	0	3	0.57
Reophax scorpiurus	1	0	2	1	0	0	0	0	0	0	0	4	0.56	14	5	19	3.59
Saccammina sp.														2	1	3	0.57
Technitella melo	0	0	0	1	0	0	0	0	0	0	0	1	0.14	1	1	2	0.38
Trochammina sp.	0	0	1	0	0	0	0	0	0	0	0	1	0.14				
Fossilising agglutinated																	
Bigenerina nodosaria	1	1	1	1	0	0	0	0	0	0	0	4	0.56	1	0	1	0.19
Karrerulina sp.														1	0	1	0.19
Pseudoclavulina crustata	0	1	0	2	0	0	0	0	0	0	0	3	0.42	8	1	9	1.70
Siphotextularia affinis	0	0	0	1	0	0	0	0	0	0	0	1	0.14				
Textularia sp.	0	0	0	1	0	0	0	0	0	0	0	1	0.14				
Textularia conica	0	0	0	0	1	0	0	0	0	0	0	1	0.14				
Total live foraminifera	148	84	141	122	174	23	12	3	1	12	0	720	100.00	448	81	529	100.00
Nbr species	26	20	28	31	24	8	7	2	1	1	0	52		43	19	44	
Glomospira spp.	0	1	4	3	27	11	8	0	6	3	0	63		41	8	49	
Arborescent indet.	5	10	10	5	6	3	11	0	0	0	0	50					
Ostracoda	3	0	0	3	2	0	1	0	0	0	0	9					

OB3B																		
Depth	0-1	1-1.25	1.25-1.50	1.5-1.75	1.75-2	2-2.5	2.5-3	3-3.5	3.5-4	4-4.5	4.5-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																		
Amphicoma scalaris	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.75
Bolivina alata	0	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	0.50
Bolivinita quadrilatera	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Bulimina costata	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0.50
Bulimina marginata	3	1	0	1	1	0	1	0	0	0	0	0	0	1	1	0	9	2.24
Chilostomella ovoidea	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0.50
Cibicides lobatulus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.50
Cibicidoides pachyderma	11	0	0	(1)	0	0	0	0	0	0	0	0	(1)	0	0	0	13	3.23
Cibicidoides ungerianus	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.75
Dentalina bradyensis	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.75
Elphidium sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Glandulina ovula	2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0.75
Globobulimina affinis	0	1	4	9	3	2	3	5	2	1	3	0	0	0	0	0	33	8.21
Gyroidina orbicularis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Hanzawaia boueana	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	0.50
Hyalinea balthica	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.50
Lenticulina peregrina	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1.00
Lenticulina vortex	3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	4	1.00
Melonis barleeanus	24	3	1	2	2	7	1	0	0	0	0	0	0	0	0	0	40	9.95
Nonionella turgida	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Nuttallides umboniferus	2	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	3	0.75
Pullenia quinqueloba	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	2	0.50
Siphogenerina columellaris	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	3	0.75
Uvigerina elongatastriata	1	1	3	2	0	1	3	0	0	0	0	0	0	0	0	0	11	2.74
Uvigerina mediterranea	54	3	5	4	5	7	1	3	0	0	0	0	2	2	1	1	88	21.89
Uvigerina peregrina	26	1	3	1	2	1	0	0	0	0	0	0	0	1	1	0	36	8.96
Porcellaneous																		
Biloculinella irregularis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.25
Cornuspira involvens	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.50
Spiroloculina tenuiseptata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Non fossilising agglutinated																		
Ammoscalaria sp.	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.50
Clavulina cylindrica	22	2	3	1	1	0	2	0	0	0	0	0	0	0	0	0	31	7.71
Cribrostomoides subglobosus	21	5	6	2	1	5	3	0	0	0	(1)	0	0	0	0	(1)	45	11.19
Cyclammina sp.2	1	0	0	0	0	(1)	0	0	(1)	0	0	0	0	0	0	(1)	4	1.00
Cyclammina sp.3	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.75
Eggerella scabra	2	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	6	1.49
Haplophragmoides bradyi	0	0	0	0	1	0	0	0	0	0	(1)	0	0	0	0	0	2	0.50
Reophax sp.	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.50
Reophax dentaliniformis	0	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	3	0.75
Reophax scorpiurus	6	1	5	1	0	1	0	0	0	0	0	0	0	0	0	0	14	3.48
Trochammina sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Fossilising agglutinated																		
Bigenerina nodosaria	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.25
Pseudoclavulina crustata	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1.00
Siphotextularia affinis	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0.75
Textularia sp.	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.25
Textularia sagittula	0	0	0	0	1	0	0	0	(1)	0	0	0	0	0	0	0	2	0.50
Total live foraminifera	206	28	36	28	23	34	15	8	4	1	5	0	3	5	3	3	402	100.00
Nbr species	30	18	13	13	14	15	8	2	3	1	3	1	2	4	3	3	45	
Glomospira spp.	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	
Arborescent indet.	40	8	4	33	4	6	0	0	0	0	0	0	0	0	0	0	95	

OB4B																		
Depth	**0-0.25**	**0.25-0.5**	**0.5-0.75**	**0.75-1**	**1-1.5**	**1.5-2**	**2-2.5**	**2.5-3**	**3-3.5**	**3.5-4**	**4-5**	**5-6**	**6-7**	**7-8**	**8-9**	**9-10**	**Total**	**%**
Perforate																		
Indet.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.36
Amphicoryna scalaris	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Bolivina alata	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Bulimina costata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Bulimina marginata	3	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	4	1.42
Chilostomella oolina	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.36
Cibicides lobatulus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Cibicides wuellerstorfi	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Cibicidoides pachydermus	8	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	2.85
Cibocidoides ungerianus	5	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	6	2.14
Globobulimina affinis	0	2	1	0	2	1	2	2	6	1	0	(1)	0	0	0	0	18	6.41
Gyroidina altiformis	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Gyroidina orbicularis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Hanzawaia boueana	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Lenticulina peregrina	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Lenticulina vortex	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Melonis barleeanus	1	7	10	13	9	3	0	0	0	0	0	0	0	0	0	0	43	15.30
Nonionella turgida	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Nuttallides umboniferus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Polymorphinidae	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Pullenia quinqueloba	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Rosalina sp.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.71
Siphogenerina columellaris	9	2	0	0	(1)	0	0	0	0	(1)	0	0	0	0	0	0	13	4.63
Uvigerina elongatastriata	0	3	8	7	2	0	0	0	0	0	0	0	0	0	0	0	20	7.12
Uvigerina mediterranea	41	5	0	0	0	1	1	0	1	1	0	0	0	0	0	0	50	17.79
Uvigerina peregrina	25	2	0	0	1	1	0	0	0	2	0	0	0	0	0	0	31	11.03
Uvigerina proboscidea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Porcellaneous																		
Biloculinella irregularis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Comuspira involvens	3	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	8	2.85
Pyrgo subsphaerica	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Non fossilising agglutinated																		
Clavulina cylindrica	0	1	1	9	3	0	0	0	0	0	0	0	0	0	0	0	14	4.98
Cribrostomoides subglobosus	5	3	2	2	1	0	0	0	0	0	0	0	0	0	0	0	13	4.63
Cyclammina sp.2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Eggerella scabra	7	2	0	2	1	0	0	0	0	0	0	0	0	0	0	0	12	4.27
Haplophragmoides bradyi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Reophax dentaliniformis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Reophax scorpiurus	6	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	3.20
Fossilising agglutinated																		
Bigenerina nodosaria	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Siphotextularia affinis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.36
Total live foraminifera	133	35	24	34	23	7	3	4	8	5	0	1	0	0	0	0	281	100.00
Nbr species	28	15	7	6	10	5	2	2	3	4	0	1	0	0	0	0	38	
Glomospira spp.	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	
Arborescent indet.	21	19	4	4	2	2	0	0	0	0	0	0	0	0	0	0	52	

OB5B																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																		
Amphicoryna scalaris	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Bolivina alata	0	0	0	0	4	4	0	0	0	0	0	0	0	0	0	0	8	2.48
Bolivinita quadrilatera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Bulimina costata	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.93
Bulimina marginata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Cibicidoides pachydermus	6	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	3.11
Cibicidoides ungerianus	0	2	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	3	0.93
Dentalina advena	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Dentalina subemaciata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Glandulina ovula	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Globobulimina affinis	0	0	0	0	2	2	0	1	4	0	3	1	0	0	0	0	13	4.04
Gyroidina orbicularis	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.62
Hanzawaia boueana	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Hyalinea balthica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0.31
Lenticulina vortex	0	0	0	1	0	0	0	0	0	0	0	(1)	0	0	0	0	2	0.62
Melonis barleeanus	0	0	1	4	18	10	1	0	0	0	0	0	0	0	0	0	34	10.56
Nodosaria sp	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Nuttallides umboniferus	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.31
Pullenia quinqueloba	1	0	0	1	1	3	0	0	0	0	0	0	0	0	0	0	6	1.86
Rectuvigerina phlegeri	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.31
Siphogenerina columellaris	1	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	6	1.86
Uvigerina elongatastriata	0	1	3	2	9	5	0	0	0	0	0	0	0	0	0	0	20	6.21
Uvigerina mediterranea	22	23	9	9	2	3	1	1	0	0	(1)	0	0	0	(3)	0	74	22.98
Uvigerina peregrina	5	7	6	4	4	0	0	0	(1)	0	0	0	0	0	0	0	27	8.39
Porcellaneous																		
Cornuspira involvens	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3	0.93
Sigmoilina sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.31
Non fossilising agglutinated																		
Indet.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Ammoscalaria sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Clavulina cylindrica	0	1	0	1	2	2	0	0	0	0	0	0	0	0	0	0	6	1.86
Cribrostomoides subglobosus	7	18	7	5	2	0	0	0	0	0	0	0	0	0	1	1	41	12.73
Cyclammina sp.2	1	1	0	1	0	0	2	0	0	1	1	1	0	0	0	0	8	2.48
Eggerella scabra	1	3	2	1	1	2	0	1	0	0	0	0	0	0	0	0	11	3.42
Reophax scorpiurus	10	5	5	4	1	0	0	0	0	0	0	0	0	0	0	0	25	7.76
Technitella melo	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Trochammina sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.31
Fossilising agglutinated																		
Bigenerina nodosaria	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.93
Pseudoclavulina crustata	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.62
Total live foraminifera	59	75	34	39	52	35	4	4	5	1	5	3	0	0	5	1	322	100.00
Nbr species	14	17	8	17	17	12	3	4	2	1	3	3	0	0	3	1	36	
Glomospira spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	
Arborescent indet.	4	13	14	6	14	8	0	0	0	0	0	0	0	0	0	0	59	
Ostracoda	0	1	0	0	3	0	0	0	0	0	0	0	0	0	0	0	4	

OB6B																		
Depth	**0-0.25**	**0.25-0.5**	**0.5-0.75**	**0.75-1**	**1-1.5**	**1.5-2**	**2-2.5**	**2.5-3**	**3-3.5**	**3.5-4**	**4-5**	**5-6**	**6-7**	**7-8**	**8-9**	**9-10**	**Total**	**%**
Perforate																		
Astacolus sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.16
Amphicoryna scalaris	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Bolivina alata	0	0	0	0	0	0	1	6	0	0	0	0	0	0	0	0	7	1.14
Bulimina costata	1	0	1	1	0	0	0	(1)	0	0	0	0	0	0	0	0	4	0.65
Bulimina marginata	0	1	1	0	1	0	0	0	2	0	(1)	0	0	0	0	0	6	0.98
Chilostomella oolina	0	0	0	0	0	0	0	1	1	0	(1)	0	0	(1)	0	0	4	0.65
Cibicidoides pachydermus	2	0	3	2	2	0	1	2	2	0	0	0	(1)	0	0	0	15	2.44
Dentalina advena	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Globobulimina affinis	0	0	0	0	0	0	0	10	12	7	16	5	5	0	0	0	55	8.94
Gyroidina altiformis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Gyroidina orbicularis	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	3	0.49
Hanzawaia boueana	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.16
Lenticulina vortex	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Melonis barleeanus	1	0	3	6	8	21	23	21	9	7	2	2	0	0	0	0	103	16.75
Nuttallides umbonifera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Siphogenerina columellaris	0	0	0	3	2	4	0	0	0	0	0	0	0	0	0	0	9	1.46
Uvigerina elongatastriata	0	0	0	0	0	4	8	4	5	0	0	0	0	0	0	0	21	3.41
Uvigerina mediterranea	17	3	48	28	63	24	4	10	5	6	6	4	4	0	3	0	225	36.59
Uvigerina peregrina	4	1	5	10	13	5	3	1	1	0	0	0	0	2	0	0	45	7.32
Porcellaneous																		
Cornuspira involvens	0	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0	3	0.49
Pyrgo sp.	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.49
Pyrgo subsphaerica	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0.33
Non fossilising agglutinated																		
Indet.	0	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	3	0.49
Ammoscalaria sp.	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.49
Clavulina cylindrica	0	0	2	0	3	2	7	5	10	3	0	0	0	0	0	0	32	5.20
Cribrostomoides subglobosus	2	0	1	2	5	2	4	4	3	1	1	0	0	0	0	0	25	4.07
Cyclammina sp.2	0	0	0	0	0	1	0	0	0	0	(1)	0	0	0	0	0	2	0.33
Cyclammina sp.3	0	0	0	0	1	2	0	0	(1)	0	0	0	0	0	0	0	4	0.65
Eggerella scabra	1	2	1	1	1	0	0	0	0	0	0	0	0	0	0	0	6	0.98
Reophax scorpiurus	2	0	7	0	3	6	2	0	0	0	0	0	0	0	0	0	20	3.25
Fossilising agglutinated																		
Bigenerina nodosaria	1	0	1	0	3	0	0	0	0	0	0	0	0	0	0	0	5	0.81
Pseudoclavulina crustata	0	0	1	1	0	0	(1)	0	0	0	0	0	0	0	0	0	2	0.33
Total live foraminifera	33	7	78	57	110	76	55	65	53	24	29	12	10	3	3	0	615	100.00
Nbr species	11	4	15	11	15	15	10	11	13	5	8	4	3	2	1	0	31	
Glomospira spp.	0	0	0	1	1	0	0	1	0	0	0	0	0	0	0	0	3	
Arborescent indet.	0	0	0	2	10	3	12	8	2	0	0	1	0	0	0	0	38	
Ostracoda	1	0	1	0	1	1	0	0	0	0	0	0	0	0	2	0	6	

OB7B																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Amphicoryna scalaris	2	0	2	0	0	(1)	0	0	0	0	0	0	0	0	0	0	5	0.90
Astacolus sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.18
Bolivina alata	0	0	0	0	7	10	2	1	0	0	0	0	0	0	0	0	20	3.61
Bolivinita quadrilatera	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.54
Bulimina marginata	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Chilostomella ovoidea	0	0	0	0	0	1	0	1	0	0	(1)	0	0	0	0	0	3	0.54
Cibicides lobatulus	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Cibicidoides pachydermus	9	6	6	2	0	0	0	0	0	0	0	0	0	0	0	0	23	4.15
Cibicidoides ungerianus	4	4	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	9	1.62
Dentalina advena	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Dentalina subemaciata	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Globobulimina affinis	0	0	0	0	3	2	3	0	9	6	10	1	3	1	0	0	38	6.86
Gyroidina altiformis	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.54
Gyroidina orbicularis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Hyalinea balthica	8	4	1	0	1	0	0	0	0	0	0	0	0	0	0	0	14	2.53
Lagena sp.	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Lenticulina peregrina	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Lenticulina vortex	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.54
Melonis barleeanus	1	0	4	3	29	3	0	0	0	0	0	0	0	0	0	0	40	7.22
Nuttallides umboniferus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Pullenia quinqueloba	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Robertinoides bradyi	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Siphogenerina columellaris	3	7	1	1	0	0	0	0	0	0	0	0	0	0	0	0	12	2.17
Uvigerina elongatastriata	0	1	0	3	19	16	3	0	0	0	0	0	0	0	0	0	42	7.58
Uvigerina mediterranea	48	54	35	22	14	1	3	0	0	(1)	0	0	0	0	0	0	178	32.13
Uvigerina peregrina	0	5	8	3	3	0	0	0	0	0	0	0	0	0	0	0	19	3.43
Uvigerina proboscidea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Porcellaneous																		
Cornuspira involvens	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Cruciloculina sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Pyrgoella sphaera	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Scutulonis sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Spiroloculina tenuiseptata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Non fossilising agglutinated																		
Adercotryma glomerata	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1.26
Ammoscalaria sp.	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.72
Clavulina cylindrica	1	0	0	2	6	4	0	0	0	0	0	0	0	0	0	0	13	2.35
Cribrostomoides subglobosus	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	1.26
Cyclammina sp.2	3	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.90
Haplophragmoides bradyi	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0.54
Reophax guttiferus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Reophax scorpiurus	15	10	8	6	4	1	0	0	0	0	0	0	0	0	0	0	44	7.94
Saccammina spp.	4	2	0	0	1	0	1	0	0	0	0	0	0	0	0	0	8	1.44
Trochammina sp.	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Fossilising agglutinated																		
Bigenerina nodosaria	1	3	2	2	0	0	0	0	0	0	0	0	0	0	0	0	8	1.44
Pseudoclavulina crustata	1	5	6	2	0	0	0	0	0	0	0	0	0	0	0	0	14	2.53
Siphotextularia affinis	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.36
Textularia conica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Total live foraminifera	128	116	80	51	93	39	14	2	9	7	11	1	3	1	0	0	554	100.00
Nbr species	29	22	17	15	15	9	7	2	1	2	2	1	1	1	0	0	49	
Glomospira spp.	5	11	8	10	10	2	6	0	0	0	0	0	0	0	0	0	52	

	OB8B																		OB8B^{bis}																	
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	Total	%
Perforate																																				
ndet																			1	0	0	0	0	0	0	0	0	0	0	1	0.22
Amphicoryna scalaris																			0	0	0	1	0	0	0	0	0	0	0	1	0.22
Bolivina alata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	0	0	0	1	3	3	1	0	(1)	0	9	1.94
Bolivina subaenariensis																			0	0	0	0	0	1	0	0	0	0	0	1	0.22
Bolivinita quadrilatera	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	1	0	0	1	0	0	0	0	0	0	2	0.43
Bulimina aculeata																			0	1	0	0	0	0	0	0	0	0	0	1	0.22
Bulimina marginata																			1	2	1	1	2	2	0	0	(1)	0	0	10	2.15
Chilostomella ovoina	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0.82	0	1	0	0	2	0	1	1	5	5	4	19	4.09
Cibicidoides pachydermus	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	3	1.22	0	0	0	0	1	0	0	0	0	0	0	1	0.22
Cibicidoides ungerianus																			0	2	0	0	0	(1)	0	0	0	0	0	3	0.65
Dentalina advena	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	0	0	0	1	0	0	0	0	0	0	1	0.22
Dentalina bradyensis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	0	0	0	1	0	0	0	0	0	0	1	0.22
Dentalina submarginata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	0	0	1		0	0	0	0	0	0	1	0.22
Glandulina ovula	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41													
Globobulimina affinis	0	0	0	0	5	4	4	1	3	6	6	1	0	0	0	0	31	12.65	0	0	1	3	6	13	13	7	8	10	10	71	15.27
Gyroidina altiformis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41	1	0	0	0	0	0	0	0	0	0	0	1	0.22
Gyroidina orbicularis	-	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82	0	0	0	0	0	0	1	0	0	0	0	1	0.22
Hanzawaia boueana																			0	0	0	1	0	0	0	0	0	0	0	1	0.22
Hyalinea baltica																			0	1	1	0	0	0	0	2	0	0	(1)	5	1.08
Lagena sp																			0	0	0	0	0	0	0	0	0	0	1	1	0.22
Lenticulina sp 2	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.41													
Lenticulina peregrina																			0	1	0	1	0	0	0	0	0	0	0	2	0.43
Lenticulina vortex	-	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	0	0	0	0	1	0	0	0	0	0	1	0.22
Marginula obesa																			0	0	0	1	0	0	0	0	0	0	0	1	0.22
Melonis barleeanus	2	5	0	3	0	0	0	0	0	0	0	0	0	0	0	0	10	4.08	0	0	2	1	10	15	5	2	0	(1)	0	35	7.74
Siphogenerina columellaris																			0	0	0	1	1	2	0	0	0	0	0	4	0.86
Uvigerina elongatastrata	8	3	0	1	10	7	3	0	0	0	0	0	0	0	0	0	32	13.06	0	1	0	3	6	5	4	3	0	0	0	22	4.73
Uvigerina mediterranea	9	7	0	22	3	1	1	0	1	3	0	3	0	0	0	0	50	20.41	7	15	3	7	25	18	5	9	0	0	0	90	19.35
Uvigerina peregrina	6	0	0	3	2	2	0	0	0	0	(1)	0	0	0	0	0	14	5.71	2	7	5	2	9	3	1	0	2	0	2	33	7.10
																			1	0	0	0	0	0	0	0	0	0	0	1	0.22
Porcellaneous																															
Cornuspira involvens	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41													
Cruciloculina sp																			0	0	0	0	1	1	0	0	0	0	0	2	0.43
Quinqueloculina sp	0	0	0	1	1	0	1	0	0	0	0	0	0	0	0	0	3	1.22													
Sigmoilina sp																			0	0	0	0	0	0	0	0	0	1	0	1	0.22
Non fossilising agglutinated																															
ndet																			0	1	1	0	1	0	0	0	0	(1)	0	4	0.86
Ammolagena sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41													
Ammoscalaria sp	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82	0	5	1	3	6	2	0	(1)	0	0	0	18	3.87
Ammoscalaria pseudospiralis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41													
Clavulina cylindrica	0	2	0	3	3	0	0	0	0	0	0	0	0	0	0	0	8	3.27	0	3	0	2	2	15	6	2	0	0	0	30	6.45
Cribrostomoides subglobosus	3	3	0	5	0	0	0	0	1	1	1	0	0	0	0	0	14	5.71	5	9	2	3	11	5	3	0	0	2	1	41	8.82
Cyclammina sp 2	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.22													
Cyclammina sp 3	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82	0	0	0	0	0	1	0	0	0	0	0	1	0.22
Eggerella scabra																			1	2	1	0	0	0	0	(1)	0	0	0	5	1.08
Haplophragmoides sp 1																			0	1	0	0	0	0	0	0	0	0	0	1	0.22
Haplophragmoides bradyi	0	2	0	1	1	1	0	0	0	0	0	0	0	0	0	0	5	2.04													
Psammosphaera fusca																			1	2	0	0	0	0	0	(1)	0	0	0	4	0.86
Reophax dentaliniformis	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.41	0	0	0	0	0	1	0	0	0	0	0	1	0.22
Reophax fusiformis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41	0	0	0	0	1	0	0	0	0	0	0	1	0.22
Reophax guttiferus																			1	0	0	1	2	0	0	0	0	0	0	4	0.86
Reophax scorpiurus	3	6	0	5	3	0	0	0	3	0	0	0	0	0	0	0	20	8.16	3	6	0	3	4	2	0	0	1	0	1	20	4.30
Saccammina spp	0	3	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	4	1.63	2	0	0	0	0	1	0	0	0	2	0	5	1.08
Technitella melo																			0	1	0	1	1	0	0	0	0	0	0	3	0.65
Trochammina sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41													
Fossilising agglutinated																															
Bigenerina nodosaria	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	1.22													
Pseudoclavulina crustata	2	5	5	9	0	1	0	0	0	0	0	0	0	0	0	0	22	8.98	0	0	0	1	1	0	(1)	0	0	0	0	3	0.65
Total live foraminifera	37	47	5	50	33	18	10	1	9	11	10	4	0	0	0	0	245	100.00	26	62	18	37	96	91	45	30	17	23	20	465	100.00
Nbr species	11	19	1	16	11	6	5	1	5	4	5	2	0	0	0	0	34		11	18	9	19	22	18	12	11	5	7	7	43	
Glomospira spp	7	8	7	5	11	11	3	5	5	2	1	2	0	0	0	0	67		0	2	1	1	5	11	8	4	2	0	0	35	
																			0	0	0	0	0	2	0	0	0	0	0	2	

OB9B

Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																		
indet	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.66
Amphicoryna scalaris																		
Astacolus sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Bolivina alata	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0.51
Bolivina spathulata																		
Bolivinita quadrilatera	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Bulimina costata																		
Bulimina marginata	4	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	9	1.53
Cassidulina carinata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Cassidulina crassa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Chilostomella oolina	0	0	0	0	0	0	1	0	0	6	3	1	1	0	0	0	12	2.04
Cibicides lobatulus																		
Cibicidoides pachydermus	1	5	5	0	0	0	0	0	0	0	0	0	0	0	0	0	11	1.87
Cibicidoides ungerianus	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Dentalina advena	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Dentalina bradyensis	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.34
Dentalina subemaciata	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0.34
Epistominella sp																		
Glandulina ovula	0	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Globobulimina affinis	0	0	0	0	0	11	14	5	3	4	9	5	0	0	0	0	51	8.67
Gyroidina altiformis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Gyroidina orbicularis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Hanzawaia boueana	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Hyalinea balthica	3	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1.70
Lenticulina sp 1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Lenticulina peregrina	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Lenticulina vortex	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Melonis barleeanus	0	2	0	3	7	12	15	0	0	0	0	0	0	0	0	0	39	6.63
Nuttallides pusillus																		
Nuttallides umboniferus	0	3	0	0	1	1	0	0	0	0	0	0	0	0	0	0	5	0.85
Pullenia quinqueloba	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	7	1.19
Robertinoides bradyi	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.34
Siphogenerina columellaris	1	3	1	3	0	0	0	0	0	0	0	0	0	0	0	0	8	1.36
Uvigerina elongatastriata	1	1	0	0	1	7	5	0	0	0	0	0	0	0	0	0	15	2.55
Uvigerina mediterranea	45	55	45	17	18	6	1	0	0	1	1	0	0	0	0	0	189	32.14
Uvigerina peregrina	7	5	3	3	8	1	0	0	0	0	0	0	0	0	0	0	27	4.59
Uvigerina proboscidea	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Porcellaneous																		
Biloculinella sp																		
Cornuspira involvens	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Cruciloculina sp	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.34
Pyrgo depressa																		
Quinqueloculina sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Non fossilising agglutinated																		
Agglutinated sp 1																		
Adercotryma glomerata	2	2	1	0	0	3	1	0	0	0	0	0	0	0	0	0	9	1.53
Ammolagena sp																		
Ammoscalaria sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Ammoscalaria pseudospiralis	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.34
Clavulina cylindrica	0	0	4	0	13	8	2	0	0	0	0	0	0	0	0	0	27	4.59
Cribrostomoides subglobosus	5	9	7	0	1	0	6	0	0	0	0	0	0	0	0	0	28	4.76
Cyclammina sp 1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Cyclammina sp 2	2	2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	6	1.02
Cyclammina sp 3	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Eggerella scabra	1	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	6	1.02
Haplophragmoides sp																		
Haplophragmoides sp 1																		
Haplophragmoides bradyi	0	2	1	0	2	1	0	0	0	0	0	0	0	0	0	0	6	1.02
Karrerella sp																		
Psammosphaera fusca																		
Reophax sp 1	1	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Reophax dentaliniformis																		
Reophax fusiformis	0	2	1	2	1	0	0	0	0	0	0	0	0	0	0	0	6	1.02
Reophax guttifera																		
Reophax scorpiurus	3	2	7	1	0	1	0	0	0	0	0	0	0	0	0	0	14	2.38
Rhabdammina cornuta	0	1	1	0	0	0	1	0	0	0	0	0	0	0	0	0	3	0.51
Saccammina spp	0	6	7	0	6	1	0	0	0	0	0	0	0	0	0	0	20	3.40
Technitella nitida																		
Trochammina sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Fossilising agglutinated																		
Bigenerina nodosaria	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.51
Pseudoclavulina crustata	7	7	5	1	4	0	0	0	0	0	0	0	0	0	0	0	24	4.08
Sigmoilopsis schlumbergeri	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.17
Siphotextularia affinis	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.34
Textularia agglutinans																		
Total live foraminifera	92	118	122	44	69	52	52	5	3	11	13	6	1	0	0	0	588	100.00
Nbr species	24	24	31	13	17	11	11	1	1	3	3	2	1	0	0	0	55	
Glomospira spp	2	4	11	5	24	10	7	0	5	2	1	0	1	0	0	0	84	
Ostracoda	0	1	3	1	1	3	0	0	1	0	0	0	0	0	0	0		

OB9B^{bis}

Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																		
indet	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Amphicoryna scalaris	1	2	0	1	2	0	0	0	0	0	0	(1)	0	0	0	0	7	1.11
Astacolus sp																		
Bolivina alata	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.32
Bolivina spathulata	0	0	0	0	0	2	1	0	0	0	0	0	0	0	0	0	3	0.48
Bolivinita quadrilatera																		
Bulimina costata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Bulimina marginata	0	2	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Cassidulina carinata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Cassidulina crassa																		
Chilostomella oolina	0	0	0	0	0	0	0	0	1	0	0	0	0	(1)	0	0	2	0.32
Cibicides lobatulus	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.48
Cibicidoides pachydermus	6	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	11	1.74
Cibicidoides ungerianus	1	0	0	3	1	0	0	0	0	0	0	0	0	0	0	0	5	0.79
Dentalina advena																		
Dentalina bradyensis	0	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Dentalina subemaciata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Epistominella sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Glandulina ovula	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Globobulimina affinis	0	0	0	0	2	5	9	2	2	2	2	0	0	0	0	0	24	3.80
Gyroidina altiformis	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.32
Gyroidina orbicularis	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Hanzawaia boueana	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Hyalinea balthica	3	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	6	0.95
Lenticulina sp 1																		
Lenticulina peregrina	1	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Lenticulina vortex	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Melonis barleeanus	9	4	4	5	14	6	3	7	0	0	0	0	0	0	0	0	52	8.24
Nuttallides pusillus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Nuttallides umboniferus	4	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0	7	1.11
Pullenia quinqueloba																		
Robertinoides bradyi	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.32
Siphogenerina columellaris	6	3	1	1	2	1	0	0	0	0	0	0	0	0	0	0	14	2.22
Uvigerina elongatastriata	1	1	1	1	5	18	9	1	0	0	0	0	0	0	0	0	37	5.86
Uvigerina mediterranea	85	50	42	27	29	9	1	5	1	1	1	0	0	0	0	0	251	39.78
Uvigerina peregrina	2	2	2	2	2	1	0	0	0	0	0	0	0	0	0	0	11	1.74
Uvigerina proboscidea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Porcellaneous																		
Biloculinella sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Cornuspira involvens	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Cruciloculina sp	2	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	3	0.48
Pyrgo depressa	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Quinqueloculina sp																		
Non fossilising agglutinated																		
Agglutinated sp 1	5	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	8	1.27
Adercotryma glomerata																		
Ammolagena sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Ammoscalaria sp	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.48
Ammoscalaria pseudospiralis	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.32
Clavulina cylindrica	0	0	0	0	4	1	10	1	0	0	0	0	0	0	0	0	16	2.54
Cribrostomoides subglobosus	31	19	6	1	1	1	2	0	0	0	0	0	0	0	0	0	61	9.67
Cyclammina sp 1																		
Cyclammina sp 2	2	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Cyclammina sp 3	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Eggerella scabra	4	0	3	2	1	0	0	0	0	0	0	0	0	0	0	0	10	1.58
Haplophragmoides sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Haplophragmoides sp 1	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Haplophragmoides bradyi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Karrerella sp	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Psammosphaera fusca	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Reophax sp 1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Reophax dentaliniformis	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.16
Reophax fusiformis																		
Reophax guttifera	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.48
Reophax scorpiurus	0	7	6	0	4	3	1	0	0	0	0	0	0	0	0	0	21	3.33
Rhabdammina cornuta																		
Saccammina spp	0	0	1	1	2	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Technitella nitida	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.32
Trochammina sp																		
Fossilising agglutinated																		
Bigenerina nodosaria	2	3	0	3	0	0	0	0	0	0	0	0	0	0	0	0	8	1.27
Pseudoclavulina crustata	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	5	0.79
Sigmoilopsis schlumbergeri																		
Siphotextularia affinis																		
Textularia agglutinans	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.32
Total live foraminifera	181	115	80	63	79	49	36	16	4	3	3	1	0	1	0	0	631	100
Nbr species	26	27	21	29	22	11	9	5	3	2	2	1	0	1	0	0	57	
Glomospira spp	2	3	13	12	19	15	5	0	0	0	0	0	0	0	0	0	71	
Ostracoda																		

Appendix C

Taxa	0B1B		0B1B^bis		0B2B		0B2B^bis		0B3B		0B4B		OB5B	
	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
Perforate														
Indet	1	0.07	2	0.60					2	1.52				
Amphicoryna scalaris	3	0.20							1	0.76				
Anomalinoides sp	1	0.07	3	0.91							2	1.40	1	1.37
Astacolus sp									1	0.76				
Baggina sp													1	1.37
Bolivina sp	6	0.53	2	0.60	3	1.20	1	0.83	4	3.03				
Bolivina sp 1					13	7.23								
Bolivina alata							3	2.48	1	0.76				
Bolivina difformis	10	0.66	7	2.11	1	0.40	1	0.83	1	0.76	1	0.70	1	1.37
Bolivina spathulata	49	3.26	44	13.29	12	4.82	8	6.61	6	4.55	2	1.40		
Bolivina striatula	2	0.13												
Bolivina subaenariensis	1	0.07												
Bolivina variabilis	5	0.33			2	0.80			1	0.76			1	1.37
Bolivinita quadrilatera	15	1.00					1	0.83			2	1.40	1	1.37
Bulimina aculeata													1	1.37
Bulimina costata	11	0.73	2	0.60	3	1.20					1	0.70	1	1.37
Bulimina inflata														
Bulimina marginata	35	2.33	5	1.51	3	1.20	4	3.31	1	0.76	2	1.40	1	1.37
Cassidulina carinata	72	4.78	47	14.20	29	11.65	11	9.09	3	2.27	2	1.40	3	4.11
Cassidulina crassa	9	0.60	4	1.21	1	0.40								
Cassidulinoides sp									1	0.76				
Ceratobulimina sp	10	0.66	3	0.91	1	0.40	2	1.65	3	2.27	2	1.40	1	1.37
Chilostomella oolina									4	3.03				
Cibicides lobatulus			1	0.30	1	0.40								
Cibicidoides pachydermus	1	0.07							1	0.76				
Cibicidoides ungerianus	2	0.13	1	0.30					1	0.76				
Coryphostoma sp	29	1.93	3	0.91							1	0.70		
Dentalina sp														
Dentalina sp 1	1	0.07												
Dentalina ariena														
Dentalina bradyensis	1	0.07					1	0.83			3	2.10	3	4.11
Dentalina subemaciata	1	0.07												
Epistominella exigua	133	8.84	30	9.06			5	4.13	1	0.76	1	0.70	2	2.74
Fissurina sp	5	0.33	2	0.60							4	2.80		
Glandulina sp	1	0.07												
Globobulimina affinis					2	0.80			60	45.45	2	1.40		
Globocassidulina subglobosa														
Gyroidina sp			1	0.30										
Gyroidina sp 1	1	0.07			1	0.40								
Gyroidina sp 2					1	0.40								
Gyroidina altiformis	6	0.40	1	0.30	1	0.40	1	0.83						
Gyroidina orbicularis	4	0.27												
Gyroidina umbonata	40	2.66	8	2.42	5	2.01	1	0.83	1	0.76	2	1.40	7	9.59
Hanzawaia boueana														
Hoeglundina elegans							1	0.83						
Hyalinea balthica	4	0.27	5	1.51	1	0.40			1	0.76				
Lagena sp			1	0.30	1	0.40								
Lagena multilatera					1	0.40								
Lenticulina sp	15	1.00			1	0.40					2	1.40	1	1.37
Lenticulina sp 1	4	0.27			2	0.80	1	0.83			1	0.70	3	4.11
Lenticulina peregrina	13	0.86	2	0.60	7	2.81	6	4.96					3	4.11
Lenticulina vortex														
Marginulina obesa														
Melonis barleeanus	41	2.72	2	0.60	1	0.40	11	9.09	7	5.30	22	15.38	4	5.48
Nonion scaphum													1	1.37
Nonionella spp	41	2.72	8	2.42	11	4.42	8	6.61	7	5.30	11	7.69	1	1.37
Nuttallides pusillus	83	5.51	1	0.30	1	0.40	2	1.65	1	0.76	1	0.70	2	2.74
Nuttallides umboniferus	8	0.53	5	1.51	5	2.01	1	0.83	1	0.76	2	1.40	2	2.74
Oolina sp	1	0.07	1	0.30									1	1.37
Parafissurina sp	1	0.07									1	0.70		
Polymorphina sp	6	0.40			1	0.40			1	0.76	2	1.40		
Pullenia quinqueloba	3	0.20	1	0.30							3	2.10	4	5.48
Robertinoides sp			1	0.30										
Rosalina sp														
Siphogenerina columellaris	46	3.06	1	0.30	3	1.20	8	6.61	5	3.79	16	11.19		
Stainforthia sp	1	0.07												
Stainforthia concava	1	0.07			1	0.40	1	0.83						
Trifarina angulosa														
Trifarina bradyi	31	2.06	5	1.51							1	0.70	2	2.74
Uvigerina elongatastriata	7	0.47	4	1.21	1	0.40	2	1.65					1	1.37
Uvigerina mediterranea	138	9.17	8	2.42	5	2.01	10	8.26	3	2.27	3	2.10	5	6.85
Uvigerina peregrina	250	16.61	10	3.02	5	2.01	2	1.65	4	3.03	11	7.69	11	15.07
Uvigerina proboscidea														
Uvigerina spp			1	0.30									1	1.37
Porcellaneous														
Biloculinella sp											1	0.70		
Cornuspira involvens	4	0.27			2	0.80	3	2.48	1	0.76	7	4.90	2	2.74
Cruciloculina sp											1	0.70		
Pyrgo subsphaerica			4	1.21										
Quinqueloculina sp	5	0.33	3	0.91	6	2.41								
Sigmoilina sp	1	0.07	1	0.30	2	0.80								
Triloculina sp			1	0.30										
Non fossilising agglutinated														
Agglut. sp A	3	0.20	1	0.30	1	0.40								
Indet	11	0.73	2	0.60	1	0.40								
Adercotryma glomerata	18	1.20	8	2.42	10	4.02	1	0.83			2	1.40	1	1.37
Ammoscalaria sp			2	0.60										
Clavulina cylindrica														
Cribrostomoides subglobosus	5	0.33	12	3.63	6	2.41	1	0.83	5	3.79	1	0.70		
Eggerella scabra	1	0.07			1	0.40					2	1.40		
Haplophragmoides sp	3	0.20	9	2.72	11	4.42			2	1.52	1	0.70		
Psammosphaera fusca	8	0.53	18	5.44	6	2.41	5	4.13			5	3.50		
Reophax sp 1	19	1.26	12	3.63	6	2.41	4	3.31						
Reophax dentaliniformis	4	0.27			1	0.40	3	2.48			3	2.10	1	1.37
Reophax fusiformis					1	0.40								
Reophax guttiferus	179	11.89	14	4.23	41	16.47	5	4.13			8	5.59		
Reophax scorpiurus	1	0.07	3	0.91	18	7.23					2	1.40	1	1.37
Reophax spiculifer	2	0.13	2	0.60										
Saccammina spp	50	3.32	1	0.30							2	1.40	1	1.37
Spiroplectinella sp			1	0.30	4	1.61								
Technitella melo	15	1.00	1	0.30			3	2.48						
Trochammina spp	19	1.26	1	0.30	1	0.40	4	3.31	1	0.76	5	3.50		
Fossilising agglutinated														
Bigenerina nodosaria	5	0.33	11	3.32	1	0.40							1	1.37
Siphotextularia affinis	1	0.07	1	0.30										
Siphotextularia concava			1	0.30										
Total live foraminifera	1505	100.00	331	100.00	249	100.00	121	100.00	132	100.00	143	100.00	73	100.00
Nbr species	65		65		49		33		30		40		34	
Ostracoda	32		5		9				2		11		3	
Glomospira spp	14				3		9		1		4		6	

	0B6B		0B7B		0B8B		0B8B^{bis}		OB9B		OB9B^{bis}		0B10B		OB10B^{bis}	
Taxa	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
Perforate																
Indet									2	0.48			2	0.52	3	0.14
Antpenoryma scalaris			1	0.32							2	0.46	4	1.04	1	0.05
Aminaceae sp			4	1.29			5	3.40	1	0.24			2	0.52	6	0.27
Astacolus sp																
Baggina sp																
Bolivina sp			1	0.32	3	1.08	1	0.68	3	0.71	4	0.91	9	2.35	4	0.18
Bolivina sp 1																
Bolivine alata													1	0.26	1	0.05
Bolivina diffusa			3	0.96	2	0.72			11	2.62	15	3.42	27	7.05	87	3.90
Bolivina spathulata			30	9.65	9	3.24	9	6.12	23	5.48	27	6.16	27	7.05	98	4.37
Bolivina striatula															2	0.09
Bolivina subaenariensis					1	0.36										
Bolivina variabilis			4	1.29					2	0.48			2	0.52		
Bolivinella quadrilatera			1	0.32	1	0.36	1	0.68	3	0.71	16	4.11	17	4.44	10	0.46
Bulimina aculeata																
Bulimina costata	1	2.70	2	0.64	2	0.72			7	1.67	1	0.23	6	1.57	8	0.36
Bulimina inflata			1	0.32												
Bulimina marginata	3	8.11	7	2.25			8	5.44	12	2.86	14	3.20	8	2.09	15	0.68
Cassidulina carinata	4	10.81	26	8.04	9	3.24	9	6.12	13	3.10	18	4.11	43	11.23	135	6.19
Cassidulina crassa			5	1.61			1	0.68	3	0.71			7	1.83	11	0.50
Cassidulinoides sp													1	0.26		
Ceratobulimina sp			2	0.64	14	5.04	4	2.72	6	1.43	1	0.23	5	1.31	18	0.87
Chilostomella oolina					1	0.36							1	0.26	1	0.05
Chrysalidinella dimorpha																
Cibicides lobatulus															1	0.05
Cibicidoides pachyderma			1	0.32												
Cibicidoides ungerianus			1	0.32	1	0.36										
Coryphostoma sp			3	0.96	1	0.36	2	1.36	1	0.24			6	1.57	8	0.36
Dentalina sp															1	0.05
Dentalina sp 1																
Dentalina anema							1	0.68								
Dentalina bradyensis			1	0.32			1	0.68							3	0.14
Dentalina subemaciata			1	0.32			1	0.68	2	0.48			1	0.26	1	0.05
Epistominella exigua			2	0.64	2	0.72	8	5.44	138	32.86	62	14.16	23	6.01	781	35.58
Fissurina sp			1	0.32			1	0.68			3	0.68	3	0.78	11	0.50
Glandulina sp					1	0.36										
Globobulimina affinis																
Globocassidulina subglobosa			1	0.32					1	0.24						
Gyroidina sp					1	0.36			2	0.48			1	0.26		
Gyroidina sp 1			1	0.32												
Gyroidina sp 2																
Gyroidina laticlava									1	0.24	1	0.23	2	0.52	5	0.23
Gyroidina orbicularis																
Gyroidina umbonata	2	5.41	2	0.64	8	2.88	2	1.36	19	4.52	18	4.11			2	
Hanzawaia boueana															2	0.09
Hoeglundina elegans			1	0.32					1	0.24					1	0.05
Hyalinea baltica			2	0.64	3	1.08	1	0.68	3	0.71					12	0.55
Lagena sp					2	0.72							1	0.26		
Lagena multilatera									1	0.24						
Lenticulina sp			8	2.57	2	0.72			1	0.24	1	0.23	4	1.04		
Lenticulina sp 1	1	2.70							2	0.48	1	0.23			2	0.09
Lenticulina peregrina			1	0.32	1	0.36	1	0.68	3	0.71	5	1.14	4	1.04	4	0.18
Lenticulina vortex															1	0.05
Marginulina obesa									1	0.23						
Miliona bateriana			5	1.61	10	3.60	1	0.68	3	0.71	1	0.23	5	1.31	19	0.87
Nonion asaphum																
Nonionella spp			3	0.96	12	4.32			6	1.43	1	0.23	3	0.78	41	1.87
Nuttallides pusillus			3	0.96	2	0.72	5	3.40	14	3.33	8	1.83	12	3.13	48	2.19
Nuttallides umbonifera			7	2.25	2	0.72			1	0.24	3	0.68			3	0.14
Oolina sp																
Parafissurina sp													2	0.52	1	0.05
Polypodina sp					3	1.08									1	0.05
Pullenia quinqueloba			1	0.32	3	1.08	3	2.04	3	0.71	1	0.23	3	0.78	84	3.83
Robertinoides sp																
Rosalina sp							1	0.68					2	0.52		
Siphogenerina columellaris	2	5.41	17	5.47	4	1.44	3	2.04			3	0.68	24	6.27	28	1.32
Stainforthia sp																
Stainforthia concava													2	0.52	3	0.14
Tritaxia exquisita															22	1.02
Trifarina bradyi			6	1.93	3	1.08	1	0.68	11	2.62	2	0.46	8	2.09	13	0.59
Uvigerina elongatastriata			4	1.29			1	0.68	20	4.76					3	0.14
Uvigerina mediterranea	5	13.51	11	3.54	10	3.60	6	4.08	7	1.67	5	1.83	15	3.92	22	1.02
Uvigerina peregrina	3	8.11	29	9.32	26	9.35	2	1.36	1	0.24	24	5.48	5	1.31	72	3.28
Uvigerina proboscidea													1	0.26	7	0.32
Uvigerina spp			2	0.64					2	0.48	1	0.23			4	0.18
Porcellaneous																
Biloculinella sp													2	0.52		
Cornuspira striolaris	1	2.70	2	0.64			2	1.36	1	0.24	1	0.23	1	0.26	7	0.32
Cruciloculina sp																
Pyrgo subsphaerica			1	0.32												
Quinqueloculina sp			3	0.96	3	1.08	1	0.68	1	0.24	5	1.14			9	0.41
Sigmoilina sp							1	0.68	3	0.71						
Triloculina sp											1	0.23				
Non fossilising agglutinated																
Aggut. sp A			5	1.61			2	1.36	2	0.48			4	1.04		
Indet															28	1.28
Adercotryma glomerata	1	2.70	8	2.57	10	3.60	5	3.40	9	2.14	9	2.05	10	2.61	36	1.79
Ammoscalaria sp			1	0.32	1	0.36	1	0.68	2	0.48	4	0.91	1	0.26	9	0.41
Clavulina cylindrica			1	0.32												
Cribrostomoides subglobosus			3	0.96	2	0.72	4	2.72	16	4.29	13	2.97	1	0.26		
Eggerella scabra			4	1.29	1	0.36					1	0.23			11	0.50
Hyperammoides sp	1	2.70	5	1.61	13	4.68	10	6.80	15	3.57					5	0.23
Psammosphaera fusca	1	2.70	10	3.22	8	2.88	5	3.40	2	0.48	3	0.68	4	1.04	35	1.59
Reophax sp 1	2	5.41	4	1.29	13	4.68	8	5.12	3	0.71	5	1.14	2	0.52	11	0.50
Reophax dentaliniformis	1	2.70	1	0.32	2	0.72	2	1.36	1	0.24					3	0.14
Reophax fusiformis									2	0.48					2	0.09
Reophax guttiferus	6	16.22	37	11.90	32	11.51	17	11.56	22	5.24	116	26.48	41	10.70	237	10.80
Reophax scorpiurus			3	0.96	35	12.59	2	1.36	2	0.48	1	0.23	1	0.26	2	0.09
Reophax spiculifer					4	1.44					1	0.23	8	2.09		
Saccammina spp									1	0.24	1	0.23				
Spiroplectinella sp			1	0.32	2	0.72							2	0.52	3	0.14
Technitella melo			3	0.96					1	0.24					7	0.32
Trochammina spp	4	10.81	13	4.18	10	3.60	3	2.04	6	1.43	20	4.56	17	4.44	194	8.84
Fossilising agglutinated																
Bigenerina nodosaria			6	1.93	1	0.36	2	1.36	1	0.24	7	1.60	1	0.26		
Spiroplectinata affins					2	0.72									1	0.05
Spirotextularia concava									1	0.24					1	0.05
Total live foraminifera	37	100.00	311	100.00	278	100.00	147	100.00	420	100.00	438	100.00	383	100.00	2195	100.00
Nbr species	15		56		45		40		52		42		45		64	
Ostracoda	1		5		11				8		8				13	
Glumospira spp	1		21		16				3		3				12	

CHAPITRE 3

Variabilité saisonnière des faunes de foraminifères benthiques à 1000 mètres de profondeur dans le Golfe de Gascogne.

Seasonal variability of benthic foraminiferal faunas at 1000 m depth in the Bay of Biscay.

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Résumé

Une étude du même type que la précédente a été faite pour une station située à 1000m de profondeur dans le Golfe de Gascogne (station A). Cette station, située à quelques dizaines de kilomètres de la station B précédemment étudiée (Fontanier et al., 2003a), a été échantillonnée 10 fois entre octobre 1997 et avril 2001 dans le but d'étudier la variabilité temporelle et spatiale des faunes de foraminifères benthiques vivants des fractions 63-150 µm et >150 µm. Deux duplicata de carottes sont disponibles. Comme sur le site à 550m de profondeur, la variabilité spatiale à méso-échelle est substantielle entre les duplicatas, mais elle ne surpasse pas la variabilité temporelle. La zone d'étude est caractérisée par des blooms de printemps long de deux mois et des blooms d'automne plus hypothétiques, lesquels induisent des enrichissements périodiques en matière organique labile du sédiment superficiel. En avril 2001, les apports de phytodétritus ont un impact remarquable sur les processus diagénétiques en provoquant une dimunution de l'oxygénation des eaux de fond et une remontée significative des fronts redox vers l'interface eau-sédiment. Les faunes de foraminifères répondent aux blooms de printemps et d'automne par des augmentations d'effectif d'espèces opportunistes. Dans la fraction >150 µm, *Uvigerina peregrina*, *Uvigerina mediterranea* et, à moindre degré, *Hoeglundina elegans* se développent et se reproduisent préférentiellement dans des microhabitats endopéliques peu profonds au cours des périodes eutrophes des blooms. Les changements saisonniers dans la fraction 63-150 µm sont beaucoup moins évidents ; néanmoins, *Nuttallides pusillus* et *Uvigerina peregrina* présentent des comportements semble-t-il opportunistes. Les changements saisonniers à 1000 mètres de profondeur sont synchrones avec ceux enregistrés à 550 mètres de profondeur (station B). A 550 comme à 1000 mètres de profondeur, les communautés de foraminifères benthiques répondent aux dépôts de phytodétritus pendant les périodes eutrophes. Néanmoins, l'amplitude des variations de densité ainsi que les changements saisonniers de composition faunistique diffèrent entre les deux stations. En considérant que les flux exportés de matière organique aux deux stations sont théoriquement différents saisonnièrement et annuellement, nous proposons un modèle conceptuel pour préciser nos interprétations concernant la dynamique des communautés de foraminifères benthiques à ces deux stations.

Mots-clés : Foraminifère benthique ; Microhabitat ; Saisonnalité ; Patchiness ; Opportunisme ; Bloom phytoplanctonique ; Flux organique.

Abstract

A 1000 metres deep station from the Bay of Biscay (station A) was sampled 10 times between October 1997 and April 2001 in purpose to study the temporal and spatial variability of live foraminiferal faunas in the 63-150 µm and >150 µm size fractions. This station is close to the previously studied station B (Fontanier et al., 2003a). Two duplicate cores are available at station A. Although meso-scale spatial variability, as suggested by duplicate cores, is substantiel, patchiness does not overshadow temporal variability. The study area is marked by two months long spring blooms and short, putative, autumn blooms that induce labile organic matter enrichment of the upper sediment. Episodic exportation of phytodetritus has only a remarkable impact on early diagenetic processes in April 2001. There, bottom water oxygenation is lower and the zero oxygen boundary shallows up to sediment-water interface. Foraminiferal faunas respond to spring and autumn blooms by a frequency increase of opportunistic taxa. In the >150 µm size fraction, *Uvigerina peregrina*, *Uvigerina mediterranea* and, in a lesser degree, *Hoeglundina elegans* preferentially reproduce and thrive in shallow infaunal microhabitats that are seasonally enriched in phytodetritus. Seasonal changes in the 63-150 µm size fraction are more less straightforward; nevertheless, *Nuttallides pusillus* and *Uvigerina peregrina* show an opportunistic tendency. Seasonal changes of foraminiferal faunas at our 1000 m deep station are synchronous with the temporal changes recorded in the 550 m deep station B. Nevertheless, although foraminiferal faunas respond at both stations to phytodetritus deposits in eutrophic periods, the range of density changes and the faunistic composition seasonal changes differ at both study areas. Because the annually and seasonally exported organic matter flux is surely lower at our 1000 m deep station than at the 550 m deep station, we suggest that that the decrease with depth of the vertically advected organic matter flux along a slope transect is a fundamental and major parameter structuring the composition and seasonal dynamics of foraminiferal faunas throughout the year. We propose a simple conceptual model to sum up our conclusions about those both stations.

Keywords: Benthic foraminifera; Microhabitat; Seasonality; Patchiness; Opportunism; Bloom; Organic flux.

Introduction

Deep-sea heterotroph benthic foraminifera are well known to respond to seasonal phytodetritus deposits at the sea floor (e.g. Gooday, 1988; Kitazato and Ohga, 1995; Kitazato et al., 2000; Duijnstee et al., 2001). Various opportunistic foraminiferal taxa are able to quickly colonize and feed on freshly deposited phytoplankton aggregates in deep-sea environments (Gooday, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Barmawidjaja et al., 1992; Gooday, 1993; Kitazato and Ohga, 1995; Jannink et al., 1998; Silva et al, 1996; Gooday and Rathburn, 1999; Kitazato et al., 2000; Duijnstee et al., 2001, Moodley et al., 2002). Recently, experimental laboratory studies on deep-sea foraminiferal taxa have confirmed the response of foraminiferal taxa to simulated phytoplankton pulses (Heinz et al., 2001; 2002; Ernst, 2002). Deep-sea foraminiferal faunas appear to play a major role in the cycling of organic carbon and other biolimiting elements (e.g. Nitrogen, Phosphorous) and in the packaging of freshly deposited organic matter (Moodley et al., 2002).

In a paper discussing the seasonal and small-scale spatial variability of deep-sea foraminiferal faunas at 550 metres deep in the Bay of Biscay, Fontanier et al. (2003a) suggest a strong linkage between the phytoplankton bloom regime and the seasonal dynamics of the foraminiferal faunas. Some weeks after chlorophyll-a production peaks in the surface waters (spring and autumn bloom), opportunistic taxa (e.g. *Epistominella exigua*, *Uvigerina peregrina*) exhibit standing stock increases in the organic matter-enriched surface sediment. The foraminiferal response is mainly restricted to the sediment surface and the first cms, into which phytodetritus aggregates are bioturbated. In the deeper part of the sediment, highly specialized taxa (e.g. *Melonis barleeanus*, *Globobulimina affinis*), which live preferentially in dysoxic and anoxic micro-biotopes, show only a minor seasonal variability. Those taxa can obviously not compete for labile food particles in the surficial and shallow infaunal niches and prefer the more stable (trophic and chemical) conditions deeper in the sediment. As suggested by Fontanier et al. (2003c), they may either live in symbiosis with deep chemiolithotroph bacterial consortia, or feed on heterotroph bacteria.

In this paper we investigate the temporal variability of live foraminiferal faunas (63-150µm, >150µm) collected from a considerably deeper open slope station (Station A, 1000 m deep) from the Bay of Biscay (44°10'N, 2°20'W; Fig. 1). We sampled our station 10 times between October 1997 and April 2001, and collected 12 cores, including two couples of duplicates. These two duplicate cores allow us to assess the importance of meso-scale spatial variability of foraminiferal faunas in comparison to temporal variability. As described by

Fontanier et al. (2003a), the Bay of Biscay is under the influence of a typical temperate, mid latitude seasonal primary production regime marked by a spring and an autumn bloom. Our main intention is to determine whether the interannual and seasonal primary production oscillations in the surface waters provoke important short term variability of the standing stocks and composition of the benthic foraminiferal faunas. To this end, we compare our faunal analyses with geochemical data of the upper sediment and with chlorophyll-a concentration values in the surface waters throughout the study period. We used on-line data archives of the Joint Research Centre (SeaWIFS data) to estimate chlorophyll-a concentration changes during the study period (Fig. 2).

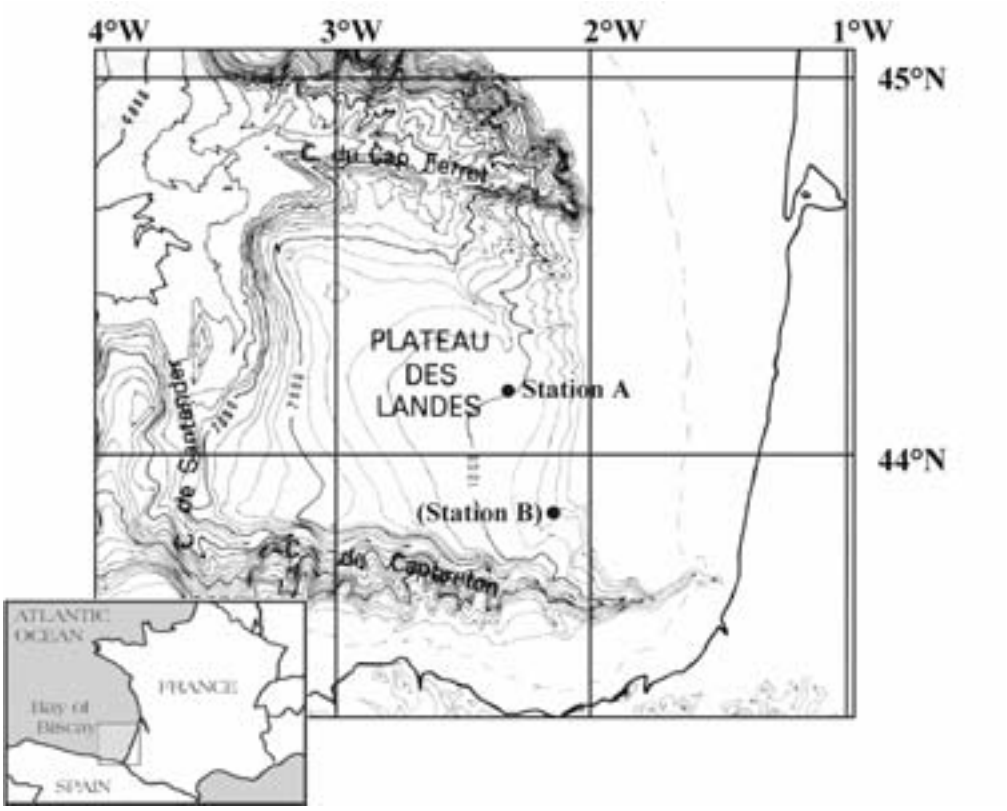


Fig. 1 Study area, bathymetry and geographical position of station A. Station B, discussed in the text, is also presented (Fontanier et al., 2003a).

Study area

Hydrographical setting

Vertical hydrological structures and major physiographic patterns of the study area are described in detail in Fontanier et al. (2002; 2003a). The Bay of Biscay is occupied by waters

that are disconnected from the North Atlantic drift. Surface waters enter generally into the Bay from the North, off Brittany (France), and turn roughly clockwise during two years within the semi-enclosed basin of the Bay of Biscay, before joining the Atlantic circulation off Galicia (Spain) (Tréguer et al., 1979). Our station A (1000 metres depth) bathes in Mediterranean Waters (MW), which are found between 800 and 1200 metres deep. They spread between upper North Atlantic Central Water (NACW) and lower Northern Atlantic Deep Water (NADW) (Ogawa et Tauzin, 1973, Vangrieshem, 1985). The Mediterranean Waters are characterized by a high salinity (35.80-35.85, Le Floch, 1968), and rather low oxygen concentration values (3.8 ml/l, Le Floch, 1968). Durrieu de Madron et al. (1999) recorded salinity of about 35.75 and temperature of about 9.5°C for MW at 1000 m depth in the Northern Cap-Ferret Canyon.

Station A is situated on the Plateau des Landes (Fig.1), which is a 200-2000 m deep continental slope area, bounded by two canyon systems in the North and South. At our open-slope station A (just as in station B; see Fontanier et al., 2003a), vertical advection of fresh organic matter (phytoplankton productivity) from surface waters is considered as the main source of exported labile organic compounds. Nevertheless, as suggested by Heussner et al. (1999), the upper part of the Plateau des Landes (<1000 m deep) may also act as a potential source of reworked sediment transported into the Northern Cap-Ferret Canyon head by strong along-slope currents. Thus, sea floor resuspension may be an important phenomenon affecting the sedimentary deposits in our study area (Heussner et al., 1999).

Primary production patterns in the north-eastern Atlantic

The temporal variability of primary production in the Bay of Biscay is described by Fontanier et al. (2003a). The Bay of Biscay is characterized by phytoplankton blooms in boreal spring, summer and autumn (Tréguer et al, 1979; Froidefond et al., 1996; Laborde et al., 1999). Spring blooms present the highest phytoplankton production of the year. They last for about two months in March, April and May (Boucher, 1985; Laborde et al., 1999, Fontanier et al., 2003a). They usually represent of a succession of individual bloom events consisting of different phytoplankton groups (Tréguer et al., 1979, Lampert, 2001). Upwelling cells are active in summer along the shelf-break off the French coasts; they induce important coccolithophorid blooms (Holligan et al., 1983; Fernandez et al., 1993; Froidefond et al., 1996, Beaufort and Heussner, 1999). The occurrence of autumn bloom is unclear, and only few papers deal with it. Autumn bloom corresponds to sub-surface primary production

triggered by in situ nutrient regeneration (Tréguer et al., 1979, Sellmer et al., 1998). According to Sellmer et al. (1998) who studied a BIOTRANS site (47°N/20°W), short fall bloom consisting in autotrophic dinoflagellates with small amount of diatoms occur at about 30 to 50 metres deep in Autumn 1996.

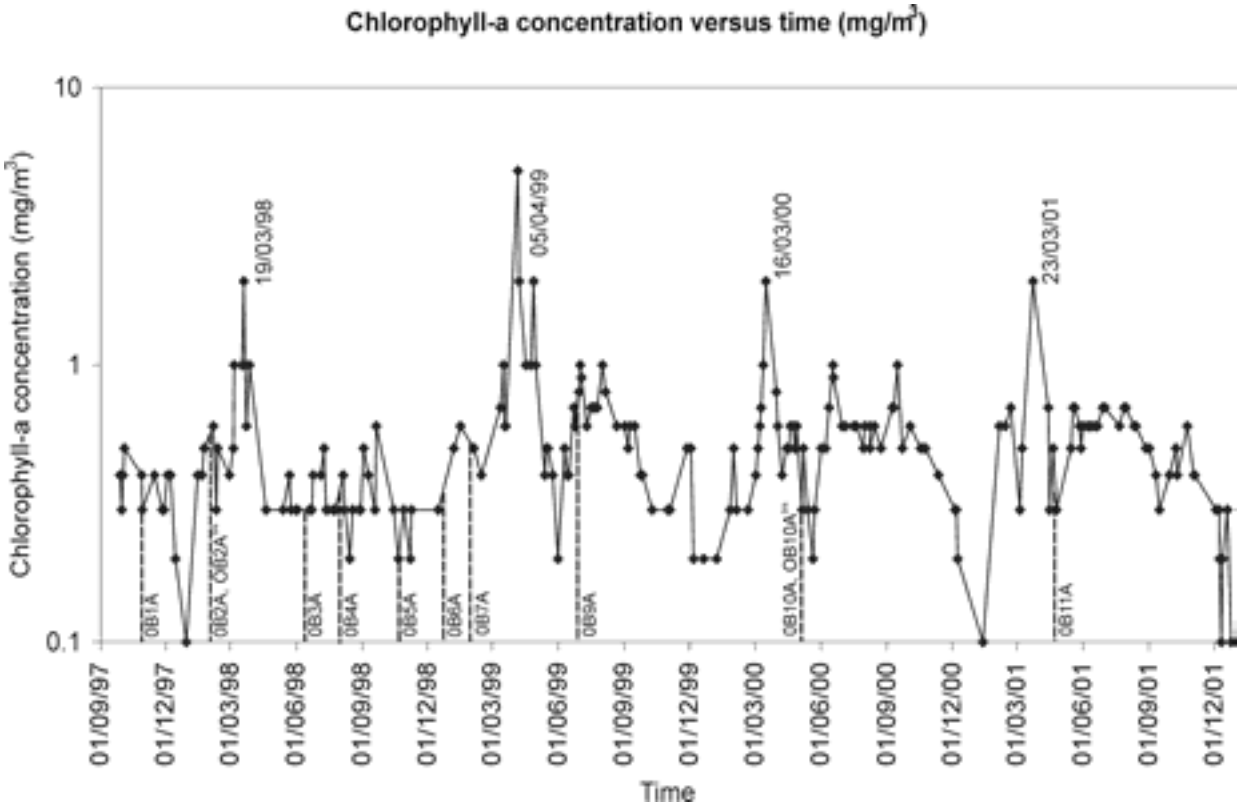


Fig. 2 Chlorophyll-a concentrations in the surface waters above our station A, between October 1997 and April 2001 (estimates based on SEAWIFS images). Vertical dotted/dashed lines indicate when the sampling cruises took place.

As suggested by Fontanier et al. (2003a), few quantitative data are available on primary production in our study area. Primary production has been estimated between 0.7 - 1.2 g C/m^2/day for the spring bloom of 1990 and 1991 in the Cap-Ferret canyon area (Laborde et al., 1999). Daily primary production in autumn 1990 was about 0.3 g C/m^2/day (Laborde et al., 1999), which is very close to the values of 0.3 - 0.4 g C/m^2/day recorded during the autumn bloom of 1972 by Le Corre and Tréguer, 1976. Laborde et al. (1999) estimate the total annual primary production between 145 and 170 gC/m²/yr, which is roughly in the range of values proposed by Antoine et al. (1996) on a the basin-wide scale (150-200 gC/m²/yr).

Material and Methods

As explained in Fontanier et al. (2003a), we used on-line data archives of the Joint Research Center (European Commission) to estimate chlorophyll-a concentrations (SeaWIFS data) in the study area for the duration of our sampling period (October 1997 to April 2001; Fig. 2). The use of this method has the inconveniency that weather conditions strongly affect the availability of images. As a consequence, we have no precise idea about the temporal variability of chlorophyll-a during late autumn and early winter.

Station A (44°10'00 N, 2°20'00 W; Fig. 1) was sampled 10 times with a Barnett multi-tube corer (Barnett et al., 1984), allowing sampling of the first decimetres of the sediment, the overlying bottom waters, and an undisturbed sediment-water interface (Table 1). Free waters were collected immediately after core recovery for dissolved O_2 measurements by the Winkler titration method (Strickland and Parsons, 1972). Profiles of pore water O_2 were obtained on board with a cathode-type mini-electrode (Revsbech and Jørgensen, 1986; Helder and Bakker, 1985; Revsbech, 1983). The temperature was maintained stable with an insulating device. This operation was completed in duplicate within 30 minutes after core recovery. Subsequently, the core used for O_2 profiling was sliced into thin horizontal sections (every 0.5 cm for the top 2 cm, 1 or 2 cm below) within 1 hour and 30 minutes. For every level a sub-sample was centrifuged under N_2 at 5000 rpm for 20 min in order to collect pore waters. Two aliquots of water were filtered (0.2 µm) and frozen at -25°C for nutrient analyses. Interstitial water compounds were analyzed by techniques adapted for small volumes of samples (Anschutz et al., 1999; Hyacinthe et al., 2001).

For faunal analysis, one entire 72 cm^2 core was sliced horizontally for each sampling, usually every 0.25 cm for the first cm of sediment, every half cm between 1 and 4 cm depth, and every cm between 4 and 10 cm. Only core OB1A was sampled slightly differently. For assessing the extent of spatial heterogeneity, the two available duplicate cores were analyzed as well. This concerns samples $OB2A^{bis}$ (normally sampled) and $OB10A^{bis}$ (top 1 cm sampled in 0.5 cm intervals; 1-5 cm interval sampled in 1 cm slices; 5-10 cm interval sliced in two 2.5 cm samples). Each duplicate pair was recovered from two different multi-corer deployments. Sediments storage and preparation were described by Fontanier et al. (2002). Foraminifera belonging to the >150 µm fraction were studied along the 10 cm long cores, whereas foraminifera from the 63-150µm fraction were only studied in the first half cm of the sediment. During picking, semi-quantitative observations were made on the residual parts of

>150 µm fractions to evaluate some perspicuous sedimentary components (phytodetritus and zooplankton compounds; Table 1).

Live foraminiferal individuals were colored with the Rose Bengal staining technique (Walton, 1952; Bernhard, 1988). Several authors (e.g. Bernhard, 1988; Corliss and Emerson, 1990; Bernhard, 2000) dealt with the potential problems of the Rose Bengal staining method. Protoplasm of dead foraminiferal individuals that has been temporarily preserved from degradation in anoxic parts of the sediment may still be colored. Furthermore, coloration in translucent tests of dead foraminifera may be due to the presence of organisms inhabiting one or several chambers of the shell (nematodes, bacterial consortia). As a consequence, we used the same strict staining criteria as those described in Fontanier et al. (2002). Non-transparent agglutinated and miliolid taxa were broken in order to inspect the test interior.

Cores Station A	Date	O2 concentration (µmol/l)	Oxygen penetration Depth (mm)	Whitish filamenteous and/or amorphous phytodetrital aggregates	Radiolarians
OB1A	10/25/1997	196	18	ND	ND
OB2A/OB2A^{bis}	1/31/1998	201	31	-/-	--/--
OB3A	6/7/1998	192	32	-	--
OB4A	7/23/1998	189	30	--	--
OB5A	10/17/1998	200	32	+	--
OB6A	12/6/1998	193	36	-	--
OB7A	1/23/1999	196	34	-	--
OB9A	6/22/1999	200	33	-	++
OB10A/OB10A^{bis}	4/30/2000	199	29	++/++	++/++
OB11A	4/16/2001	138	8	+	+

Cores Station A	Foraminiferal density (/72cm²) (63-150 µm)	(>150 µm)	Specific richness (63-150 µm)	Specific richness (>150 µm)
OB1A	1115	517	48	38
OB2A/OB2A^{bis}	834, 1543	443, 343	37, 38	51, 44
OB3A	695	225	58	33
OB4A	483	177	34	28
OB5A	544	228	37	36
OB6A	95	305	19	35
OB7A	141	411	19	39
OB9A	603	509	48	38
OB10A/OB10A^{bis}	523, 963	216, 539	26, 31	54, 61
OB11A	881	639	43	53

Table 1 Sampling dates, bottom water oxygen concentration, depth in the sediment of the zero oxygen level, foraminiferal density and specific richness in 63-150 and >150 µm fraction, and semi-quantitative analysis performed on the sedimentary residual parts of the first quarter of sediment for 12 cores at station A for the 10 sampling cruises; Phytoplankton and zooplankton components were observed and described according to the following classes: ++ abundant, + common, - rare, -- absent. Bottom water oxygen concentration is measured 5 mm above the sediment-water interface. Foraminiferal density is expressed as number of individuals per 72 cm².

Fragments of the very fragile arborescent agglutinating foraminiferal fragments (such as *Hyperammina* spp., *Bathysiphon* spp. and most species of *Rhabdammina* spp.) were not included in the quantitative analyses. Our taxonomical framework is given in Appendix A. All foraminiferal census data are listed in Appendices B and C. Census data of core OB1A (>150 μm fraction) have already been presented in Fontanier et al. (2002) (see Chapter 1). The total density of the live foraminiferal fauna total density has been determined by summing up the number of individuals for all levels between 0 to 10 cm depth for the >150 μm fraction, but only for the 0-0.5 cm interval for the 63-150 μm fraction. Thus, the total density per core is expressed as number of individuals found at and below a 72 cm² sediment surface. In all graphs depicting the vertical distribution of the foraminifera in the >150 μm fraction (Figs. 5a-l), the faunal densities have been standardised for a 50 cm^3 sediment volume.

The average living depth (ALD_x, Jorissen et al., 1995) seems the best way to describe the overall vertical distribution of the total foraminifera fauna or of individual taxa, and to get a general idea about the microhabitat patterns. To this end, we used the methods and formula presented in Fontanier et al. (2003a). For all stations, ALD_{10} was calculated for the whole fauna, as well as for individual taxa, on the basis of the numbers of stained individuals found in the successive sediment slices. Isolated individuals separated from the main population by more than 1 cm of "sterile" sediment (without live individuals of the studied taxon) were not integrated in the calculations of the ALD_{10}. In Appendix B, those individuals are present between brackets. We suppose that such isolated individuals have been transported downward (outside their normal microhabitat) by bioturbation, or correspond to dead organisms that have been counted erroneously**.**

In order to evaluate the differences between duplicate and temporally distinct samples, a non-standardised principal component analysis (Davis, 1986) was applied for both size fractions, using the percentages of all taxa with an occurrence of more than 2.5% in at least one sample.

Results

Chlorophyll-a concentrations from October 1997 to April 2001

At the basin-wide scale of the Bay of Biscay, higher Chlorophyll-a concentrations in the surface waters (≥ 1 mg/m^3) are systematically recorded at the end of winter and the beginning of boreal spring (second half of March and April). As shown by our observations and as suggested by Tréguer et al. (1979), Laborde et al. (1999) and Fontanier et al. (2003a), spring blooms last for about two months till June. Also in July and August, enhanced Chlorophyll-a concentrations can be noticed over the shelf and shelf-break off French coasts. Large plume-like structures with high Chlorophyll-a concentration spread from the highly productive shelf-break areas seaward into the open ocean. Such structures are rather stable for several weeks and generally disappear at the end of boreal summer (in September). Those estival structures do not exhibit the same magnitude and geographical distribution throughout the investigated years; they are spatially limited in summer 1998. They may be associated with well known coastal upwelling cells that are mainly related to Northern winds blowing along the coast (Holligan et al., 1983; Froidefond et al., 1996). As suggested by Beaufort and Heussner (1999) and as shown by our observations, the spreading of the upwelling systems and the intensity of the accompanying phytoplankton production may present a strong interannual variability. In autumn and winter, oceanic waters of the Bay of Biscay become oligotrophic with very low Chlor-a concentrations and minima were recorded in late autumn and early winter. No Chlorophyll-a maximum is recorded in surface waters in autumn periods during our 3.5 years long study. It does not mean that autumn blooms do not occur in the Bay of Biscay. Indeed, as suggested by Sellmer et al. (1998), autumn bloom may be related to sub-surface or deep Chlorophyll-a maximum that is not detectable on satellite images of surface waters.

At our station A (Fig. 2), the temporal variability of chlorophyll-a concentrations in the overlying surface waters exhibit the same trends as those previously described for the whole basin. The spring blooms are recurrent throughout the three and half years of our investigation. They are associated with eutrophic conditions prevailing in the surface waters of our study area (≥ 1 mg/m^3). Chlorophyll-a maxima are recorded on March 19th 1998, on April 5th 1999, on March 16th 2000 and on March 23rd 2001. In estival periods (except for summer 1998, when primary production stays weak through summer), station A is under the moderate influence of the mesotrophic plume-like structures that spread from the highly productive French shelf-break area. Chlorophyll-a concentration ranges from 0.6 to 0.8 mg/m^3. From late summer to early winter, chlorophyll-a concentrations generally decrease gradually to oligotrophic values (0.2 mg/m^3). No autumn bloom is detectable in surface waters.

Organic sedimentary components

Semi-quantitative observations of the sieve residues of the first half centimetre of the >150 μm fraction are presented in Table 1. No observation could be performed for October 1997 (OB1A core) because the samples have been stored dry after picking, and therefore, hypothetical organic compounds have not been preserved. However, as observed for OB1B (core collected at station B in October 1997; Fontanier et al., 2003a), organic matter deposits related to a putative 1997 autumn bloom may also have occurred at station A (although there are no increased chlorophyll-a values here) but are not detectable in samples of OB1A.

Cores sampled in June 1999, April 2000 and April 2001 (OB9A, OB10A, OB10A^{bis} and OB11A respectively) contain high amounts of whitish amorphous aggregates and abundant radiolarians. Because the spring bloom started several weeks before these three cruises (Table 1, Fig. 2), we suppose that those organic detritus result from the vertical advection of spring bloom zooplankton and phytoplankton remains to the sea floor. OB9A was indeed collected 7 weeks after the 1999 spring bloom. OB10A and OB10A^{bis} were collected 6 weeks after the 2000 spring bloom. OB11A was collected 3 weeks after the 2001 spring bloom. Phytodetritus deposits have been observed for the same period at the 550 metres depth station B close to our study area (June 1999 and April 2000; Fontanier et al., 2003a) (Fig. 1). Cores collected during summer and early autumn (OB3A, OB4A and OB5A) do not exhibit any zooplankton and phytoplankton remains that might be related to enhanced surface water primary production.

Oxygen concentration and redox conditions of interstitial waters

Bottom water oxygen concentrations measured 5 mm above the sediment-water interface (Table 1) vary from 138 to 201 μmol/l (from 3.07 to 4.47 ml/l). At the sediment-water interface, oxygen concentration values range from 20 to 201 μmol/l (respectively in April 2001 and in January 1998). The zero oxygen boundary depth is only 8 mm in April 2001 (OB11A). For the other cores, oxygen concentration profiles from the sediment-water interface to deeper layer are rather similar, although the exact zero oxygen boundary varies from 18 mm (0B1A, October 1997) to 36 mm depth (OB6A, December 1998) (Fig. 3).

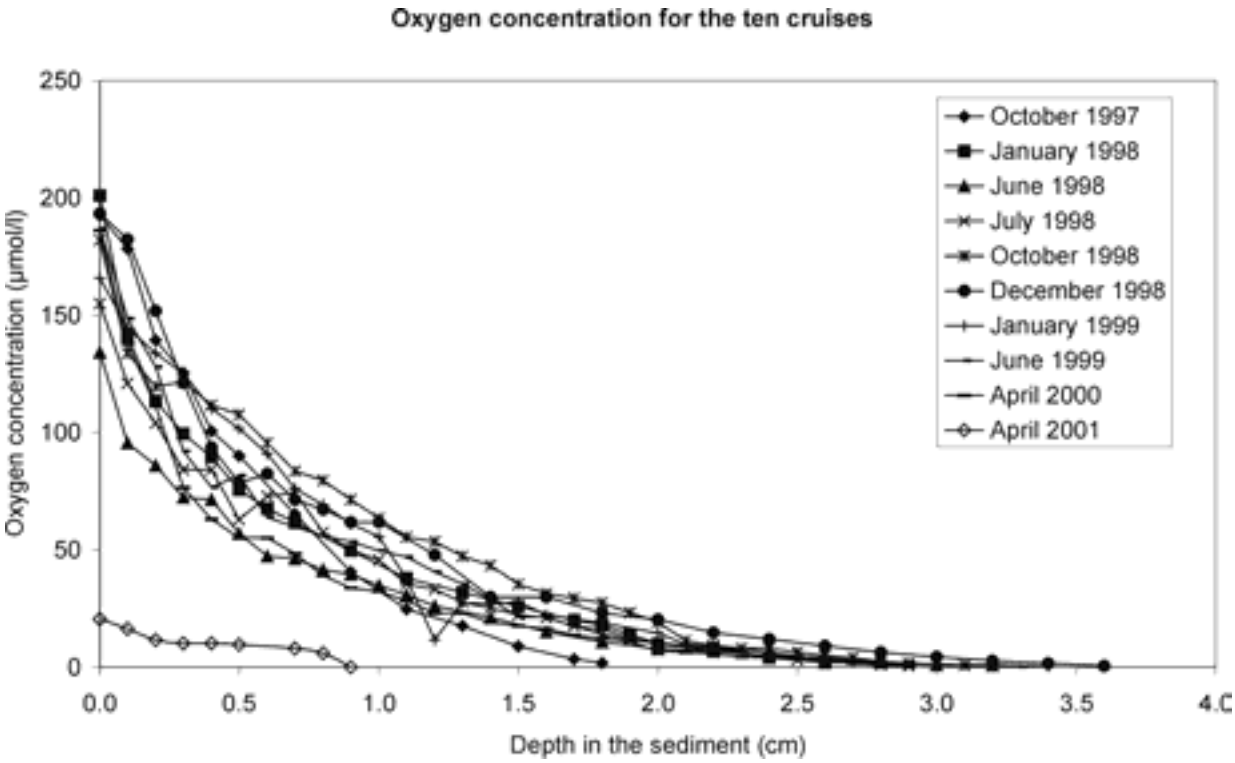


Fig. 3 Dissolved oxygen concentrations in the sediment for the ten cruises.

Faunal density and number of taxa

In the >150 µm fraction, foraminiferal densities vary from 177 to 963 individuals per 72 cm^2 core (Table 1). Maxima of 963 and 639 individuals are recorded in April 2000 ($OB10A^{bis}$) and in April 2001 (OB11A) respectively. The minimum value is found in July 1998 (OB4A, 177 individuals par core). For the 63-150 µm fraction, foraminiferal densities (only for the topmost 0.5 cm) vary from about 95 to 1543 individuals (Table 1). Maxima of 881, 1115 and 1543 individuals are recorded in April 2001 (OB11A), October 1997 (OB1A) and in January 1998 ($OB2A^{bis}$) respectively. Minimum values are found in December 1998 (OB6A, 95 individuals) and in January 1999 (OB7A, 141 specimens). Part of this large variability, however, may be due to the variable sample size of the first 0.5 cm in the case of oblique sediment surfaces.

In the >150 µm fraction, perforate foraminifera form the main faunal component (64% to 78% of the fauna). Non fossilising agglutinated taxa account for 20 to 36 %. Miliolids (maximum 6.5%) are rare in all cores. Fossilising agglutinated taxa are almost absent. Also, in the 63-150 µm fraction, perforate taxa form the largest group (62-87%). Non fossilising agglutinated foraminifera represent between 12 and 36% of the total fauna. Miliolids and fossilising agglutinated foraminifera account for less than 2.5% of the foraminiferal faunas.

The number of taxa in the >150 µm fraction varies from 28 (July 1998, OB4A) to 61 (April 2000, OB10A^{bis}), with a clear positive correlation to faunal density. In the 63-150 µm fraction, for which only the topmost 0.5 cm was studied, the number of taxa varies from 19 (December 1998, OB6A) to 58 (June 1998, OB3A), with no clear correlation to the faunal density.

Faunal composition and microhabitat

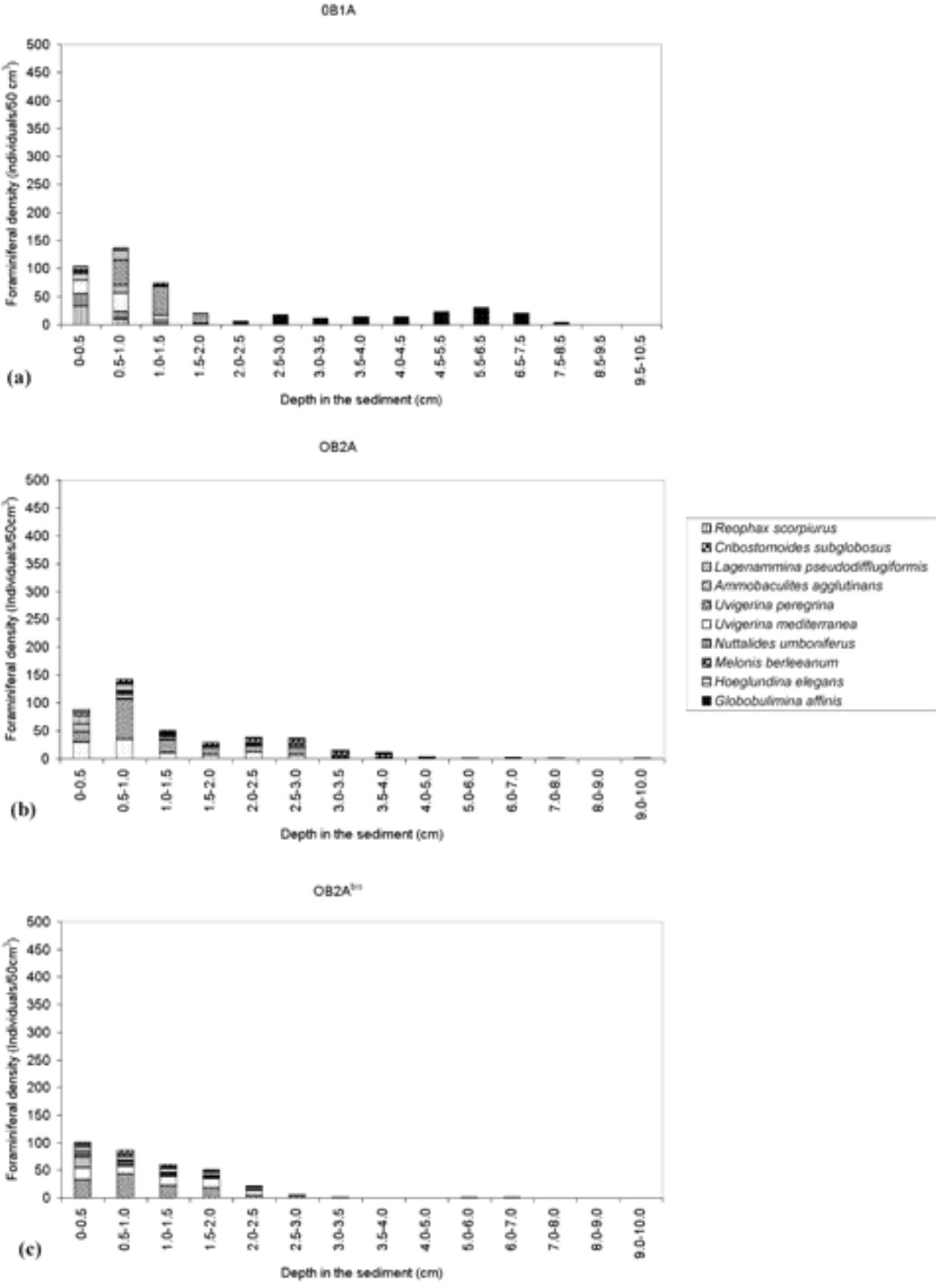
1. >150µm fraction

Live foraminiferal faunas are normally concentrated in the upper 0.5 to 1.0 cm of the sediment (Fig. 4a-l). The highest superficial foraminiferal density is recorded in April 2001 (OB11A; ~400 specimen/50 cm^3). In one of the duplicate cores collected in April 2000, we record a spectacular subsurface density maximum in the 0.5-1 cm interval (OB10A^{bis}; ~450 specimen/50 cm^3). In most cores, foraminiferal density quickly decreases down to 2 cm depth. Consequently, for most of the cores, the ALD_{10} of the total fauna is between 0.5 and 1.5 cm. The shallowest microhabitat depth is observed in June 1998 (ALD_{10} = 0.5 cm). In the deeper sediment layers, foraminiferal densities increase moderately in October 1997 (OB1A) and in April 2001 (OB11A). There, monospecific assemblages consisting of *Globobulimina affinis* individuals appear in anoxic sediment (with maximum values close to 30 individuals/50 cm^3). In June 1999 (OB9A), a deep plurispecific foraminiferal assemblage is found in 7-10 cm depth interval. As a consequence, maximum ALD_{10} values are found in October 1997 (OB1A; 1.9 cm) and June 1999 (OB9A; 2.0).

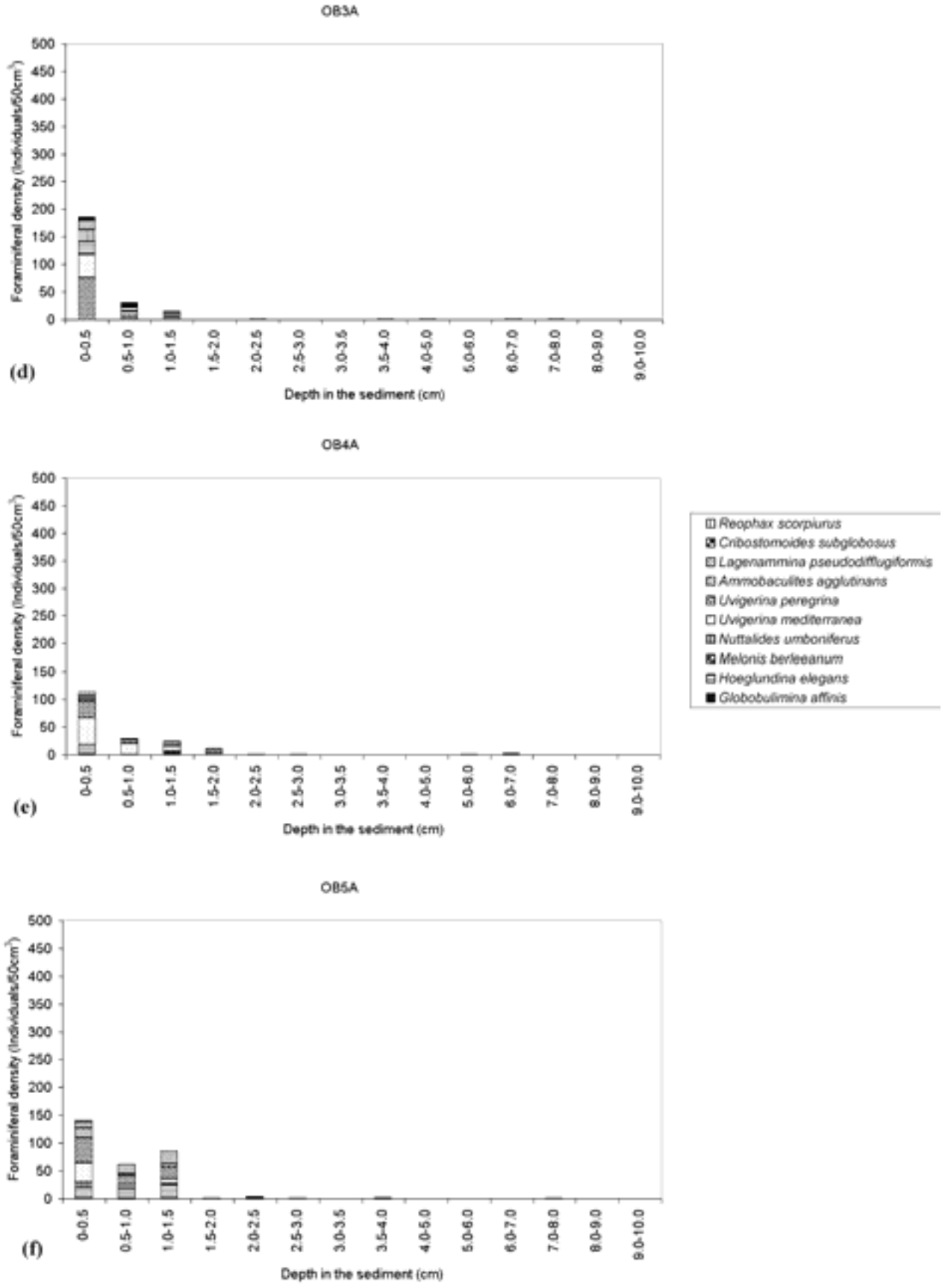
Uvigerina peregrina dominates the faunas in most cores (Appendix B); its relative abundances range from 14.0 to 27.1% with maximum percentages recorded in January 1998 (both replicate cores), June 1998 (OB3A), April 2000 (OB10A) and April 2001 (OB11A). Minimum values are recorded in the second replicate core collected in April 2000 (OB10A^{bis}), in October 1997 (OB1A) and in December 1998 (OB6A). *Uvigerina mediterranea* is the second dominant taxon. It exhibits its highest relative abundance in April 2000 (OB10A^{bis}, 39.6%), and its lowest percentage in October 1997 (OB1A; 8.7%). As the third dominant taxon, *Hoeglundina elegans* presents percentages ranging from 4.1 to 19.0%. Low values are recorded in October 1997 (OB1A) and January 1998 (both replicate cores) whereas high percentages occur in December 1998 and in January 1999. *Lagenammina pseudodifflugiformis* ranges from 2.3 to 10.5% with the highest value recorded in October

1998 (OB5A). *Globobulimina affinis* exhibits spectacularly high percentages in October 1997 (OB1A; 26.5%) and April 2001 (OB11A; 7.0%). *Ammobaculites agglutinans*, *Melonis barleeanus*, *Reophax scorpiurus*, *Cribrostomoides subglobosus* and *Nuttallides umboniferus* are minor species with percentages generally below 10.0%.

ALD values for most taxa are presented in Table 2. *Nuttallides umboniferus* (overall weighed ALD_{10} = 0.56 cm), *Reophax scorpiurus* (overall weighed ALD_{10} = 0.57 cm), *Ammobaculites agglutinans* (overall weighed ALD_{10} = 0.72 cm), *Cribrostomoides subglobosus* (overall weighed ALD_{10} = 0.74 cm) and *Hoeglundina elegans* (overall weighed ALD_{10} = 0.86 cm) consistently present shallow infaunal microhabitats. *Uvigerina mediterranea*, *Uvigerina peregrina* and *Lagenammina pseudodifflugiformis* exhibit overall weighed values of ALD_{10} close to 1cm depth (respectively 0.96, 0.99 and 1.04 cm). For all these taxa, microhabitats are rather constant throughout the study period (Table 2). The exception is the core collected in June 1999 (OB9A). There, the occurrence of a consistent number of individuals belonging to these usually superficially living species in the deeper part of the sediment is apparently related to the presence of an irrigated burrow between 5 and 9 cm depth. This induces a significant deepening of ALD_{10} values (Table 2, Fig.5h). *Melonis barleeanus* with a weighed ALD_{10} of 2.05 cm lives at an intermediate/deep infaunal microhabitat. In the years of our study the microhabitat of *M. barleeanus* varies over a rather wide depth range (1.0-3.1 cm), but always coincides with weakly oxygenated conditions. *Globobulimina affinis* occupies deep infaunal niches in anoxic sediments (overall weighed ALD_{10} = 4.05 cm). Its microhabitat ranges from 3.6 to 5.6 cm.



Figs. 4a-l Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for 12 available cores.



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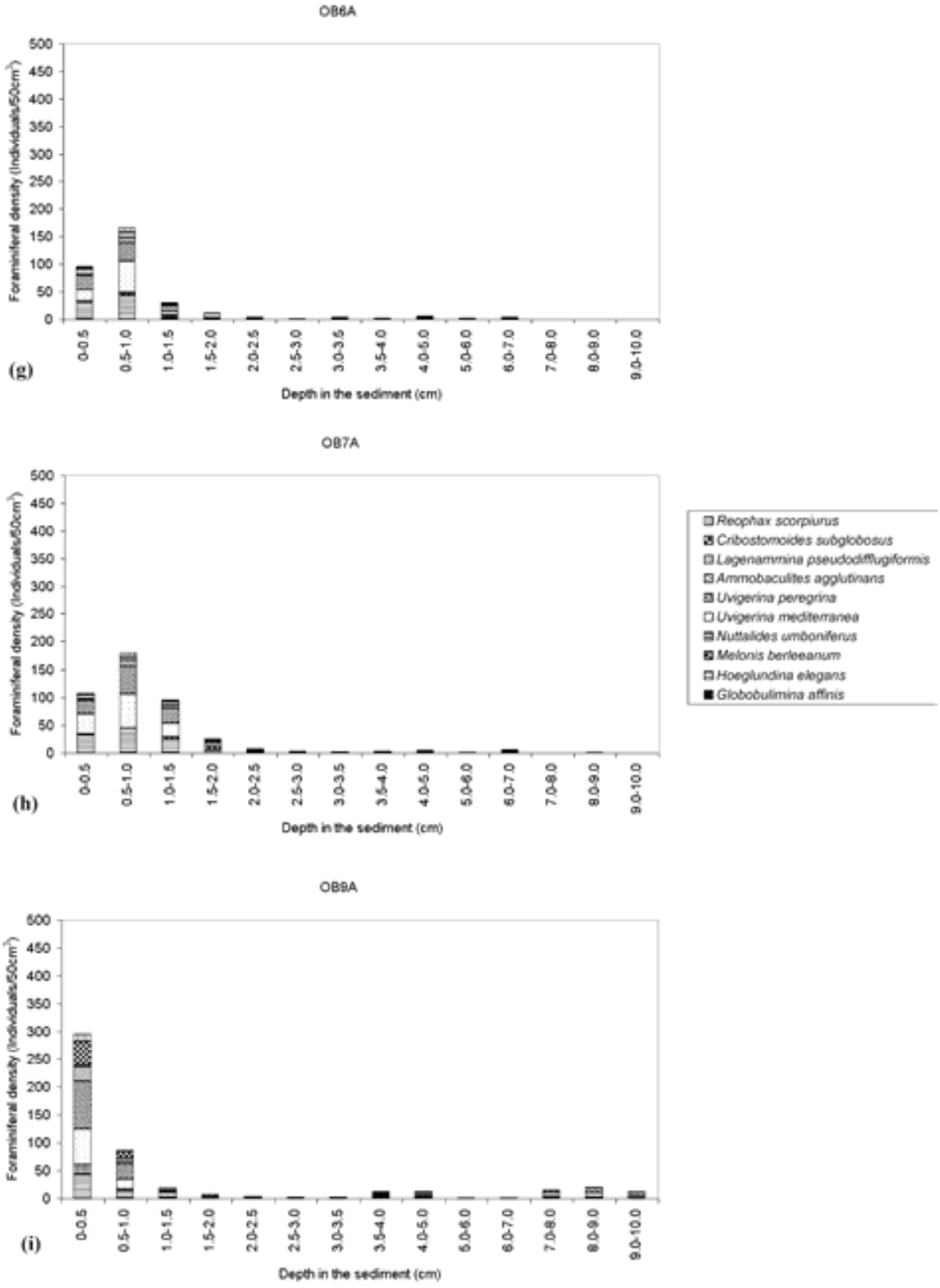

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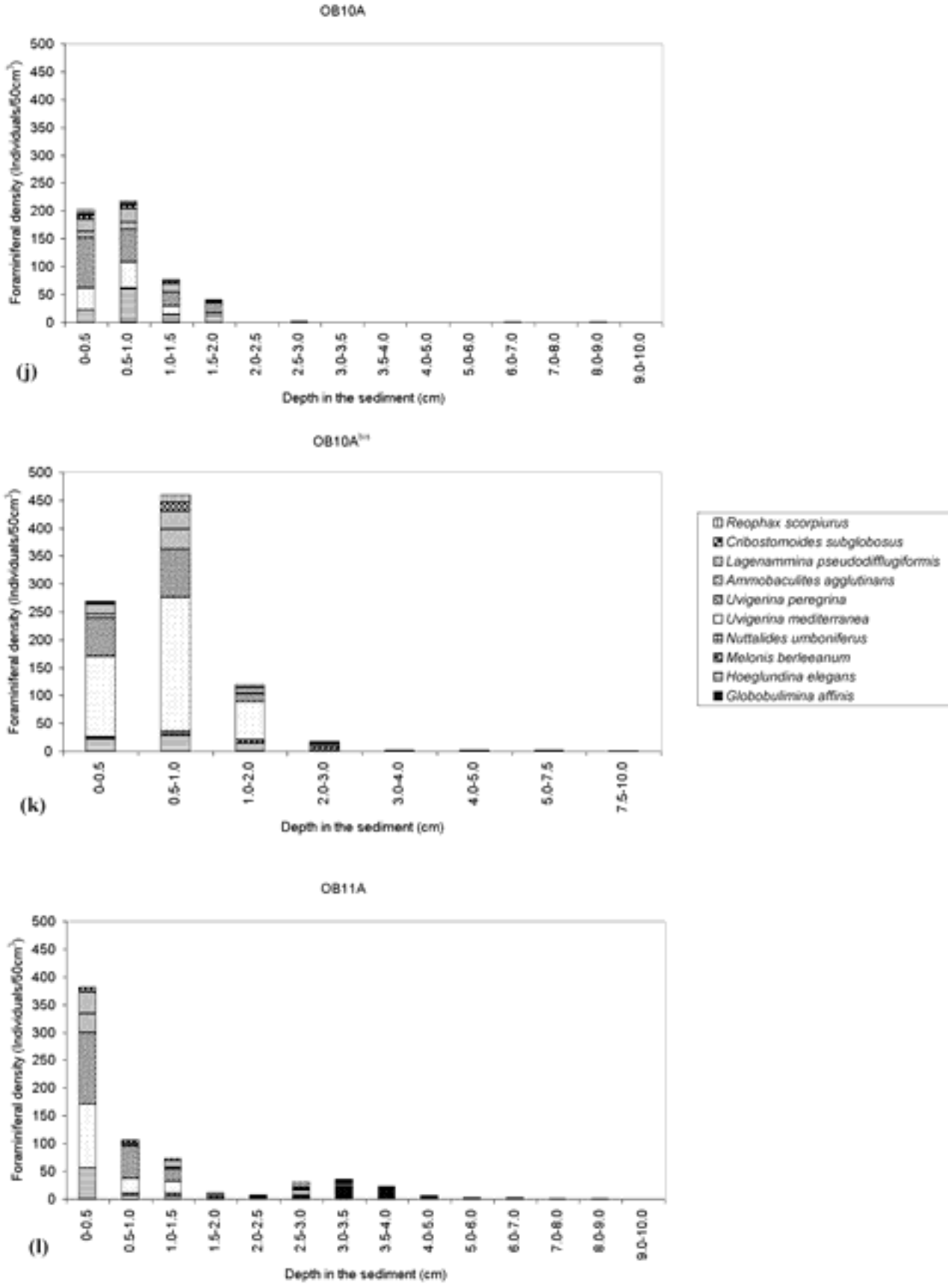

Figs. 4a-l Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume) for 12 available cores.

Taxa	Cores, ALD_{10}											Average weighted ALD_{10}	Microhabitat
	C01A	C02A	C02A^{rep}	C03A	C04A	C05A	C06A	C07A	C09A	C10A	C10A^{rep}	C011A	
Anomalinoides sp.	0.3 (7)												0.34	SI
Bulimina inflata	0.4 (5)								4.2 (13)	0.7 (12)	0.8 (22)	0.7 (11)	1.42	=
Cibicidoides pachyderma	0.4 (11)												0.40	SI
Globobulimina affinis	4.7 (137)	3.6 (14)					5.0 (20)	4.7 (11)	4.0 (13)		5.6 (10)	3.9 (45)	4.50	DI
Gyroidina orbicularis		2.3 (14)	1.8 (15)	1.8 (6)	1.9 (5)	2.3 (7)	1.8 (6)	3.0 (12)	3.2 (9)		1.9 (11)	1.4 (5)	2.18	II/DI
Hoeglundina elegans	0.8 (26)	0.5 (18)	1.0 (19)	0.5 (23)	0.3 (15)	0.5 (20)	0.6 (54)	0.8 (78)	1.9 (53)	0.8 (76)	0.9 (57)	0.9 (61)	0.86	SI
Melonis barleeanus	1.7 (6)	2.4 (37)	1.0 (18)			1.6 (5)	1.6 (11)	2.2 (15)	3.1 (16)	1.7 (5)	2.1 (27)	1.8 (13)	2.05	II/DI
Nuttallides umbonifera	0.4 (27)		1.2 (11)			0.2 (7)	0.5 (5)		0.3 (15)	0.8 (13)	0.8 (6)	0.4 (6)	0.56	SI
Triloculina trigonula											0.5 (5)	0.7 (5)	0.59	SI
Uvigerina mediterranea	0.6 (45)	1.3 (75)	1.2 (59)	0.4 (40)	0.5 (60)	0.4 (34)	0.8 (67)	1.0 (97)	2.7 (94)	0.7 (77)	0.8 (361)	0.6 (126)	0.96	SI
Uvigerina peregrina	1.1 (85)	1.3 (154)	1.0 (88)	0.2 (60)	0.6 (37)	0.4 (46)	0.7 (53)	1.1 (83)	2.4 (125)	0.7 (136)	0.7 (138)	0.8 (168)	0.99	SI
Pyrgo depressa	0.1 (10)												0.06	SI
Pyrgo murrina										0.7 (8)	0.6 (5)		0.62	SI
Pyrgo subsphaerica	1.3 (5)										0.9 (16)		0.98	SI
Pyrgoella sphaera												0.9 (8)	0.92	SI
Quinqueloculina sp 2			0.8 (12)										0.84	SI
Triloculina tricarinata		1.5 (21)											1.49	=
Agglutinated sp 11	0.6 (5)		0.8 (5)									0.5 (12)	0.59	SI
Agglutinated sp 29								0.9 (7)		1.2 (9)			1.03	SI
Agglutinated sp 46		1.7 (8)							1.2 (6)		4.0 (5)		2.13	DI
Ammobaculites agglutinans	0.6 (10)	1.3 (9)	0.8 (12)			0.3 (16)	1.1 (11)	0.8 (12)	0.9 (24)	0.6 (18)	0.8 (36)	0.4 (28)	0.72	SI
Ammolagena clavata											1.1 (26)		1.06	=
Cribrostomoides sp.						0.1 (7)							0.13	SI
Cribrostomoides subglobosus									0.7 (41)	0.7 (13)	0.8 (16)	0.7 (12)	0.74	SI
Crithionina aldystorum					1.2 (5)								1.20	=
Eggerella bradyi		0.9 (5)									1.3 (10)		1.14	SI/II
Kamerlella bradyi	0.5 (5)	0.7 (9)									1.3 (9)		0.86	SI
Lagenammina pseudodifflugiformis	1.4 (17)	1.2 (18)	0.7 (22)	0.6 (18)		0.6 (23)	0.6 (16)	1.5 (19)	2.6 (14)	0.8 (47)	1.4 (56)	0.8 (44)	1.04	SI/II
Paratrochammina challengeri										0.6 (7)			0.55	SI
Psammosphaera spp.		0.8 (5)	0.5 (6)				0.6 (5)			1.0 (8)	2.2 (7)	0.5 (5)	0.98	SI
Recurvoides sp.	1.7 (6)												1.67	=
Reophax guttiferus		0.7 (5)									0.8 (6)		0.70	SI
Reophax scorpiurus	0.3 (31)	0.6 (20)	0.5 (8)	0.2 (18)	0.2 (6)		0.6 (9)	1.0 (11)	0.3 (13)	0.8 (5)	1.1 (21)		0.57	SI
Saccammina spp.										0.9 (9)	0.8 (6)		0.75	SI
Thurammina albicans	0.9 (16)	1.1 (13)					1.2 (5)	1.6 (14)		1.4 (6)	1.4 (11)	1.1 (7)	1.22	=
Thurammina papillata			1.3 (6)	1.2 (5)		1.4 (6)				2.0 (6)	2.3 (8)		1.67	=
Oxygen penetration depth (cm)	1.8	3.1	3.1	3.2	3.0	3.2	3.6	3.4	3.3	2.9	2.9	0.8		

Table 2 Average living depth (ALD_{10}) of foraminiferal species and (in parentheses) the number of individuals on which the calculation is based. Only occurrences of ≥ 5 individuals are shown. The grey boxes represent dominant taxa with a relative proportion ≥ 5% at least one of the stations. Microhabitat patterns are summarised as shallow infaunal (SI), intermediate infaunal (II) or deep infaunal taxa (DI).

2. 63-150 µm fraction

The densities of the main taxa in the topmost half cm of the twelve cores are shown in Fig. 5a and Appendix C. The percentages of the main taxa are presented in Fig. 5b and Appendix C. Because of the large variability of foraminiferal density, which may be partially due to a varying sampling volume, the faunal variability is probably better represented by percentage data. *Nuttallides pusillus* is the most abundant taxon. Its relative abundances range from 9.6 to 39.7% (respectively in April 2001 and in October 1997). When *N. pusillus* is less dominant, juvenile specimens of *Uvigerina peregrina* dominate the foraminiferal assemblage. *Uvigerina peregrina* accounts for 6.9 to 24.3% of the total faunas. Highest percentages are recorded in July 1998 (OB4A), in April 2000 (both duplicate cores) and in April 2001 (OB11A). Its lower abundance is recorded in October 1997 (OB1A). This variability largely coincides with that found in the >150 µm fraction. *Trifarina pauperata* is the third dominant taxon, which exhibits much less temporal variability than the previous two taxa. It shows high percentages in June 1998 (OB3A), in December 1998 (OB6A) and in January 1999 (OB7A) (about 16%). Its lowest percentage is recorded in October 1997 (OB1A, 6.5%). Other taxa, such as agglutinated sp. 46, *Anomalinoides* sp., Agglutinated sp. 22 show some isolated and minor relative abundance peaks. *Epistominella exigua* and *Trochammina globigeriniformis* each represent always less than 10% of total fauna. They both present their highest relative abundance in June 1999 (OB9A), in April 2000 (both duplicate cores) and in April 2001 (OB11A). Finally, *Reophax guttiferus* shows a small percentage maximum in June 1999 (OB3A; 5.3%).

3. Taxonomic precision

Agglutinated sp.22 only occurs in 63-150 µm size fraction. This slightly elongate agglutinated taxon is mainly made of a chaotic aggregation of small test of planktonic foraminifera or fragments (rarely terrigeneous material). No chamber inner structure is visible and no aperture is detectible. This taxon may belong to Psammosphaeridae family according to Loeblich and Tappan (1988). Agglutinated sp.46 occurs in both size fractions. This monothalamous soft-shelled taxon presents an oval, more or less elongate, flask-shaped test made of white very fine grains. A single aperture is visible at the tapered end. This taxon may belong to Saccamminidae family according to Loeblich and Tappan (1988).

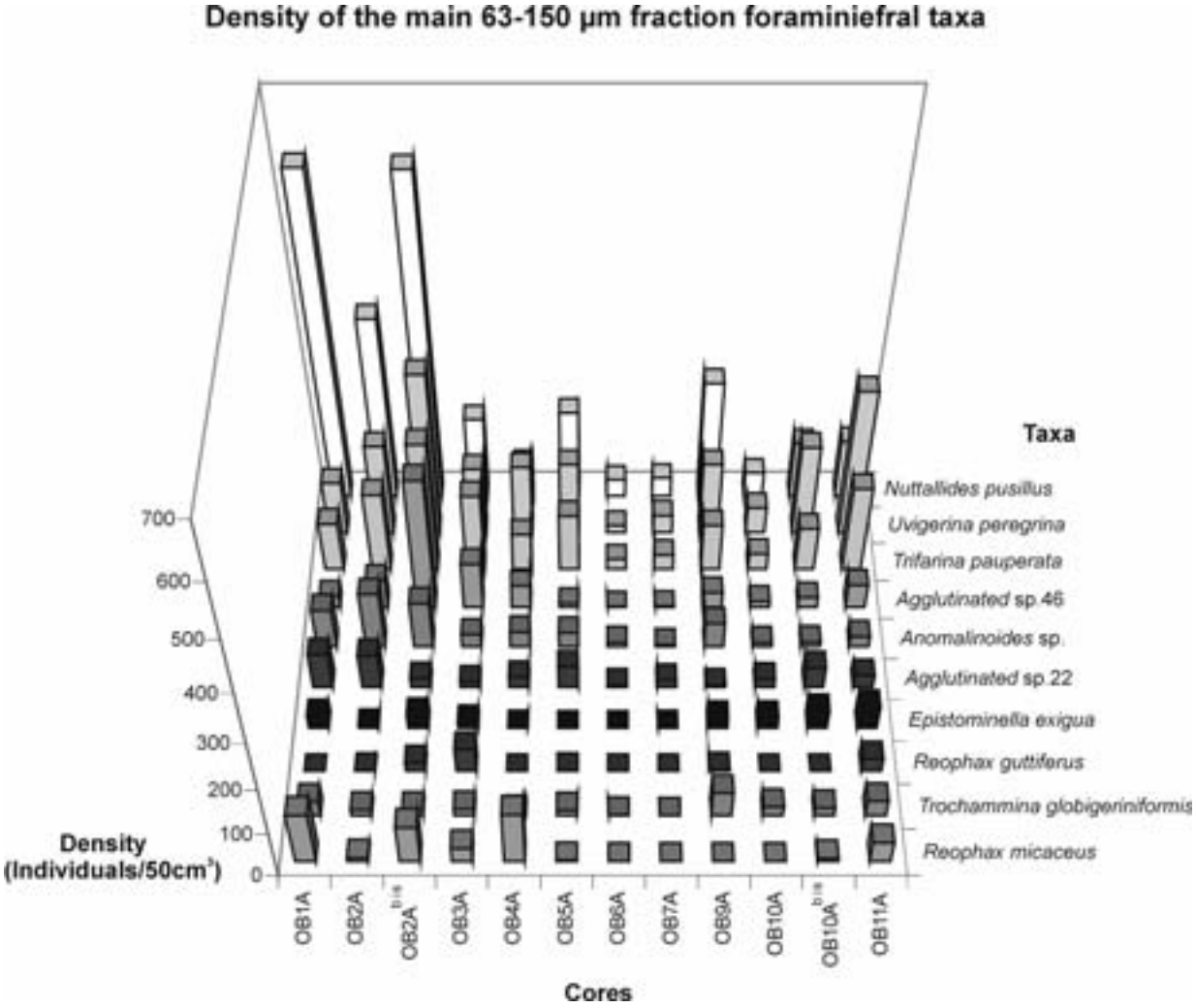

Fig. 5a Foraminiferal density of the main foraminiferal taxa in the 63-150 µm fraction for the 12 cores. Densities are standardised to a 50 cm^3 sediment volume.

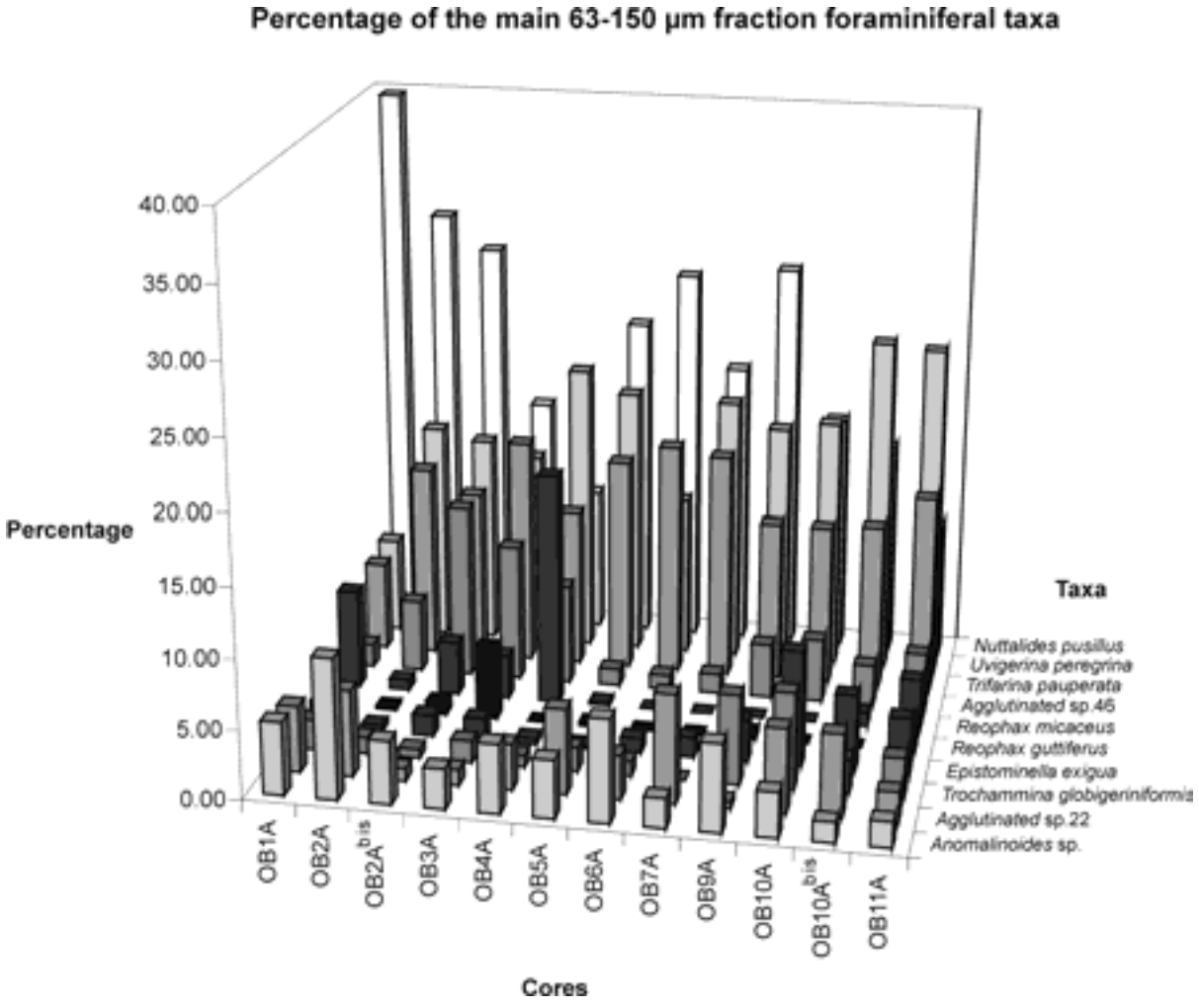

Fig. 5b Percentages of the main foraminiferal taxa in the 63-150 µm fraction for the 12 cores.

Discussion and Conclusions

Temporal variability of bottom and pore water chemical characteristics at station A

Our data show a surprising constancy in the chemistry of the bottom waters at station A. Bottom water oxygen concentration values range from 138 to 201 µmol/l (4.07-4.47 ml/l), close to the value of 202 µmol/l (4.49 ml/l) measured by Vangrieshem (1985) at 900 metres depth off Brittany (47°35'N-9°39'W; EDYLOC 82 campaign). Our oxygen concentration values are a bit higher than the value presented by Le Floch (1968) for Mediterranean Waters entering into the Bay of Biscay (171 µmol/l, 3.8 ml/l). A gradual mixing of Mediterranean Waters along its circulation in the Bay of Biscay with more oxygenated surrounding water masses (NACW, NADW) could explain this discrepancy.

At the sediment-water interface, oxygen concentrations are much more variable than in the bottom waters (Fig. 3). Marked oxygen concentration decrease in the first half cm of the bottom waters over sediment-water interface can be recorded in June 1998, July 1998, January 1999 and April 2001. The most spectacular oxygen concentration gradient is recorded in April 2001, with a marked decrease of 120 µmol/l. This may be due to an enhanced oxygen consumption at the sediment water interface related to biogenic degradation of freshly deposited organic matter deposits (Table.1).

Vertical profiles of dissolved oxygen in the uppermost sediment are intriguing (Fig. 3). For most cores, oxygen concentration decreases sharply in the first cm and zero oxygen boundary is reached at 3 cm depth, showing intense oxygen consumption due to degradation of reactive organic matter available in the topmost sediment. As predicted by oxygen concentration gradient in the lower 5 mm of bottom water, the zero oxygen boundary is limited to 8 mm depth in April 2001, which suggest a very strong oxygen consumption in the first half cm of sediment. For most cores, we think that most labile organic matter deposits (phytodetritus) are remineralised in a very shallow bioturbation zone (less than 1 cm according to ^{210}Pb and ^{234}Th data, Jouanneau, pers comm., 2003). Aerobic bacteria adapted to respond immediately to seasonal phytodetritus deposits are able to quickly consume these labile organic compounds (Turley et al., 1988; Lochte and Turley, 1988; Thiel et al., 1990; Della Groce et al., 1996, Danovaro et al., 2000b). This may be especially the case in April 2001 (OB11A) and in a lesser degree in October 1997 (OB1A) where oxygen is totally consumed in the 2 fisrt cms of sediment as a direct echo to bacterial response to organic

matter deposits. In the deeper parts of the sediment, only small portions of labile organic compounds may be found in relation to major bioturbation structures. Refractory organic matter consisting of resistant polymer biomolecules dominates the sedimentary organic load (Carney, 1989, Bruland et al., 1989, Jørgensen, 2000). Only highly specialized bacterial consortia can take advantage of this low value organic matter. These are mainly denitrifying, metal-reducing and sulphate-reducing bacteria (Froelich et al., 1979, Fenchel and Finlay, 1995, Jørgensen, 2000). Contrary to station B sampled in the Bay of Biscay (550 metres depth) (Fontanier et al., 2003a), it appears that the deposit of phytoplankton (and zooplankton) detritus originating from a local marine source and produced in the eutrophic period (June 1999, April 2000, April 2001) induces marked episodic changes of early diagenetic processes in the upper sediment of station A.

Spatial heterogeneity of the benthic ecosystem at station A

It is commonly thought that spatial variability of benthic organisms (patchiness) is mainly related to a heterogeneous repartition of phytoplankton aggregates at the sea floor; high density and highly diversified faunas generally thrive in patches of organic matter at the sediment-water interface (Grassle and Morse-Porteous, 1987; Grassle, 1989; Snelgrove et al., 1994; 1996), which tend to concentrate in topographic depressions. The study of seasonal and interannual variability of live benthic foraminiferal faunas from a 550 metres depth station in the Bay of Biscay (station B) depicts the importance of spatial variability (patchiness) of live benthic foraminifera (Fontanier et al., 2003a). Patchiness at station B appears to be mainly food controlled, and, as a consequence, is most important in eutrophic periods (spring bloom and autumn bloom) (Fontanier et al., 2003a). However, at this 550 m deep station, the spatial variability of the foraminiferal faunas is definitely lower than the observed temporal changes, both for the 63-150 µm and >150 µm fractions.

In purpose to objectively compare the extent of spatial variability of the foraminiferal faunas (as shown by the two couples of duplicate cores) with temporal changes at station A, we performed a non-standardised principal component analysis (Davis, 1986) on the basis of the percentage data of all taxa which appear with at least 2.5% in one of the cores. Since both sets of duplicate cores issue from two successive multicorer deployments, we deal with meso-scale (one to several hundred metres) spatial variability. For the >150µm fraction, this multivariate analysis is based on 12 samples (10 samples and 2 duplicates) and 19 taxa, and

>150 µm fraction	PCA1	PCA2	PCA3	PCA4
Eigenvalues column	95.6	53.1	25.6	9.6
Percent of trace	46.6	25.9	12.5	4.7
Cumulative percent of trace	46.6	72.5	85.0	89.6
Taxa				
Bulimina inflata	0.02	0.00	0.00	-0.06
Globobulimina affinis	-0.54	0.66	0.09	0.13
Gyroidina orbicularis	0.04	-0.09	-0.06	0.08
Hoeglundina elegans	0.07	-0.23	0.88	0.34
Melonis barleeanus	0.02	-0.03	-0.20	0.15
Nuttallides umboniferus	-0.12	0.02	0.02	-0.23
Uvigerina mediterranea	0.82	0.42	-0.05	0.10
Uvigerina peregrina	-0.08	-0.50	-0.34	0.40
Quinqueloculina sp.2	-0.01	-0.02	-0.08	-0.07
Triloculina tricarinata	-0.01	-0.02	-0.15	0.15
Ammobaculites agglutinans	0.02	-0.06	0.08	-0.38
Ammalagena clavata	0.05	0.06	0.01	-0.11
Cribrostomoides sp.	-0.01	-0.04	0.03	-0.20
Cribrostomoides subglobosus	0.01	-0.06	-0.02	-0.08
Crithionina abyssorum	0.03	0.01	-0.03	-0.01
Lagenammina pseudodifflugiformis	-0.01	-0.21	0.11	-0.45
Reophax scorpiurus	-0.07	0.07	-0.09	0.38
Thurammina albicans	-0.03	0.05	0.02	0.16
Thurammina papillata	0.03	-0.05	-0.04	-0.10

(a)

63-150 µm fraction	PCA1	PCA2
Eigenvalues column	95.6	53.0
Percent of trace	46.6	25.9
Cumulative percent of trace	46.6	72.5
Taxa		
Anomalinoides sp.	0.16	0.06
Bolivina sp.39	-0.05	-0.06
Bulimina inflata	-0.03	-0.05
Ceratobulimina sp.	0.02	0.05
Epistominella exigua	-0.08	-0.15
Gavelinopsis translucens	-0.04	0.01
Hoeglundina elegans	-0.04	0.00
Nuttallides pusillus	0.87	-0.03
Nuttallides umboniferus	0.02	-0.09
Trifarina bradyi	-0.04	-0.16
Trifarina pauperata	-0.09	-0.23
Uvigerina mediterranea	-0.05	0.12
Uvigerina peregrina	-0.42	-0.21
Agglutinated sp.22	0.00	-0.19
Agglutinated sp.29	0.07	0.07
Agglutinated sp.46	-0.05	0.35
Haplophragmoides sp.5	0.02	-0.04
Psammosphaera spp.	-0.06	0.14
Reophax guttiferus	-0.04	0.04
Reophax micaceus	-0.11	0.78
Trochammina sp.103	0.04	-0.05
Trochammina globigeriniformis	-0.01	-0.11

(c)

>150 µm	OB2A	OB2A^{bis}	OB3A	OB4A	OB5A	OB6A	OB7A	OB9A	OB10A	OB10A^{bis}	OB11A
OB1A	28.0	29.8	30.4	37.0	29.6	27.7	32.3	28.0	31.5	40.9	26.0
OB2A		**6.4**	8.4	19.2	16.1	18.3	18.3	8.8	14.4	26.5	8.6
OB2A^{bis}			6.9	19.3	10.9	17.0	17.0	6.3	10.5	25.6	6.9
OB3A				18.6	11.0	13.6	12.4	4.5	7.0	26.5	6.4
OB4A					22.2	16.3	14.7	16.7	22.7	9.5	16.7
OB5A						13.1	14.3	8.7	7.0	27.1	9.3
OB6A							5.4	10.9	13.8	22.1	10.5
OB7A								11.1	13.0	21.7	11.7
OB9A									7.9	23.7	2.3
OB10A										**29.5**	9.6
OB10A^{bis}											23.3

(b)

63-150 µm	OB2A	OB2A^{bis}	OB3A	OB4A	OB5A	OB6A	OB7A	OB9A	OB10A	OB10A^{bis}	OB11A
OB1A	12.7	13.9	24.5	34.4	22.3	15.6	25.5	16.3	27.1	31.6	35.6
OB2A		**7.1**	14.3	27.2	9.7	3.0	13.0	3.7	14.9	19.5	24.4
OB2A^{bis}			10.6	21.3	11.4	8.6	13.8	7.4	14.6	18.7	21.8
OB3A				14.0	9.2	13.4	8.5	11.5	7.2	9.6	11.2
OB4A					23.1	26.9	21.7	25.1	19.5	18.9	14.1
OB5A						7.1	3.4	6.0	5.7	10.2	16.1
OB6A							10.5	1.9	12.6	17.2	22.6
OB7A								9.3	2.6	6.8	13.1
OB9A									11.3	15.8	21.0
OB10A										**4.6**	10.5
OB10A^{bis}											7.0

(d)

Tables 3a-c Results of non standardised principal component analyses based on the percentages of the main foraminiferal taxa in the >150 and 63-150 µm fraction (percentage ≥ 2.5%). Table 3a. Eigenvalues and species loadings of the four significant axes for the >150 µm fraction. Table 3b. The normative distance between cores in the 4-dimensional space (normative distance between the five pairs of replicate cores are given in bold letters). Table 3c. Eigenvalues and species loadings of the two significant axes for the 63-150 µm fraction. Table 3d. The normative distance between cores in the 2-dimensional space (normative distance between the five pairs of replicate cores are given in bold letters).

yields four significant axes, explaining 90% of the total variability. The eigenvalues for these four axes and the species loadings on the axes are given in Table 3a. We calculated the normative distance between the two couples of duplicates cores in the 4 dimensional space defined by the four significant axes (Table 3b). This table shows that differences between duplicate samples in January 1998 (6 units) are minimal. For the duplicate cores collected in April 2000, on the contrary, spatial variability is much higher (30 units), and is comparable to the largest difference of 41 units found between October 1997 (OB1A) and April 2000 ($OB10A^{bis}$). Since only 2 sets of replicate cores are compared with 10 samples separated in time, it may be concluded that spatial variability is at least as large as temporal variability. Of course this seriously hampers the interpretation of the differences between our cores in terms of seasonal variation. For the 63-150 μm fraction, a similar multivariate analysis is based on 12 samples (10 samples and 2 duplicates) and 22 taxa, and presents two significant axes, that explain 72% of the total variability. The eigenvalues for these two axes and the species loadings on the axes are given in Table 3c. The positive side of axis 1 is highly dominated by *Nuttallides pusillus* (0.87) and *Anomalinoides* sp. (0.16), whereas *Uvigerina peregrina* (-0.42) and *Reophax micaceus* (-0.11) load negatively on the first axis. The positive side of the second axis is strongly dominated by *Reophax micaceus* (0.78) and agglutinated sp.46 (0.35), whereasile *Trifarina pauperata, Uvigerina peregrina* and agglutinated sp.22 load negatively. Fig. 7 shows the position of the 12 cores in the axial plot. After looking at the figure 6, it is not easy to give a clear ecological significance to the two main axes. Nevertheless, we can notice that cores from April 2000 and 2001 (OB10A, $OB10A^{bis}$ and OB11A) regroup in a graphic zone defined by the strong percentages of *Uvigerina peregrina* (negative side of axis 1) and *Trifarina pauperata* (negative side of axis 2). We calculated the normative distance between the two couples of duplicates cores in the 2 dimensional space defined by the two significant axes (Table 3d). As observed in figure 6, distances between the two couples of duplicate cores (5-7 units) are definitely lower than the maximum of temporal variability recorded between October 1997 and April 2001 (36 units).

These multidimensional analyses show that the spatial variability have a considerable extent, and may have amplitude comparable to that of temporal variability. We would expect that patchiness would be especially high in eutrophic periods, when abundant food will be irregularly distributed over the sea floor relief. Although it is impossible to base firm conclusions on only 2 duplicate cores, it is evident that differences between our 10 samplings can not been interpreted straightforward as seasonal variation. This is a problem that makes questionable the results of all studies about temporal variability without any duplicates cores.

A simple comparison between station A and station B studied by Fontanier et al. (2003a) could considerably strengthen the idea that foraminiferal faunas at both stations respond to a similar seasonal signal and have got a real temporal variability. If foraminiferal densities in both stations vary in the same way, this would be a strong argument in favour of a response to temporal changes in food availability and against patchiness.

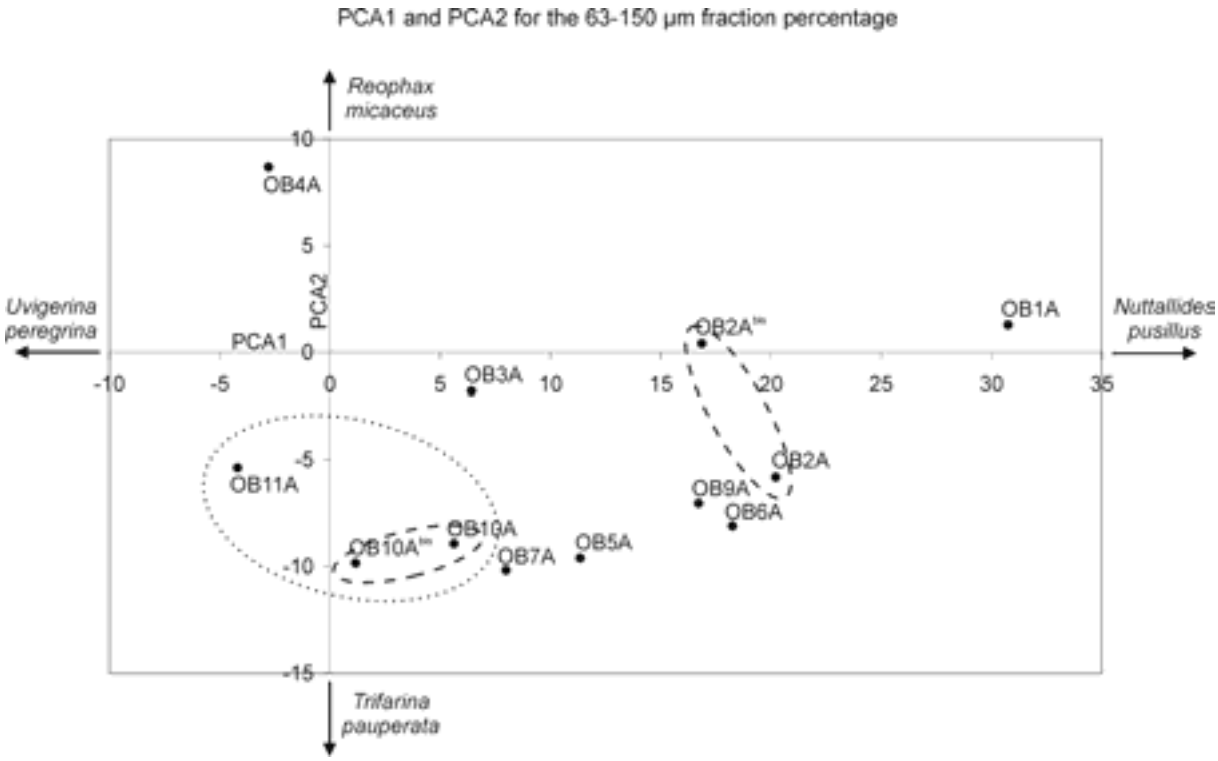

Fig. 6 Plot of the 12 cores in the 2-D space defined by the two main axes of the non standardised principal component analysis (PCA1, PCA2). Duplicate cores are circled by dotted line.

Comparison of temporal variability of foraminiferal density between station A and station B

In figure 7, foraminiferal densities for both size fractions at stations A and B, between September 1997 and April 2001, are expressed in standardised densities (*SD*) according the following formula:

$$SD_{core\ i} = \left(D_{core\ i} - \overline{D}\right) / Se$$

,where $SD_{core\ i}$ is the standardised density for *core i* in 63-150 µm or >150 µm size fraction, $D_{core\ i}$ is the initial density of core i, $\overline{D}$ is the mean density for all cores in the same size fraction and Se is the standard error related to mean density. The foraminiferal density for the >150 µm fraction is initially calculated as the total number of live individuals per core of 72 cm^2. The foraminiferal density for the 63-150 µm fraction is calculated as the total number of live foraminifera in the first half cm of the core. Standardised density allow a better comparison between density changes for both fraction at station A and station B. Station B (550 m depth, fig. 1) is close to station A and was studied by Fontanier et al. (2003a). At station B, foraminiferal faunas in 63-150 µm and >150 µm fractions exhibit significant seasonal variability with a clear foraminiferal response to increased organic matter input recorded in eutrophic periods (autumn bloom and spring bloom).

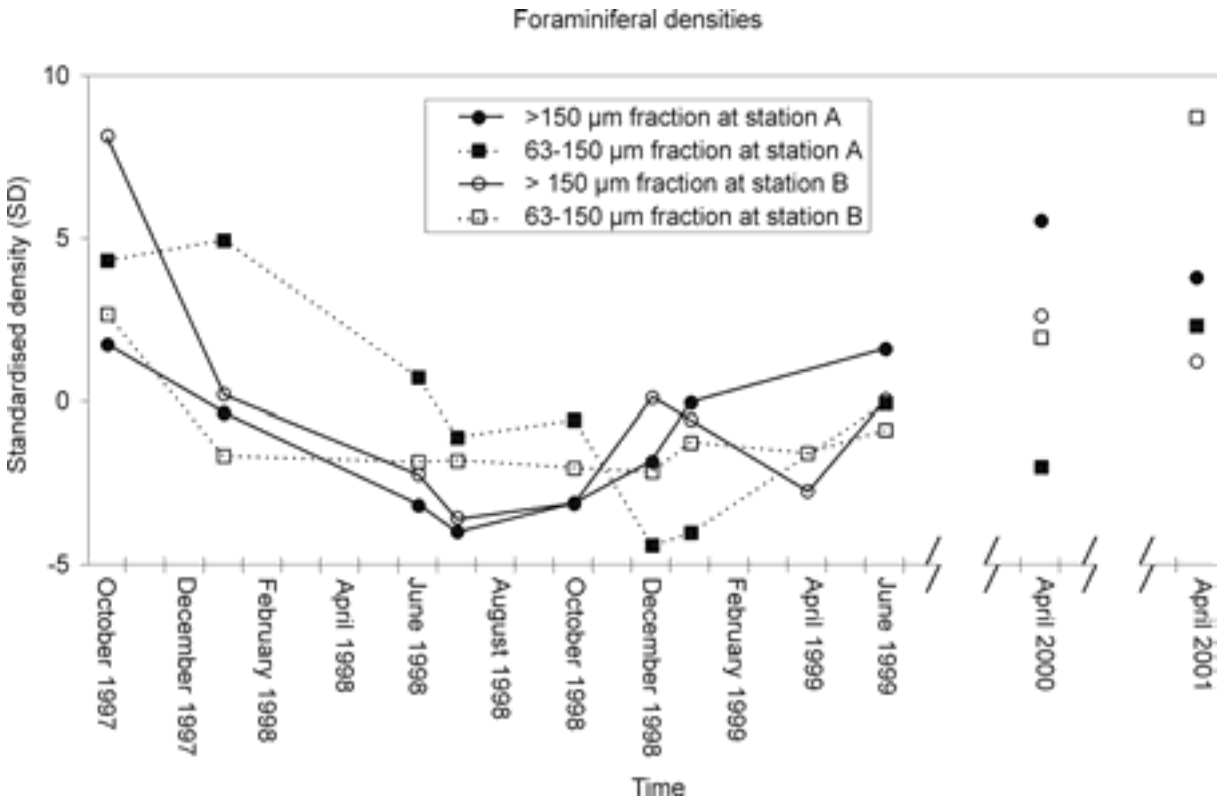

Fig. 7 Foraminiferal standardised density (SD) for both size fractions at station A and B between September 1997 and April 2001 (see discussion for calculation details of SD).

For >150 µm fraction, a simple linear regression between both stations shows a clear positive correlation ($R^2 = 0.45$). The seasonal trends are roughly the same for both stations;

the lowest standardised densities are recorded in oligotrophic periods (winter, summer) whereas the highest standardised density values are recorded in eutrophic periods (spring blooms, autumn blooms) (Fig. 7). This comparison also suggests that foraminiferal faunas collected in October 1997 at station A (OB1A core) may have reacted to organic matter deposits related to the putative autumn bloom described at station B (Fontanier et al., 2003a). That's why in the further discussion, we suppose that OB1A core was sampled in autumn bloom period. In spite of the potentially important patchiness, it appears that the foraminiferal density of the >150 µm fraction has recorded the same seasonal trends at both stations.

A simple linear regression between the foraminiferal standardised densities in 63-150 µm fraction for stations A and B does not exhibit any effective correlation ($R^2 = 0.13$). Such a discrepancy surely reflects the difficulty of working directly with density values for the 63-150 µm fraction in the top half cm. As discussed above, the variable sample size volume for the 0-0.5 cm interval is probably the main responsible of the differences in foraminiferal density.

Temporal variability of foraminiferal faunas at station A

In the >150 µm fraction, most of foraminifera concentrate in the oxygenated layers of the sediment and more specifically in the oxic zone where dissolved oxygen concentration exceeds 50 µmol/l (Fig. 4a-l). Only *Globobulimina affinis* individuals are found in purely anoxic sediments. Fontanier et al. (2002) present an adaptation in the Bay of Biscay of the TROX-model of Jorissen et al. (1995). They suggest that foraminiferal microhabitats at station A are mainly food controlled. According to this model, most foraminiferal taxa thrive indeed preferentially in the well-oxygenated surficial sediment, enriched by fresh organic matter that originates from the labile organic matter flux to the ocean floor. Intermediate and deep infaunal taxa, which are minor species, thrive in close relation to redox gradients and with buried organic matter.

When looking at our present results, the occurrence of high-density foraminiferal faunas in the upper sediment of the cores collected in October 1997, June 1999, April 2000 and April 2001 (OB1A, OB9A, OB10A^{bis} and OB11A) suggests a significant foraminiferal response to phytodetritus enrichment of the topmost cores. The shallow infaunal species *Uvigerina peregrina* and *Uvigerina mediterranea* exhibit the largest density variations (Fig. 4a-l; Appendix C). Their highest absolute densities are exclusively recorded some weeks after the spring bloom in shallow infaunal niches (June 1999, April 2000 and April 2001) (Fig. 4a-

l). As suggested by Fontanier et al. (2003a) for foraminiferal faunas at a 550 m depth station (station B), these taxa can be considered as the most opportunistic taxa in the >150 µm fraction. Our observations are in agreement with a recent experimental study by Ernst and Van der Zwaan (2002) who show that *U. peregrina* is able to respond clearly to simulated phytoplankton deposits in the shallow infaunal microhabitat. *Hoeglundina elegans,* the third dominant taxon in the >150 µm fraction, shows the highest relative densities in the most oligotrophic periods. Nevertheless, in spite of its lower percentages during eutrophic periods, the absolute values show an increase in spring bloom periods (June 1999, April 2000 and April 2001; OB9A, OB10A^{bis} and OB11A) (Appendix C). Therefore, we suggest thus that also *H. elegans* may have a moderately opportunistic response to a sudden exported organic flux, albeit much less strong than that of both *Uvigerina* species. Indeed, Fontanier et al. (2003c) describe this species as opportunistic taxon able to respond to periods of slightly increased food supply in deep and oligotrophic environments (a 3000 m depth station). *H. elegans* dominates foraminiferal faunas thriving in oligotrophic periods of our 1000 metres depth station (December 1998 and January 1999). This in agreement with numerous observations describing *H. elegans* as typical of low organic carbon areas (Lutze and Coulbourne, 1984; Corliss, 1985; Corliss and Emerson, 1990; Corliss, 1991; Fontanier et al., 2002; Morigi et al., 2001). A recent study by Fontanier et al. (2002) shows that *H. elegans* is a typical species of meso-oligotrophic bathyal environments from the Bay of Biscay (deeper than station A). This explains the absence of *H. elegans* at the shallower and more eutrophic station B (550 m depth; Fontanier et al., 2003a). At station A, we consider *H. elegans*, just as *U. mediterrenea* and *U. peregrina,* as a "background" species, capable to react to seasonal blooms, and to maintain a viable population nucleus during more oligotrophic periods. Finally, *Lagenammina pseudodifflugiformis* exhibits a higher density in April 2000 (both duplicate cores) and April 2001 (OB11A). Also this shallow/intermediate infaunal taxon appears to have an opportunistic response to phytodetritus deposits.

At station A, where stable redox conditions prevail throughout the year, the exported labile organic matter flux from the surface waters represents an essential food source for most benthic foraminifera. In oligotrophic periods, foraminiferal faunas benefit from lower exported organic matter flux by strongly concentrating in the surficial sediments. In eutrophic periods, opportunistic taxa thrive abundantly in shallow infaunal and deeper microhabitats in well-oxygenated sediments where short-term phytodetritus is available. Thus, as suggested by TROX-model adapted to the Bay of Biscay by Fontanier et al. (2003a), shallow infaunal microhabitats at station A are strongly controlled by the exported organic matter flux.

Melonis barleeanus occupies an intermediate/deep infaunal microhabitat (Table 2; Fig. 4a-l). It lives preferentially in an ecological niche where oxygen concentrations range from 40 to 1 µmol/l (dysoxic to suboxic conditions according to Tyson and Pearson, 1991). Similar observations were presented and commented in numerous other in situ studies (e.g. Corliss, 1988; Corliss et Emerson, 1990; Jorissen et al., 1995; 1998; Jorissen, 1999a, Fontanier et al., 2002; 2003a). The lower densities recorded at station A (1000 m depth) (13 individuals per core as a mean value) in comparison with *M. barleeanus* populations thriving at station B (500 m depth) (51 individuals per core as a mean value; Fontanier et al., 2003a) are an argument for a linkage between exported organic matter fluxes at the sea floor at both stations and *M. barleeanus* standing stocks. Higher organic matter fluxes may sustain richer populations of adult *M. barleeanus*. *M. barleeanus* adults (>150 µm) may feed on very small portions of labile organic matter buried in their intermediate infaunal niches by meifaunal and/or macrofaunal organisms. Moreover, burial of organic matter in the deep sediment may induce coupling between heterotroph and chemotroph bacterial activity (Jørgensen, 2000). Thus, as suggested by Licari et al. (2003) and Fontanier et al. (2003a; 2003c), we also suggest that *M. barleeanus* may behave as a highly specialized taxon that can feed on heterotroph bacteria or live in mutualism with chemoautotroph nitrifying bacterial consortia that thrive in the dysoxic part of the sediment. We further think that oxygen concentrations where *M. barleeanus* adults thrive (Dissolved Oxygen Threshold < 0.1-40 µmol/l >) are close to the body threshold for the vital functions of this intermediate/deep infaunal taxon.

When present in our cores, *Globobulimina affinis* always settles in a deep infaunal microhabitat in anoxic sediments (Table 2; Fig. 4a-l). This is in agreement with numerous studies describing *Globobulimina* spp. as a deep infaunal taxon (e.g. Corliss, 1985; Mackensen et Douglas, 1989; Corliss, 1991; Jorissen et al., 1995; 1998, Schmiedl et al., 2000; Fontanier et al., 2002, 2003a, 2003c). In Fontanier et al. (2003a and 2003c), *G. affinis* is a highly specialized taxon which lives in a stable biogeochemical microhabitat where phytodetritus is supposed to be scarce or only related to macrofaunal burrowing. According to Fontanier et al. (2003a), seasonal frequency variations of *G. affinis* may be related to the burrowing of labile organic matter some weeks after initial phytodetritus deposits (in autumn and spring bloom) and an associated increase of bacterial activity. In the present study, the relatively high densities of *G. affinis* in October 1997 and in April 2001 (OB1A and OB11A; Fig. 4a and Fig. 4l) suggests that *G. affinis* is responding to (1) an organic matter enrichment of the deeper sediment parts related to intensified bioturbation in eutrophic periods (autumn bloom 1997 and spring bloom 2001) and (2) the upward migration of zero oxygen boundary

in organic matter enriched surficial sediment. Bioturbation structures (burrows) are indeed very abundant along the 10 cm long cores collected in October 1997 and April 2001 and oxygen penetration is limited for both samplings. Mature *Globobulimina* populations that strictly tolerate suboxic and anoxic conditions prevailing close to zero oxygen boundary are able to migrate in close relation to it (Kitazato and Ohga, 1995; Ohga and Kitazato, 1997). Heteretroph bacterial consortia associated with the degradation of bioturbated organic matter compounds may act as an alternative food source for *G. affinis*. A very similar increase of the population density was observed by Heinz et al. (2001) in a culture experiment after addition of low quality organic matter.

The interpretation of our results for the smaller fraction (63-150 µm) is less straightforward. Because of the possibility of strongly varying sediment volume the density variations cannot be used as a criteria of temporal variability of foraminiferal faunas. As suggested in Fontanier et al. (2003a), in cases where the sediment surface is oblique, the volume of the top half cm layer may show important differences between cores. Thus, we are forced to base our discussion mainly on percentage values.

Nuttallides pusillus is the dominant taxon and shows the highest temporal variability in the 63-150 µm fraction (Fig. 5a-b). At station B (550 m depth) (Fig. 1), *Nuttallides pusillus* behaves as a moderate opportunistic taxon that is able to feed and reproduce on ephemeral organic matter deposits preferentially related to autumn primary production (Gooday and Hughes, 2002; Fontanier et al., 2003a). At our station A, *N. pusillus* dominates foraminiferal faunas collected in autumn 1997 and in early winter 1998 (OB1A, OB2A and OB2A^{bis}). That is why we think that this species could be an opportunistic taxon responding preferentially to phytodetritus related to autumn primary production events, such as the putative autumn bloom 1997. However its high percentage in June 1999 (OB9A) may also plead for a significant response to spring bloom phytodetritus (Fig.6b). *Epistominella pusilla* (= *Nuttallides pusillus*) is described by Heinz et al. (2001) as an opportunistic taxon responding to food addition in laboratory studies based on material collected at a 900 metres depth station in the Gulf de Lions. Gooday and Hughes (2002) describe very large population of *Eponides pusillus* (= *Nuttallides pusillus*) living embedded in lumps of phytodetritus related to spring bloom at a 1920 m deep bathyal station in the NE Atlantic. In autumn 1998 and winter 1999, the weaker frequencies of *N. pusillus* in the very low-density faunas collected in our study area are rather striking in comparison with the previous year (Fig. 5a). It suggests a differential response of *N. pusillus* to strong interannual variability of phytodetritus inputs. Juveniles of *Uvigerina peregrina* (63-150 µm) dominate the faunas in spring (April 2000 and April 2001) (Fig. 5b),

which pleads for a reproductive behaviour strongly related to the ephemeral spring bloom phytodetritus. As a main result, *U. peregrina* exhibits in the >150 µm fraction absolute frequency increase in spring bloom periods. This confirms the highly opportunistic behaviour of *U. peregrina*. Its high percentages in both size fractions throughout the year suggest also that *U. peregrina* is able to sustain it metabolic activity and to reproduce as more competitive species in the more oligotrophic periods of the year.

The significant occurrence of *Epistominella exigua, Trochammina globigeriniformis* and *Reophax guttiferus* in the samples from June and April (June 1999, April 2000, April 2001) appears to be connected to the impact of freshly deposited phytodetritus. *E. exigua* is well known to respond to ephemeral organic matter deposits at the sea floor (Gooday, 1988; Gooday and Lambshead, 1989; Gooday and Turley, 1990; Gooday, 1993; Loubere, 1998; Jannink et al., 1998). In station B (550 metres depth), *E. exigua* and *R. guttiferus* responds indeed clearly to spring and/or autumn bloom phytodetritus deposits with spectacular frequency and percentage increases (Fontanier et al., 2003a). At station A, the response of *E. exigua* and *R. guttiferus* is not so strong; probably because the spring bloom organic matter flux at station A is much lower than at station B. Nevertheless, their presence reflects phytoplankton deposits at the sediment-water interface.

In view of our results for the 63-150 µm fraction, it appears that the temporal variability of the foraminiferal fauna is lower at station A than at station B (Fontanier et al., 2003a). In view of the spectacular occurrence of major opportunistic taxa (e.g. *E. exigua*), seasonality is surprisingly more marked at the upper slope station B than at station A where more moderately opportunistic species thrive (e.g. *N. pusillus*). In the next paragraph, we propose a simple conceptual model explaining the differences in the foraminiferal response between stations A and B.

Conceptual model of opportunist dynamics along a slope transect in the Bay of Biscay

Figure 8 presents a conceptual model depicting the seasonal variability of foraminiferal faunas (63-150 µm and >150 µm) at station A (1000 metres depth) and station B (550 metres depth) in the Bay of Biscay (model of Opportunist DYnamics along a Slope tranSEct in the (B)ay of (B)iscaY: ODYSSEY model). These two open slope stations are under the influence of a typical temperate regime of primary production characterized by two chlorophyll-a maxima in the surface waters: a strong, two months long, spring bloom and a short, and weaker, autumn bloom. We suppose that primary production regimes in surface

waters over our both station are qualitatively and quantitatively similar (with a annual mean value of 150 g C/m²/yr). The dotted lines represent the density profiles of foraminiferal faunas in the >150 µm size fraction. Dominant and opportunistic foraminiferal taxa in the >150 µm size fraction are underlined in figure 8. The dashed lines represent the density profiles in the 63-150 µm size fraction. Non-underlined taxa are dominant and/or remarkable species in the 63-150 µm size fraction.

The figure insists on the foraminiferal response to phytodetritus deposits. The organic matter flux controls the foraminiferal density in both size fractions. In spring and autumn bloom periods, foraminiferal frequencies increase some weeks after chlorophyll-a maxima due to the response of opportunistic foraminiferal taxa. At station A, the occurrence of autumn bloom is questionable. Despite some doubts, we suggest that a putative fall bloom occurring in September/October 1997 may be responsible with the faunistic density and composition observed in both size fractions in OB1A core.

At 550 m and 1000 m depth stations, *Uvigerina peregrina* and *Uvigerina mediterranea* dominate the >150 µm size fraction foraminiferal faunas throughout the year. They behave both as opportunistic taxa reproducing and thriving abundantly in eutrophic periods. It is striking that *U. peregrina* is the dominant opportunistic taxon in the autumn bloom period at 550 m depth as well as in the spring bloom at 1000 m depth. This suggests that spring bloom organic matter fluxes at station B and autumn bloom organic matter fluxes at station A are quantitatively similar and provoke the same foraminiferal response. The 550 m spring bloom, on the contrary, appears to be surprisingly too strong for *U. peregrina.* Or perhaps, *U. peregrina* is less opportunistic than the shallow infaunal *U. mediterranea*, a taxon that apparently needs a higher organic input than *U. peregrina* and dominates the foraminiferal faunas at station B (Fontanier et al., 2002).

In the 63-150 µm size fraction, *U. peregrina* is generally the most opportunistic taxon for both periods. Moreover, we suggest that the weaker spring bloom phytodetritus flux recorded in our station A in comparison to station B limits the response of the very opportunistic taxa recorded in the 63-150 µm fraction at station B such as *E. exigua* and *R. guttiferus*. *Nuttalides pusillus* which is a minor opportunistic taxon at station B, occuring in autumn and spring bloom periods, is apparently more adapted to thrive in the relatively more oligotrophic conditions prevailing at station A. Accompanied by *Trifarina pauperata*, it dominates the 63-150 µm foraminiferal faunas throughout the year and shows a marked opportunistic behaviour in and after the autumn bloom period.

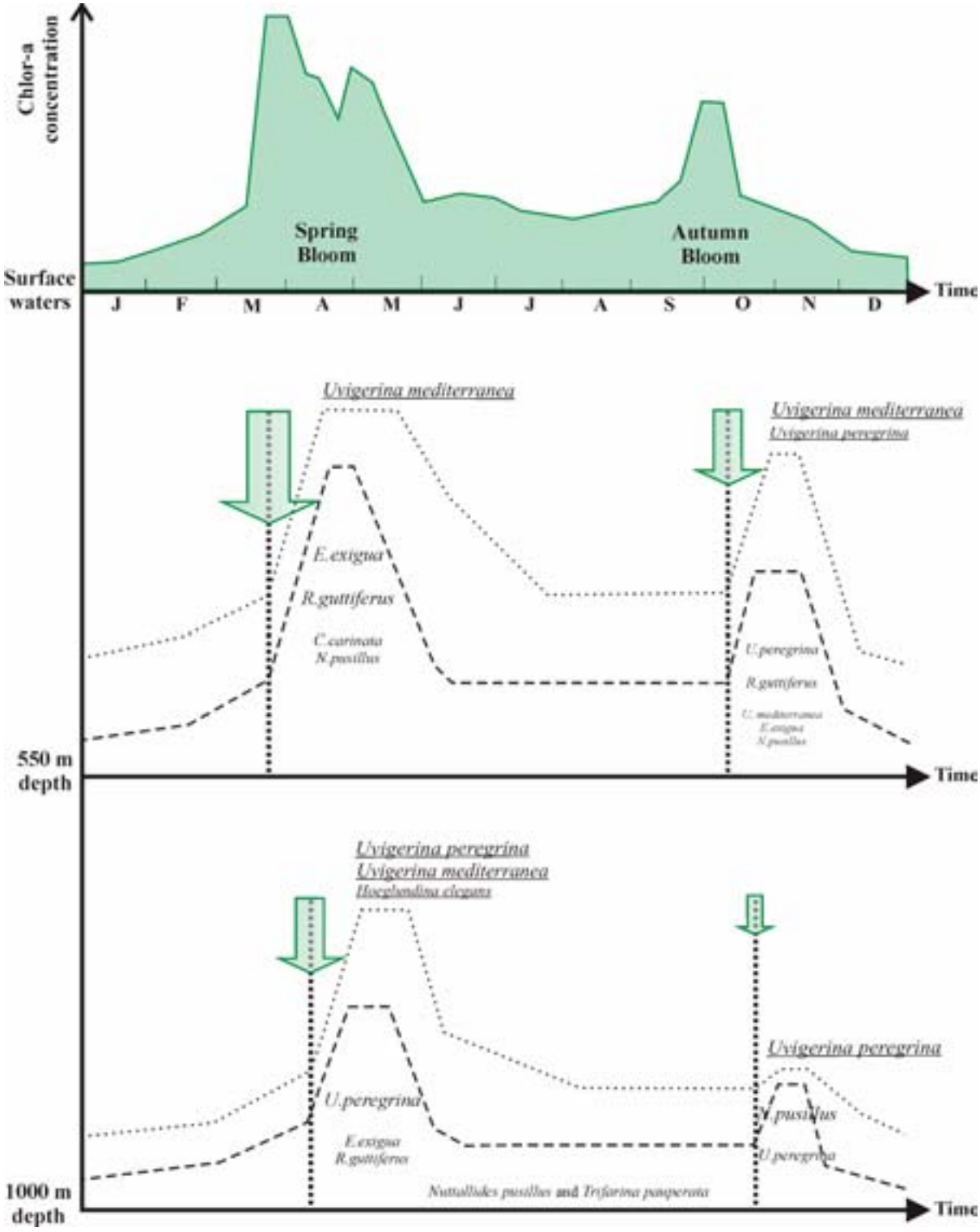

*Fig. 8 Pelagic-benthic coupling and stepwise benthic ecosystem response to phytodetritus input at station B (550 metres) and station A (our station; 1000 metres depth)**:** ODYSSEY model. See text for further explanation.*

Because of the occurrence of very opportunistic taxa (e.g. *E. exigua*, *U. mediterranea*) and higher exported organic matter fluxes, temporal variability is widely more marked at the station B than at station A. The gradual decrease with depth of the periodic organic matter flux along a slope transect is a fundamental parameter structuring the composition and seasonal dynamics of foraminiferal faunas. At both stations, opportunistic faunas respond to phytodetritus deposits; but the general trophic level decides which species are most successful to thrive. Foraminiferal faunas composition and density directly reflect the seasonal and absolute organic matter flux reaching the sea floor.

Acknowledgements

We would like to thank the French national program PROOF (INSU-CNRS) for sponsoring the OXYBENT program. We have special and kind thoughts for the crews and the captains of the Côte de la Manche, our scientific ship during all campaigns. We would like to thank the Space Applications Institute/Marine Environment Unit (SAI/ME) from the Joint Research Center (European Commission) (JRC/EC) and more precisely N. Hoepffner and G. Zibordi, for the easy access to the on-line archives of chlorophyll-a concentration (SeaWIFS data). We are grateful for the SeaWIFS project (NASA/ GSFC DAAC), which provides very useful satellite images. We also thank Stéphanie Caradec, Jean-Claude Sorbe and Pierre Carbonel for the very interesting and helpful discussions we had about macro- and meiofaunal ecology in the Bay of Biscay. We have particular thanks for Emmanuelle Geslin and for the precise and necessary taphonomic work we made with her in the laboratory of l'Ile d'Yeu (France). We thank Gert-Jan Reichart for helpful suggestions during writing of this paper.

Appendix A

Species of benthic foraminifera recognised at station A from the Bay of Biscay, with references to plates and figures in the literature about Atlantic and Mediterranean foraminifera.

Species	References
Adercotryma glomerata (Brady), 1878	Jones (1994), pl. 34, Figs. 15-18
Ammobaculites agglutinans (d'Orbigny), 1846	Hess (1998), pl. 4, Fig. 4
Ammolagena clavata (Jones and Parker), 1860	Jones (1994), pl. 41, Figs. 12-16
Amphicoryna scalaris (Batsch), 1791	Jones (1994), pl. 63, Figs. 28-31
Biloculinella irregularis(d'Orbigny) 1839	d'Orbigny (1839), pl. 8, Fig. 20 and 21
Bolivina albatrossi Cushman, 1922	Schiebel (1992), pl.1, Fig. 1a-b
Bolivina spathulata (Williamson), 1858	Jorissen (1987), pl. 1, Fig. 5
Bulimina costata d'Orbigny, 1826	Van Leeuwen (1989), pl. 8, Fig 2 and 3
Bulimina inflata Seguenza, 1862	Van Leeuwen (1989), pl. 8, Fig. 4
Bulimina marginata d'Orbigny, 1826	Hess (1998), pl. 10, Fig. 7
Cassidulina carinata Silvestri, 1896	Phleger et al.(1953), pl 9, Figs. 32-37
Cassidulina crassa d'Orbigny, 1839	Jones (1994), pl. 54, Fig 4 and 5
Chilostomella oolina Schwager, 1878	Jones (1994), pl. 55, Figs. 12-14
Cibicides lobatulus Walker & Jacob, 1798	Jones (1994), pl. 92, Fig. 10
Cibicidoides pachydermus (Rzehac), 1886	Jones (1994), pl. 94, Fig 9
Cibicidoides robertsonianus (Brady), 1881	Van Leeuwen (1989), pl. 9, Figs. 1-3
Cibicidordes ungerianus d'Orbigny, 1846	Jones (1994), pl. 94, Fig. 9
Cornuspira foliacea (Philippi), 1844	Jones (1994), pl. 11, Fig. 5 and 6
Cornuspira involvens (Reuss), 1950	Jones (1994), pl. 11, Figs. 1-3
Cribrostomoides subglobosus (Cushman), 1910	Jones (1994), pl. 34, Figs. 8-10
Crithionina abyssorum Kiaer, 1899	Kiaer (1899), pl.1, Figs.1-4
Cystammina argentea Earland, 1934	Timm (1992), pl.3, Fig. 8
Cystammina pauciloculata (Brady), 1879	Jones (1994), pl. 41, Fig 1
Dentalina albatrossi (Cushman), 1923	Jones (1994), pl. 64, Figs. 11-14
Dentalina bradyensis (Dervieux), 1894	Jones (1994), pl. 62, Fig. 19 and 20
Dentalina subsoluta (Cushman), 1923	Jones (1994), pl.62, Figs. 13-16
Eggerella bradyi (Cushman), 1911	Jones (1994), pl. 47, Figs. 4-7
Eggerella scabra (Williamson), 1858	Jones (1994), pl. 47, Figs. 15-17
Epistominella exigua (Bradyi), 1884	Schiebel (1992), pl.5, Fig.9
Gavelinopsis translucens (Phleger & Parker), 1951	Schiebel (1992), pl. 4, Fig 5
Glandulina ovula d'Orbigny, 1846	Jones (1994), pl. 61, Figs. 17-22
Globobulimina affinis (d'Orbigny), 1839	Phleger et al.(1953), pl. 6, Fig. 32
Globocassidulina subglobosa (Bradyi), 1881	Jones (1994), pl. 54, Fig.17
Gyroidina altiformis Stewart & Stewart, 1930	Jorissen (1987), pl. 1, Fig. 11
Gyroidina orbicularis (sensu Parker, Jones and Brady), 1865	Jones (1994), pl. 115, Fig. 6
Gyroidina umbonata (Silvestri), 1898	Parker (1958), pl. 3, Fig. 19 and 20
Haplophragmoides bradyi (Robertson), 1891	Schiebel (1992), pl. 7, Fig. 1a
Hoeglundina elegans (d'Orbigny), 1826	Phleger et al (1953), pl 9, Fig. 24 and 25
Hormosina globulifera Brady, 1879	Jones (1994), pl. 39, Figs. 1-4, 6
Hyalinea balthica (Schroeter), 1783	Jones (1994), pl. 112, Fig. 1 and 2
Karreriella bradyi (Cushman), 1911	Jones (1994), pl. 41, Figs. 1-4
Laganammina pseudodifflugiformis Nogan, 1964	Nogan (1964), pl 1, Fig.1
Lenticulina gibba (d'Orbigny), 1839	Hess (1998), pl.13, Fig. 1
Lenticulina peregrina (Schwager), 1866	Cushman and McCulloch (1950), pl. 39, Fig. 5
Lenticulina vortex (Fichtel and Moll), 1798	Jones (1994), pl.69, Figs. 14-16
Marginula obesa (Cushman), 1923	Jones (1994), pl. 65, Fig 5 and 6
Melonis barleeanus (Williamson), 1858	Van Leeuwen (1989), pl. 13, Fig. 1 and 2
Nonionella turgida (Williamson), 1858	Jones (1994), pl. 109, Figs. 17-19
Nuttallides pusillus (Parr), 1950	Phleger et al (1953), pl 9, Fig. 5 and 6
Nuttallides umboniferus (Cushman), 1933	Van Leeuwen (1989), pl. 15, Figs. 11-13; pl. 16, Figs. 1-7
Oridorsalis umbonatus Reuss, 1851	Van Leeuwen (1989), pl. 17, Figs. 1-13
Paratrochammina challengeri Brönnimann and Whittaker, 1988	Jones (1994), pl. 35, Fig. 10
Pullenia quinqueloba (Reuss), 1851	Jones (1994), Pl. 84, Fig. 14 and 15
Pyrgo depressa (d'Orbigny), 1826	Jones (1994), Pl. 2, Figs. 12, 16 and 17
Pyrgo murrhina (Schwager), 1866	Hess (1998), pl.9, Fig. 1
Pyrgo subsphaerica d'Orbigny, 1839	Cushman (1929), pl. 18, Fig 1 and 2
Pyrgoella sphaera (d'Orbigny), 1839	Jones (1994), pl. 2, Fig. 4
Quinqueloculina seminula (Linné), 1758	Jones (1994), pl. 5, Fig. 6
Reophax bilocularis Flint, 1899	Hess (1998), pl.2, Fig. 13 and 14
Reophax guttiferus Brady, 1881	Jones (1994), pl. 31, Fig. 10-15
Reophax micaceus Eerland, 1934	Schiebel (1992), pl. 8, Fig. 7
Reophax scorpiurus Montfort, 1808	Loeblich and Tappan (1988), pl. 44, Figs. 1-3
Rhabdamina cornuta (Brady), 1879	Jones (1994), pl. 22, Fig. 11 and 13
Robertinoides bradyi (Cushman and Parker), 1936	Jones (1994), pl. 50, Fig 18
Rotamorphina? involuta (Parker), 1958	Parker (1958), pl. 4, Figs. 28-30
Sigmoilopsis schlumbergeri Silvestri, 1904	Jones (1994), pl. 8, Figs. 1-4
Siphogenerina columellaris (Brady), 1881	Jones (1994), pl. 75, Figs. 15-17
Siphotextularia affinis Fornasini, 1883	Kohl (1985), pl. 2, Fig. 5
Siphotextularia concava (Karrer), 1868	Jones (1994), pl.42, Figs. 13-14
Spirophtalmidium acutimargo (Brady), 1884	Jones (1994), pl.10, Fig. 13
Stainforthia fusiformis (Williamson), 1858	Schiebel (1992), pl. 2, Fig. 10
Technitella legumen Norman, 1878	Jones (1994), pl.25, Figs. 8-10
Textularia earlandi Parker, 1952	Timm (1992), pl.3, Fig 1a-b
Thurammina albicans Bradyi, 1879	Jones (1994), pl.37, Figs. 2-7
Thurammina papillata Bradyi, 1979	Jones (1994), pl.36, Figs. 7-18
Trifarina angulosa (Williamson), 1858	Jones (1994), pl. 74, Fig. 17 and 18
Trifarina bradyi Cushman, 1923	Jones (1994), pl. 67, Figs. 1-3
Trifarina pauperata (Heron-Allen and Earland), 1932	Schiebel (1992), pl. 3, Fig 3
Triloculina tricarinata d'Orbigny, 1826	Hess (1998), pl.9, Fig. 10
Trochammina globigeriniformis (Parker and Jones), 1865	Timm (1992), pl.4, Fig. 2a-b
Uvigerina elongatastriata (Colom), 1952	Van der Zwaan et al. (1986), pl. 6, Figs. 1-8
Uvigerina mediterranea Hofker, 1932	Van der Zwaan et al (1986), pl. 5, Figs. 1-7
Uvigerina peregrina Cushman, 1923	Van der Zwaan et al. (1986), pl. 1, Figs.1-6
Uvigerina proboscidea Schawger, 1866	Van der Zwaan et al. (1986), pl. 12, Figs. 1-4

Appendix B

Census data for benthic foraminifera in the >150 µm size fraction for all 12 cores.

N.B. Numbers are not standardized for sediment volume.

OB1A																			
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-4.5	4.5-5.5	5.5-6.5	6.5-7.5	7.5-8.5	8.5-9.5	9.5-10.5	Total	%
Perforate																			
Indet	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Epistinc Indet	0	0	10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1.93
?Anomalinoides sp	4	0	3	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	8	1.55
Bulimina inflata	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.97
Bulimina marginata	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.19
Cibicidoides pachydermus	4	2	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	11	2.13
Glandulina ovula	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.19
Globobulimina affinis	0	0	0	0	0	0	3	13	8	10	10	17	44	27	5	0	0	137	26.50
Gyroidina altiformis	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.58
Hoeglundina elegans	4	4	4	6	7	1	0	0	0	0	0	0	0	0	0	0	0	26	5.03
Lenticulina sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Lenticulina sp.1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Lenticulina gibba	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Lenticulina peregrina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Melonis barleeanus	0	0	0	0	3	1	2	0	0	0	0	0	0	0	0	0	0	6	1.16
Nuttallides pusillus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Nuttallides umbonifera	8	8	6	2	1	0	0	0	0	0	0	0	0	0	0	0	0	27	5.22
Rosalina sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Siphogenerina columellaris	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.19
Uvigerina mediterranea	5	12	12	12	4	0	0	0	0	0	0	0	0	0	0	0	0	45	8.70
Uvigerina peregrina	2	1	10	22	37	13	0	0	0	0	0	0	0	0	0	0	0	85	16.44
Porcellaneous																			
Biloculinella sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Cornuspira foliacea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Cornuspira involvens	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.58
Pyrgo depressa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	10	1.93
Pyrgo murrhina	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Pyrgo subsphaerica	0	0	1	1	2	0	1	0	0	0	0	0	0	0	0	0	0	5	0.97
Pyrgoella sphaera	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.58
Quinqueloculina seminula	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Quinqueloculina sp 2	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Non fossilising agglutinated																			
Agglutinated sp 11	0	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.97
Agglutinated sp 29	0	2	2	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	5	0.97
Agglutinated sp 46	0	0	1	0	0	0	0	2	0	0	0	0	0	0	0	0	0	3	0.58
Ammobaculites agglutinans	0	5	3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	10	1.93
Ammolagena clavata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Cribrostomoides subglobosus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Cyclammina sp 1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Cystammina pauciloculata	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.77
Eggerella bradyi	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Karreriella bradyi	1	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.97
Lagenammina pseudodifflugiformis	0	2	12	1	0	0	0	0	0	0	0	0	0	2	0	0	0	17	3.29
Paratrochammina challengeri	1	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.77
Recurvoides sp	0	0	0	0	1	5	0	0	0	0	0	0	0	0	0	0	0	6	1.16
Reophax sp.6	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Reophax guttiferus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Reophax scorpiurus	15	9	6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	31	6.00
Thurammina albicans	0	2	5	4	4	1	0	0	0	0	0	0	0	0	0	0	0	16	3.09
Fossilising agglutinated																			
Sigmoilopsis schlumbergeri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Siphotextularia concava	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Total live foraminifera	57	57	103	54	65	27	11	15	9	12	11	18	44	29	5	0	0	517	100.00
Nbr species	20	17	28	13	12	9	5	2	2	3	2	2	1	2	1	0	0	48	
Arborescent indet	3	26	76	112	267	72	2	0	0	0	0	0	0	0	0	0	0	560	

OB2A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina inflata	0	0	2	0	0	0	0	(1)	0	0	0	0	0	0	0	0	3	0.68
Cibicidoides pachydermus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.45
Cibicidoides ungerianus	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.23
Dentalina subsoluta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Fissurina spp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Glandulina ovula	1	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	3	0.68
Globobulimina affinis	0	0	0	0	0	0	2	2	2	2	5	1	0	0	0	0	14	3.16
Gyroidina altiformis	0	0	0	0	1	0	0	0	0	0	0	0	(1)	0	0	0	2	0.45
Gyroidina orbicularis	0	0	2	0	0	2	4	4	1	1	0	0	0	0	0	0	14	3.16
Hoeglundina elegans	3	8	2	4	1	0	0	0	0	0	0	0	0	0	0	0	18	4.06
Lenticulina peregrina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Marginula obesa	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Melonis berleeanus	0	0	1	3	3	5	6	7	6	6	0	0	0	0	0	0	37	8.35
Nuttallides umboniferus	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.45
Rotamorphina involuta	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.23
Trifarina bradyi	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.23
Trifarina carinata	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.23
Uvigerina mediterranea	10	11	16	9	7	5	8	5	0	0	0	1	2	1	0	(1)	76	17.16
Uvigerina peregrina	2	11	40	12	17	10	9	10	3	0	0	0	(1)	0	0	0	115	25.96
Porcellaneous																		
Pyrgo murrhina	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Pyrgo subsphaerica	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.68
Quinqueloculina sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Quinqueloculina sp.2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Quinqueloculina sp.53	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Spiroloculina sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Triloculina tricarinata	0	1	6	1	2	4	6	0	1	0	0	0	0	0	0	0	21	4.74
Non fossilising agglutinated																		
Agglutinated sp.11	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Agglutinated sp.31	0	0	1	0	0	0	0	0	0	0	0	1	0	0	0	0	2	0.45
Agglutinated sp.46	0	0	2	0	1	3	1	0	1	0	0	0	0	0	0	0	8	1.81
Ammobaculites agglutinans	2	3	0	2	2	0	0	0	0	0	0	0	(1)	0	0	0	10	2.26
Ammolagena sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Ammolagena clavata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Cribrostomoides sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Cribrostomoides subglobosus	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.45
Cyclammina sp.1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0.45
Cystammina pauciloculata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Eggerella bradyi	0	0	3	0	2	0	0	0	0	0	0	0	0	0	0	0	5	1.13
Glomospira spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Karreriella bradyi	1	0	4	4	0	0	0	0	0	0	0	0	0	0	0	0	9	2.03
Lagenammina pseudodifflugiformis	2	1	6	3	1	0	2	3	0	0	0	0	0	0	0	0	18	4.06
?Miliammina sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Psammosphaera spp.	1	2	0	0	3	0	0	0	0	0	0	0	0	0	0	0	6	1.35
Recurvoides sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Reophax guttiferus	0	3	0	1	1	0	0	0	0	0	0	0	0	0	0	0	5	1.13
Reophax micaceus	0	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.90
Reophax scorpiurus	10	1	2	1	4	1	1	0	0	0	0	0	0	0	0	0	20	4.51
Saccammina spp.	0	1	1	1		1	0	0	0	0	0	0	0	0	0	0	4	0.90
Technitella legumen	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.23
Thurammina albicans	1	1	4	1	2	2	2	0	0	0	0	0	0	0	0	0	13	2.93
Thurammina papillata	0	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0	2	0.45
Fossilising agglutinated																		
Sigmoilopsis schlumbergeri	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.23
Total live foraminifera	36	49	100	50	55	35	44	34	15	9	5	3	3	2	0	1	443	100.00
Nbr species	13	15	22	20	21	11	13	9	7	3	1	3	4	2	0	1	51	
Arborescent indet.	3	13	39	36	44	7	2	3	0	0	0	0	0	0	0	0	147	
Ostracoda	1	0	3	2	3	1	2	2	0	0	0	0	0	0	0	0	14	

OB2A bis																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
?Anomalinoides sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.29
Bulimina inflata	0	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0.87
Cibicidoides pachydermus	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.87
Cibicidoides ungerianus	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	3	0.87
Dentalina bradyensis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Glandulina ovula	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Globobulimina affinis	0	0	0	0	0	0	1	0	0	0	0	2	0	0	0	0	3	0.87
Gyroidina orbicularis	0	0	1	4	3	1	2	1	3	0	0	0	0	0	0	0	15	4.37
Hoeglundina elegans	5	0	3	2	4	2	3	0	0	0	0	0	0	0	0	0	19	5.54
Melonis barleeanus	0	3	4	4	4	2	1	0	0	0	0	0	0	0	0	0	18	5.25
Nuttalides umbonifera	2	1	1	0	1	5	1	0	0	0	0	0	0	0	0	0	11	3.21
Parafissurina spp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Pullenia quinqueloba	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.29
Rosalina sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Rotamorphina involuta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.29
Uvigerina mediterranea	9	7	3	7	12	12	6	3	0	0	0	0	0	0	0	0	59	17.20
Uvigerina peregrina	9	14	15	16	16	13	3	2	0	0	0	0	0	0	0	0	88	25.66
Porcellaneous																		
Biloculinella irregularis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Pyrgo subsphaerica	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Pyrgoella sphaera	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Quinqueloculina sp.2	2	1	3	1	4	1	0	0	(1)	0	0	0	0	0	0	0	13	3.79
Quinqueloculina sp.53	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Non fossilising agglutinated																		
Indet	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.87
Agglutinated sp.11	1	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	5	1.46
Agglutinated sp.29	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	2	0.58
Agglutinated sp.46	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.58
Ammobaculites agglutinans	2	2	0	4	3	1	0	0	0	0	0	0	0	0	0	0	12	3.50
Cribrostomoides sp.	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.29
Cribrostomoides subglobosus	0	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	3	0.87
Cribrostomoides subglobosus	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.87
Cribrostomoides subglobosus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Cribrostomoides subglobosus	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0.58
Karrerella bradyi	1	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	3	0.87
Lagenammina pseudodifflugiformis	8	6	0	3	2	1	1	0	1	0	0	0	(1)	0	0	0	23	6.71
?Miliammina sp	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.58
Psammosphaera spp.	0	4	0	2	0	0	(1)	0	0	(1)	0	0	0	0	0	0	8	2.33
Recurvoides sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.29
Reophax sp.12	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Reophax scorpiurus	3	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	6	1.75
Rhabdammina cornuta	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Saccammina spp	1	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.87
Technitella legumen	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.29
Thurammina albicans	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	4	1.17
Thurammina papillata	1	1	1	0	0	0	3	0	0	0	0	0	0	0	0	0	6	1.75
Vanhoeffenella sp.	0	2	1	0	0	0	0	0	0	0	(1)	0	0	0	0	0	4	1.17
Total live foraminifera	48	58	36	50	66	44	24	6	5	2	1	2	1	0	0	0	343	100.00
Nbr species	16	22	11	15	22	15	12	3	3	2	1	1	1	0	0	0	44	
Arborescent indet.	9	32	39	22	65	105	46	10	11	2	0	0	0	0	0	0	341	
Ostracoda	0	2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	3	

OB3A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina inflata	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.89
Cibicidoides pachydermus	1	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.89
Fissurina spp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Globobulimina affinis	0	0	0	0	0	0	0	0	0	1	0	0	(1)	0	0	0	2	0.89
Gyroidina altiformis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Gyroidina orbicularis	0	0	0	0	3	3	0	2	0	0	0	0	0	0	0	0	8	3.56
Hoeglundina elegans	3	13	4	2	1	0	0	0	0	0	(1)	0	0	0	0	0	24	10.67
Lenticulina sp.26	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Marginula obesa	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.89
Melonis berleeanus	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0.89
Nuttallides umboniferus	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.89
Pullenia sp.1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Robertinoides bradyi	0	0	0	1	1	1	1	0	0	0	0	0	0	0	0	0	4	1.78
Uvigerina mediterranea	22	9	2	3	4	0	0	0	0	0	0	0	0	0	0	0	40	17.78
Uvigerina peregrina	39	18	5	0	0	0	0	0	0	0	0	0	0	(1)	0	0	61	27.11
Porcellaneous																		
Biloculinella irregularis	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Cornuspira involvens	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Pyrgo subsphaerica	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.33
Quinqueloculina sp.53	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Non fossilising agglutinated																		
Agglutinated sp.11	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	4	1.78
Agglutinated sp.29	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.33
Agglutinated sp.46	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Ammobaculites agglutinans	2	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4	1.78
Cribrostomoides subglobosus	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.89
Eggerella bradyi	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1.78
Karrerielta bradyi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
?Miliammina sp	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Lagenammina pseudodifflugiformis	2	10	0	2	4	0	0	0	0	0	0	0	0	0	0	0	18	8.00
Psammosphaera spp		1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.89
Reophax scorpiurus	13	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	18	8.00
Technitella legumen	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.44
Thurammina albicans	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.89
Thurammina papillata	0	1	1	0	1	2	0	0	0	0	0	0	0	0	0	0	5	2.22
Total live foraminifera	90	58	27	16	18	6	3	3	0	1	1	0	1	1	0	0	225	100.00
Nbr species	14	11	14	11	10	3	3	2	0	1	1	0	1	1	0	0	33	
Arborescent indet	3	4	36	15	78	28	1	9	0	0	0	0	0	0	0	0	174	
Ostracoda	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	

OB4A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Indet	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.56
Bulimina inflata	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	2	1.13
Cibicides lobatulus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Fissurina spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Globobulimina affinis	0	0	0	0	0	0	0	0	0	0	0	2	1	0	0	0	3	1.69
Gyroidina orbicularis	0	1	1	0	0	1	0	1	0	1	0	0	0	0	0	0	5	2.82
Hoeglundina elegans	13	0	0	0	2	0	0	0	0	0	0	0	(1)	0	0	0	16	9.04
Lenticulina sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.56
Melonis barleeanus	0	0	0	0	3	0	1	0	0	0	0	0	0	0	0	0	4	2.26
Uvigerina mediterranea	31	4	5	10	6	3	0	1	0	0	0	0	(1)	0	0	0	61	34.46
Uvigerina peregrina	18	4	0	5	6	4	0	0	0	0	0	0	0	0	0	0	37	20.90
Porcellaneous																		
Cornuspira involvens	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Pyrgo subsphaerica	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Quinqueloculina seminula	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	1.13
Triloculina tricarinata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Non fossilising agglutinated																		
Indet	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	1.13
Agglutinated sp.29	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.56
Ammobaculites agglutinans	4	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	5	2.82
Ammolagena clavata	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	1.13
Cribrostomoides subglobosus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Cribrostomoides subglobosus	0	0	0	2	2	1	0	0	0	0	0	0	0	0	0	0	5	2.82
Karreriella bradyi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Lagenammina pseudodifflugiformis	3	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	4	2.26
Psammosphaera spp.	0	0	0	0	2	0	0	(1)	0	0	0	0	0	0	0	0	3	1.69
Reophax micaceus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Reophax scorpiurus	5	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	6	3.39
Rhabdammina cornuta	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Saccammina spp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.56
Thurammina albicans	1	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	3	1.69
Thurammina papillata	0	0	0	0	0	4	0	0	0	0	0	0	0	0	0	0	4	2.26
Total live foraminifera	81	12	7	22	27	18	1	3	0	1	0	2	3	0	0	0	177	100.00
Nbr speries	13	6	2	7	11	9	1	3	0	1	0	1	3	0	0	0	28	
Arborescent indet	6	3	4	18	43	14	0	5	0	0	1	0	1	3	0	0	98	
Ostracoda	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	

0B5A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina inflata	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Cibicidoides pachydermus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.44
Dentalina sp.33	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.44
Dentalina sibatrassi	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Globobulimina affinis	0	0	0	0	0	0	0	0	0	2	0	0	0	(1)	0	0	3	1.32
Gyroidina altiformis	1	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	1.32
Gyroidina orbicularis	0	0	0	0	0	3	1	3	0	0	0	0	0	0	0	0	7	3.07
Hoeglundina elegans	4	10	9	4	1	0	0	0	0	0	0	0	0	0	0	0	28	12.28
Marginula obesa	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Melonis berleeanus	0	0	0	1	2	0	2	0	0	0	0	0	0	0	0	0	5	2.19
Nuttallides umboniferus	5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	3.07
Robertinoides bradyi	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Rosalina sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Rotamorphina involuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Trifarina bradyi	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Uvigerina mediterranea	18	8	3	2	3	0	0	0	0	0	0	0	0	0	0	0	34	14.91
Uvigerina peregrina	21	11	7	4	3	0	0	0	0	0	0	0	0	0	0	0	46	20.18
Porcellaneous																		
Pyrgo sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Non fossilising agglutinated																		
Indet	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Agglutinated sp.31	0	1	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.88
Agglutinated sp.46	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Ammobaculites agglutinans	7	6	3	0	0	(1)	0	0	0	0	0	0	0	0	0	0	17	7.46
Ammolagena clavata	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Cribrostomoides sp.	7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	3.07
Cribrostomoides subglobosus	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0.88
Cuthiomina abyssorum	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Eggerella bradyi	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.32
Glomospira spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Karrerielta bradyi	0	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1.32
Lagenammina pseudodifflugiformis	3	5	8	4	3	0	0	(1)	0	0	0	0	0	0	0	0	24	10.53
Psammosphaera spp.	1	1	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	3	1.32
Recurvoides sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Reophax guttiferus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.44
Reophax scorpiurus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Saccammina spp.	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.88
Thurammina albicans	0	0	0	1	0	0	(1)	0	0	0	0	0	0	0	0	0	2	0.88
Thurammina papillata	0	0	0	1	3	2	0	0	0	0	0	0	0	0	0	0	6	2.63
Total live foraminifera	73	53	36	23	21	7	5	5	1	2	1	0	0	1	0	0	228	100.00
Nbr species	13	15	11	13	12	4	4	3	1	1	1	0	0	1	0	0	36	
Arborescent indet	8	15	45	45	110	27	6	8	0	0	0	0	0	0	0	0	264	
Ostracoda	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0	6	

OB6A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina inflata	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Globobulimina affinis	0	0	0	0	0	0	0	0	1	1	9	4	5	0	0	0	20	6.56
Gyroidina altiformis	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Gyroidina orbicularis	0	0	0	1	1	2	4	0	0	0	0	0	0	0	0	0	8	2.62
Hoeglundina elegans	6	15	22	9	2	0	0	0	0	0	0	0	0	0	0	0	54	17.70
Lagena sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Lenticulina sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Marginula obesa	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Melonis berleeanus	0	0	1	2	3	2	1	1	1	0	0	0	0	0	0	0	11	3.61
Nuttallides umboniferus	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	5	1.64
Pullenia quinqueloba	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.33
Rotamorphina involuta	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Trifarina sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Trifarina bradyi	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Uvigerina mediterranea	6	9	27	14	4	5	0	0	1	1	0	0	0	0	0	0	67	21.97
Uvigerina peregrina	3	16	21	4	8	1	0	0	0	0	0	0	0	0	0	0	53	17.38
Porcellaneous																		
Cornuspira involvens	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Pyrgo depressa	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Pyrgo murrhina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Pyrgo subsphaerica	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Quinqueloculina sp.2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Non fossilising agglutinated																		
Indet	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Agglutinated sp.31	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Ammobaculites agglutinans	0	1	4	2	2	0	2	0	0	0	0	0	0	0	0	0	11	3.61
Ammolagena clavata	3	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	1.31
Cribrostomoides subglobosus	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Cyclammina sp.1	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0.66
Eggerella bradyi	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Karrerella bradyi	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.66
Lagenammina pseudodifflugiformis	1	6	7	1	1	0	0	0	0	0	0	0	0	0	0	0	16	5.25
Psammosphaera spp.	1	0	3	1	0	0	0	0	0	0	(1)	0	0	0	0	0	6	1.97
Recurvoides sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.33
Reophax guttiferus	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Reophax scorpiurus	1	1	5	1	1	0	0	0	0	0	0	0	0	0	0	0	9	2.95
Saccammina spp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.33
Thurammina albicans	0	0	1	1	2	1	0	0	0	0	0	0	0	0	0	0	5	1.64
Thurammina papillata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.33
Total live foraminifera	26	56	102	41	32	15	7	2	3	2	10	4	5	0	0	0	305	100.00
Nbr species	10	14	20	14	16	8	3	2	3	2	2	1	1	0	0	0	35	
Arborescent indet	0	3	31	51	146	32	4	0	1	0	0	0	0	0	0	0	268	
Ostracoda	0	1	2	4	1	2	0	1	0	0	0	0	0	0	0	0	11	

OB7A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Indet	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Bulimina inflata	0	0	0	0	2	0	2	0	0	0	0	0	0	(1)	0	0	5	1.22
Cibicidoides pachydermus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Fissurina spp.	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	2	0.49
Glandulina ovula	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.24
Globobulimina affinis	0	0	0	0	0	0	0	0	0	3	5	0	3	0	0	0	11	2.68
Gyroidina altiformis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Gyroidina orbicularis	0	0	0	0	2	0	2	1	1	5	1	0	0	0	0	0	12	2.92
Hoeglundina elegans	6	17	27	6	18	4	0	0	0	0	0	0	0	0	0	0	78	18.98
Lenticulina sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Melonis barleeanus	0	0	0	0	3	5	2	2	2	0	1	0	0	0	0	0	15	3.65
Nuttallides umbonifera	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.49
Oridorsalis umbonatus	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.49
Polymorphina sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Pullenia sp	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Pullenia quinqueloba	0	0	0	0	1	1	2	0	0	0	0	0	0	0	0	0	4	0.97
Robertinoides bradyi	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.24
Rotamorphina involuta	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.49
Uvigerina mediterranea	9	17	23	21	18	4	2	0	0	0	0	1	2	0	(1)	0	98	23.84
Uvigerina peregrina	4	14	22	15	20	3	0	1	0	0	1	0	3	0	0	0	83	20.19
Porcellaneous																		
Cornuspira involvens	0	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0	4	0.97
Pyrgoella sphaera	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.24
Quinqueloculina seminula	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Quinqueloculina sp.2	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Non fossilising agglutinated																		
Agglutinated sp.29	0	1	2	3	0	1	0	0	0	0	0	0	0	0	0	0	7	1.70
Agglutinated sp.46	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Ammobaculites agglutinans	1	1	5	1	3	1	0	0	0	0	0	0	0	0	0	0	12	2.92
Cribrostomoides subglobosus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Cyclammina sp.1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0.73
Eggerella bradyi	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Karrerella bradyi	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	2	0.49
Lagenammina pseudodifflugiformis	0	5	3	2	5	1	1	0	0	0	0	0	2	0	(1)	0	20	4.87
Psammosphaera spp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.24
Recurvoides sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Reophax sp.19	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Reophax guttiferus	0	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0.73
Reophax scorpiurus	0	2	3	2	2	1	1	0	0	0	0	0	0	0	0	0	11	2.68
Rhabdammina cornuta	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
Saccammina spp	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.49
Thurammina albicans	0	0	0	1	4	8	1	0	0	0	(1)	0	0	0	0	0	15	3.65
Total live foraminifera	24	62	91	54	91	30	18	5	3	8	9	2	11	1	2	0	411	100.00
Nbr species	8	11	13	11	23	11	11	4	2	2	5	2	5	1	2	0	39	
Arborescent indet	0	0	6	17	26	29	12	4	1	1	0	0	0	0	0	0	96	
Ostracoda	1	0	3	0	0	0	1	2	0	0	0	0	0	0	0	0	7	

OB9A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Indet	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	1	0.20
?Animalinoides sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Bulimina inflata	4	1	0	0	0	0	0	0	0	2	1	0	0	1	3	1	13	2.55
Cibicidoides sp.	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Cibicidoides ungerianus	1	1	0	0	1	0	0	0	0	0	0	0	0	0	(1)	0	4	0.79
Dentalina bradyensis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Glandulina ovula	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Globobulimina affinis	0	0	0	0	0	0	0	0	1	7	4	1	0	0	0	0	13	2.55
Gyroidina affiformis	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Gyroidina orbicularis	0	0	1	0	0	0	1	0	4	0	3	0	0	(1)	0	0	10	1.96
Hoeglundina elegans	21	10	6	3	2	0	1	0	0	0	0	0	0	4	4	2	53	10.41
Marginula obesa	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Melonis berleeanus	0	1	0	0	0	3	2	1	1	2	6	0	0	(1)	0	0	17	3.34
Nonionella sp	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.59
Nuttallides umbonifera	8	4	2	1	0	0	0	(1)	0	0	0	0	0	0	0	0	16	3.14
Pullenia quinqueloba	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0.20
Robertinoides bradyi	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.20
Rotamorphina involuta	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Trifarina bradyi	2	1	1	0	0	0	0	0	0	0	(1)	0	0	0	0	0	5	0.98
Uvigerina mediterranea	35	11	13	0	5	0	0	0	0	0	4	0	1	9	11	5	94	18.47
Uvigerina peregrina	50	13	13	7	2	3	0	0	0	0	3	0	1	6	13	9	120	23.58
Porcellaneous																		
Cornuspira involvens	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Pyrgo depressa	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Pyrgo murrhina	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Pyrgo subsphaerica	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Pyrgoella sphaera	0	0	1	0	0	0	0	0	0	0	0	0	0	0	(1)	0	2	0.39
Quinqueloculina sp 53	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Non fossilising agglutinated																		
Indet	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.59
Agglutinated sp.11	2	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	4	0.79
Agglutinated sp.29	1	0	2	0	0	0	0	0	0	0	0	0	0	0	(1)	0	4	0.79
Agglutinated sp.31	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.20
Agglutinated sp.46	3	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	6	1.18
Ammobaculites agglutinans	17	1	3	0	1	0	0	0	0	0	0	0	0	1	1	0	24	4.72
Cribrostomoides subglobosus	27	3	5	3	0	0	0	0	0	0	1	0	0	2	0	0	41	8.06
Cyclammina sp.1	0	0	1	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	0.39
Eggerella bradyi	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.79
Glomospira spp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Hormosina globulifera	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Karrerilla bradyi	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.59
Lagenammina pseudodifflugiformis	2	1	1	4	3	0	0	0	0	0	0	0	0	0	1	2	14	2.75
?Miliammina sp	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Psammosphaera spp	0	1	0	1	0	0	(1)	0	0	0	0	0	0	0	0	0	3	0.59
Recurvoides sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Reophax sp.19	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Reophax scorpiurus	8	2	1	1	1	0	0	0	0	0	0	0	0	0	0	(1)	14	2.75
Rhabdammina cornuta	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Thurammina albicans	0	0	1	0	0	(1)	0	0	(1)	0	0	0	0	0	0	(1)	4	0.79
Thurammina papillata	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.79
Trochammina sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.20
Fossilising agglutinated																		
Sigmoilopsis schlumbergeri	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.39
Total live foraminifera	190	62	62	24	23	10	5	2	9	11	24	1	2	26	37	21	509	100.00
Nbr species	21	25	20	11	15	6	4	2	5	3	9	1	2	9	9	7	48	
Arborescent indet	28	38	94	52	46	22	7	9	7	1	1	0	0	0	1	0	306	
Ostracoda	5	2	2	1	0	0	0	0	0	1	0	0	0	0	2	0	13	

OB10A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Indet	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Epilithic Indet	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
?Anomalinoides sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Bulimina costata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Bulimina inflata	1	4	3	2	1	1	0	0	0	0	0	0	0	0	0	0	12	2.29
Bulimina marginata	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Cibicidoides pachydermus	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.38
Cibicidoides robertsonianus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Cibicidoides ungerianus	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Dentalina sp.40	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.19
Epistominella exigua	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Glandulina ovula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Globobulimina affinis	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.19
Gyroidina orbicularis	0	0	0	0	0	0	0	1	1	0	0	0	0	0	0	0	2	0.38
Hoeglundina elegans	2	14	25	18	9	8	0	0	0	0	0	0	0	0	(1)	0	77	14.72
Lagena sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Melonis barleeanus	0	0	0	2	1	0	0	2	0	0	0	0	0	0	0	0	5	0.96
Nuttallides umbonifera	0	6	1	2	3	1	0	0	0	0	0	0	0	0	0	0	13	2.49
Oridorsalis umbonatus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Parafissurina spp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.19
Pullenia quinqueloba	0	0	0	1	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.38
Robertinoides bradyi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Siphogenerina columellaris	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	2	0.38
Trifarina bradyi	0	0	2	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0.76
Uvigerina mediterranea	11	18	17	16	11	4	0	0	0	0	0	0	0	0	0	0	77	14.72
Uvigerina peregrina	30	35	28	15	18	13	0	0	0	0	0	0	0	0	0	0	139	26.58
Uvigerina proboscidea	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Porcellaneous																		
Biloculinella irregularis	0	0	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	2	0.38
Cornuspira foliacea	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Pyrgo murrhina	1	3	1	1	2	0	0	0	0	0	0	0	0	0	0	0	8	1.53
Pyrgo subsphaerica	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0.38
Pyrgoella sphaera	0	0	2	0	0	(1)	0	0	0	0	0	0	0	0	0	0	3	0.57
Quinqueloculina seminula	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.38
Non fossilising agglutinated																		
Indet	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Agglutinated sp.11	0	0	2	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.57
Agglutinated sp.29	1	2	3	0	1	0	0	1	0	1	0	0	0	0	0	0	9	1.72
Agglutinated sp.31	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0.38
Ammobaculites agglutinans	1	7	8	1	0	1	0	0	0	0	0	0	0	0	0	0	18	3.44
Cribrostomoides sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Cribrostomoides subglobosus	1	4	2	3	3	0	0	0	0	0	0	0	0	0	0	0	13	2.49
Cyclammina sp.1	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0.57
Cystammina pauciloculata	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Eggerella bradyi	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Karreriella bradyi	0	0	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	2	0.38
Lagenammina pseudodifflugiformis	3	13	11	7	11	2	0	0	0	0	0	0	0	0	0	0	47	8.99
Paratrochammina challengeri	0	3	3	1	0	0	0	0	0	0	0	0	0	0	0	0	7	1.34
Psammosphaera spp	1	3	0	0	1	3	0	0	0	0	0	0	0	0	0	0	8	1.53
Recurvoides sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Reophax guttiferus	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.76
Reophax micaceus	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.76
Reophax scorpiurus	0	2	1	1	0	1	0	0	0	0	0	0	0	0	0	0	5	0.96
Rhabdammina comuta	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Saccammina spp	0	0	5	1	3	0	0	0	0	0	0	0	0	0	0	0	9	1.72
Thurammina albicans	0	0	0	1	2	3	0	0	0	0	0	0	0	0	0	0	6	1.15
Thurammina papillata	0	0	0	0	2	0	3	1	0	0		0	0	0	0	0	6	1.15
Fossilising agglutinated																		
Sigmoilopsis schlumbergeri	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Textularia sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.19
Total live foraminifera	53	125	131	82	76	39	7	6	1	1	0	0	1	0	1	0	523	100.00
Nbr species	11	23	29	24	20	12	5	5	1	1	0	0	1	0	1	0	54	
Arborescent indet	4	12	33	22	255	54	42	19	6	4	0	0	0	0	0	0	451	
Ostracoda	0	2	5	2	1	3	0	0	1	0	0	0	0	0	0	0	14	

OB10A^{bis}										
Depth	**0-0.5**	**0.5-1**	**1-2**	**2-3**	**3-4**	**4-5**	**5-7.5**	**7.5-10**	**Total**	**%**
Perforate										
Amphycorina scalaris	0	0	1	1		0	0	0	2	0.21
Bolivina sp	1	1	0	0	0	0	0	0	2	0.21
Bulimina inflata	5	13	4	0	0	0	0	0	22	2.28
Cibicidoides pachyderma	0	1	0	0	0	0	0	0	1	0.10
Cibicidoides robertsonianus	1	0	0	0	0	0	0	0	1	0.10
Cibicidoides ungerianus	0	1	1	0	0	0	0	0	2	0.21
Dentalina bradyensis	0	0	0	1	0	0	0	0	1	0.10
Fissurina spp	0	2	2	0	0	0	0	0	4	0.42
Glandulina ovula	0	0	0	0	1	0	0	0	1	0.10
Globobulimina affinis	0	0	0	0	1	2	7	0	10	1.04
Gyroidina altiformis	1	1	0	0	0	0	0	0	2	0.21
Gyroidina orbicularis	0	3	2	5	1	0	0	0	11	1.14
Hoeglundina elegans	16	20	21	0	0	0	0	0	57	5.92
Lenticulina sp.1	2	0	0	0	0	0	0	0	2	0.21
Marginula obesa	0	0	2	0	0	0	0	0	2	0.21
Melonis barleeanus	1	2	9	13	1	1	0	(1)	28	2.91
Nonionella sp	0	1	0	0	0	0	0	0	1	0.10
Nuttallides pusillus	1	0	0	0	0	0	0	0	1	0.10
Nuttallides umboniferus	2	4	0	0	0	0	0	0	6	0.62
Parafissurina spp	0	0	1	0	0	0	0	0	1	0.10
Rotamorphina involuta	1	2	1	0	0	0	0	0	4	0.42
Siphogenerina columellaris	1	0	0	0	0	0	0	0	1	0.10
Trifarina bradyi	3	2	0	0	0	0	0	0	5	0.52
Uvigerina mediterranea	104	174	98	5	0	0	0	0	381	39.56
Uvigerina peregrina	50	62	21	2	0	0	0	0	135	14.02
Uvigerina proboscidea	2	0	0	0	0	0	0	0	2	0.21
Porcellaneous										
Biloculinella irregularis	1	0	0	0	0	0	0	0	1	0.10
Cornuspira foliacea	0	1	0	0	0	0	0	0	1	0.10
Cornuspira involvens	0	2	0	0	0	0	0	0	2	0.21
Pyrgo depressa	0	1	1	0	0	0	0	0	2	0.21
Pyrgo murrhina	2	3	0	0	0	0	0	0	5	0.52
Pyrgo subsphaerica	3	8	5	0	0	0	0	0	16	1.66
Pyrgoella sphaera	1	0	2	0	0	0	0	0	3	0.31
Quinqueloculina sp 2	0	2	2	0	0	0	0	0	4	0.42
Quinqueloculina sp 53	0	1	0	0	0	0	0	0	1	0.10
Non fossilising agglutinated										
Indet	0	1	0	0	0	0	0	0	1	0.10
Agglutinated sp.11	1	1	0	0	0	0	0	0	2	0.21
Agglutinated sp.29	0	0	0	1	0	0	0	0	1	0.10
Agglutinated sp.31	0	0	2	1	0	0	0	0	3	0.31
Agglutinated sp.46	0	0	0	3	0	0	2	0	5	0.52
Ammobaculites agglutinans	5	27	2	2	0	0	0	0	36	3.74
Ammolagena clavata	2	16	5	3	0	0	0	0	26	2.70
Ammolagena pseudodifflugiformis	13	23	13	2	1	1	1	2	56	5.82
Cribrostomoides subglobosus	2	11	3	0	0	0	0	0	16	1.66
Eggerella bradyi	0	3	7	0	0	0	0	0	10	1.04
Eggerella scabra	1	0	0	0	0	0	0	0	1	0.10
Hormosina globulifera	1	0	1	0	0	0	0	0	2	0.21
Karreriella bradyi	0	3	6	0	0	0	0	0	9	0.93
?Miliammina sp	0	1	0	0	0	0	0	0	1	0.10
Paratrochammina challengeri	1	0	0	0	0	0	0	0	1	0.10
Psammosphaera spp	1	0	3	1	1	1	0	0	7	0.73
Recurvoides sp.	0	0	1	0	0	0	0	0	1	0.10
Reophax sp 19	1	0	0	0	0	0	0	0	1	0.10
Reophax guttiferus	0	6	0	0	0	0	0	0	6	0.62
Reophax micaceus	2	1	0	0	0	0	0	0	3	0.31
Reophax scorpiurus	2	10	7	2	0	0	0	0	21	2.18
Saccammina spp	2	4	0	0	0	0	0	0	6	0.62
Thurammina albicans	0	2	9	0	(1)	0	0	0	12	1.25
Thurammina papillata	0	0	2	6	0	0	0	0	8	0.83
Trochammina sp 103	1	1	1	0	0	0	0	0	3	0.31
Fossilising agglutinated										
Sigmoilopsis schlumbergeri	1	2	1	0	0	0	0	0	4	0.42
Textularia sp.	0	1	0	0	0	0	0	0	1	0.10
Total live foraminifera	234	420	236	48	7	5	10	3	963	100.00
Nbr species	34	38	31	15	7	4	3	2	61	
Arborescent indet	13	52	100	67	14	3	1	0	65	
Ostracoda	3	0	2	1	1	0	0	0	3	

OB11A																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina inflata	5	1	0	1	3	1	0	0	0	(1)	0	0	0	0	(1)	0	13	2.03
Bulimina marginata	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Cibicidoides pachydermus	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Dentalina sp.56	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Dentalina bradyensis	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Fissurina spp.	0	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	2	0.31
Globobulimina affinis	0	0	0	0	0	0	0	5	17	12	4	4	2	1	0	0	45	7.04
Gyroidina altiformis	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Gyroidina orbicularis	1	1	0	0	1	0	1	1	0	0	0	0	0	0	0	0	5	0.78
Hoeglundina elegans	17	23	0	5	4	1	1	6	3	0	1	0	0	0	0	0	61	9.55
Lagena sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Lenticulina sp.	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Lenticulina sp.5	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Lenticulina vortex	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.16
Melonis barleeanus	0	0	0	2	3	4	1	2	1	0	0	0	0	0	0	0	13	2.03
Nonionella sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.16
Nuttalides umbonifera	3	2	0	0	1	0	0	0	0	(1)	0	0	0	0	0	0	7	1.10
Polymorphina sp.	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Rotamorphina involuta	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Trifarina bradyi	2	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	5	0.78
Uvigerina elongatastriata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Uvigerina mediterranea	38	46	2	18	16	2	2	2	0	2	0	0	(1)	0	(1)	0	130	20.34
Uvigerina peregrina	27	66	8	34	16	1	2	7	2	2	3	0	0	0	0	0	168	26.29
Uvigerina proboscidea	0	1	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	2	0.31
Porcellaneous																		
Biloculinella irregularis	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Pyrgo sp.6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Pyrgo murrhina	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	2	0.31
Pyrgo subsphaerica	1	2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Pyrgoella sphaera	0	3	0	0	5	0	0	0	0	0	0	0	0	0	0	0	8	1.25
Quinqueloculina sp.53	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Spiroplectammina acutimargo	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Triloculina tricarinata	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Non fossilising agglutinated																		
Indet	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Agglutinated sp.11	2	6	2	1	1	0	0	0	0	0	0	0	0	0	0	0	12	1.88
Agglutinated sp.29	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.16
Agglutinated sp.46	0	1	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.31
Ammobaculites agglutinans	10	15	0	1	2	0	0	0	0	0	0	0	0	0	0	0	28	4.38
Cribrostomoides subglobosus	1	5	0	3	3	0	0	0	(1)	0	0	0	0	0	0	0	13	2.03
Cyclammina sp.2	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	4	0.63
Eggerella bradyi	0	0	0	1		0	0	0	0	0	0	0	0	0	0	0	1	0.16
Glomospira spp.	0	0	0	1	1	0	0	(1)	0	0	0	0	0	0	0	0	3	0.47
Karrerilla bradyi	0	1	0	2	1	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Lagenammina pseudodifflugiformis	9	19	0	3	9	0	0	0	2	1	1	0	0	0	(1)	0	45	7.04
Psammosphaera spp	0	3	2	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0.78
Reophax sp.19	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Reophax guttiferus	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Reophax micaceus	1	2	0	1	0	0	0	0	0	0	0	0	0	0	0	0	4	0.63
Reophax scorpiurus	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Rhabdammina cornuta	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.31
Saccammina spp	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.47
Technitella legumen	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.16
Thurammina albicans	0	1	0	2	3	1	0	0	0	0	0	0	0	0	0	0	7	1.10
Thurammina papillata	0	0	1	2	0	0	0	0	0	0	0	0	0	0	0	0	3	0.47
Fossilising agglutinated																		
Sigmoilopsis schlumbergeri	0	3	0	1	0	0	0	1	0	0	0	0	0	0	0	0	5	0.78
Total live foraminifera	120	216	18	89	77	15	10	28	26	19	10	4	3	1	3	0	639	100.00
Nbr species	15	29	8	26	22	10	7	11	6	6	5	1	2	1	3	0	53	
Arborescent indet	0	10	2	19	103	35	4	2	0	0	0	0	0	0	0	0	175	
Ostracoda	0	4	0	2	4	1	0	0	0	0	0	0	0	0	0	0	11	

Appendix C

Census data for benthic foraminifera in the 63-150 µm size fraction for all 12 cores.

N.B. Numbers are not standardized for sediment volume

	OB1A		OB2A		OB2A^{bis}		OB3A		OB4A		OB5A	
Taxa	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
Perforate												
Indet	13	1 20	4	0 48	23	1 50	12	1 73	5	1 04	7	1 23
Epistic Indet			6	0 72	14	0 88					1	0 25
Ammotiamnoides sp	59	5 26	84	10 07	70	4 54	20	2 88	24	4 97	23	4 17
Baggina sp	3	0 24	6	0 72			4	0 58			8	1 47
Bolivina sp					3	0 21						
Bolivina sp 39	21	1 91	4	0 48	7	0 44	9	1 29	3	0 62		
Bolivina albatrossi	5	0 48	4	0 48			2	0 29			5	0 98
Bolivina spathulata	3	0 24	2	0 24	3	0 21	1	0 14				
Bolivina striata	3	0 24					5	0 72	5	1 04	21	3 92
Bolivina variata			2	0 24							1	0 25
Cassidulina carinata	5	0 48	4	0 48							1	0 25
Cassidulina crassa			2	0 24			1	0 14				
Ceratobulimina sp	5	0 48	10	1 20	37	2 42	6	0 86	3	0 62	1	0 25
Chrysostomella pollita							1	0 14				
Epistominella exigua	21	1 91	4	0 48	23	1 50	11	1 58	2	0 41	1	0 25
Fissurina spp							6	0 86			1	0 25
Gavelinopsis translucens					7	0 46	11	1 58				
Globocassidulina subglobosa	3	0 24	6	0 72	4	0 23	2	0 29				
Gyroidina sp	3	0 24			3	0 21	1	0 14				
Gyroidina altiformis									2	0 41		
Gyroidina orbicularis												
Gyroidina umbonata							1	0 14	2	0 41		
Hoeglundina elegans					3	0 21	5	0 72	8	1 66		
Hyalinea balthica	3	0 24	6	0 72	10	0 65					1	0 25
Lagena spp			2	0 24			1	0 14			1	0 25
Lenticulina sp							2	0 29	2	0 41		
Lenticulina peregrina							2	0 29				
Melonis barleeanus			2	0 24	7	0 44			1	0 21		
Nonionella sp			2	0 24	24	1 54	5	0 72				
Nonionella turgida									1	0 21	1	0 25
Nuttallides pseudo	443	39 71	259	30 94	441	28 56	118	16 98	50	10 35	128	23 53
Nuttallides umbonifera	13	1 20			27	1 75	16	2 30	2	0 41	8	1 47
Oolina spp	3	0 24	2	0 24								
Parafissurina spp	11	0 96										
Polymorphina spp												
Pullenia spp	5	0 48					2	0 29				
Robertina sp							1	0 14	2	0 41		
Robertinoides bradyi	3	0 24					1	0 14	2	0 41		
Siphogeneroides columelliformis			4	0 48								
Stainforthia fusiformis	3	0 24										
Trifarina sp			2	0 24	3	0 21						
Trifarina bradyi	15	1 44	4	0 48	17	1 08	9	1 29	6	1 24	15	2 70
Trifarina pauperata	72	6 46	115	13 91	189	12 26	114	16 40	55	11 39	84	15 44
Uvigerina sp									2	0 41	1	0 25
Uvigerina mediterranea	8	0 72			7	0 44	5	0 72	20	4 14		
Uvigerina peregrina	77	6 94	132	15 83	233	15 11	98	14 10	101	20 91	105	19 36
Uvigerina proboscidea			2	0 24								
Porcellaneous												
Indet			2	0 24	6	0 41						
Biloculinella sp							1	0 14	2	0 41		
Biloculinella irregularis												
Cornuspira involvens									3	0 62		
Miliolinella sp			2	0 24			1	0 14				
Quinqueloculina seminula											1	0 25
Quinqueloculina sp.53							1	0 14				
Sigmoilina sp			2	0 24								
Spiroplectinella dentata					4	0 23	7	1 01			4	0 74
Triloculina tricarinata			2	0 24								
Non fossilising agglutinated												
Indet	32	2 87	4	0 48	14	0 90	13	1 87	4	0 83	24	4 41
Agglutinated sp 11	3	0 24					1	0 14	2	0 41		
Agglutinated sp 22	53	4 78	52	6 24	14	0 90	8	1 15	16	3 31	33	6 13
Agglutinated sp 29	43	3 83			7	0 46	2	0 29				
Agglutinated sp 46	18	1 67	44	5 28	194	12 55	69	9 93	35	7 25	7	1 23
Adercotryma glomerata							1	0 14			4	0 74
Ammobaculites agglutinans					4	0 23	1	0 14				
Cribrostomoides sp					4	0 23						
Cribrostomoides subglobosus							2	0 29			1	0 25
Cystammina argentea	5	0 48			7	0 44	2	0 29	1	0 21	9	1 72
Eggerella sp 128	3	0 24			11	0 69					1	0 25
Eggerella bradyi	3	0 24	2	0 24			3	0 43	2	0 41	1	0 25
Eggerella scabra							1	0 14				
Haplophragmoides sp 5					7	0 46	1	0 14			4	0 74
Haplophragmoides bradyi												
Lagenammina pseudodifflugiformis	5	0 48			7	0 44	6	0 86			3	0 49
Miliammina sp.			4	0 48	7	0 46	4	0 58	2	0 41	1	0 25
Psammosphaera spp.	16	1 44			7	0 46	1	0 14	18	3 73	1	0 25
Recurvoides spp												
Reophax sp	3	0 24	2	0 24	4	0 23	1	0 14				
Reophax bilocularis							1	0 14				
Reophax guttifera			2	0 24	14	0 92	37	5 32			1	0 25
Reophax micaceus	80	7 18	6	0 72	59	3 85	22	3 17	81	16 77	1	0 25
Reophax scorpiurus							1	0 14	2	0 41	1	0 25
Saccammina spp												
Textularia earlandi	11	0 95	2	0 24	7	0 44	5	0 72			3	0 49
Trochammina sp 1			2	0 24			13	1 87	9	1 86		
Trochammina sp 5							1	0 14				
Trochammina sp 103	5	0 48	26	3 12	4	0 23	5	0 72			15	2 45
Trochammina globigeriniformis	24	2 15	10	1 20	10	0 65	11	1 58	4	0 83	9	1 72
Fossilising agglutinated												
Sigmoilopsis schlumbergeri	3	0 24										
Siphotextularia affinis	8	0 72					1	0 14			1	0 25
Siphotextularia concava									4	0 83		
Textularia sp												
Total live foraminifera	1115	100 00	834	100 00	1543	100 00	695	100 00	483	100 00	544	100 00
Nbr species	39		37		38		58		34		38	

	OB6A		OB7A		OB9A		OB10A		OB10A bis		OB11A	
Taxa	Total	%	Total	%	Total	%	Total	%	Total	%	Total	%
Perforate												
Indet	9	9 47	2	1 42	4	0 66	5	2 31	8	1 45	11	1 30
Epilthic Indet			4	2 84							3	0 30
Ammobaculoides sp	7	7 37	3	2 13	38	6 30	7	3 24	8	1 45	16	1 86
Baggina sp									3	0 50	8	0 88
Bolivina sp												
Bolivina sp 39			5	3 55	2	0 33	3	1 39	19	3 47	22	2 47
Bolivina albatrossi			2	1 42	2	0 33					3	0 30
Bolivina spathulata											11	1 21
Bulimina inflata					3	0 50	1	0 46	13	2 48		
Bulimina marginata												
Cassidulina carinata					2	0 33	1	0 46			8	0 86
Cassidulina crassa			1	0 71			1	0 46			5	0 61
Ceratobulimina sp					16	2 65					8	0 91
Chilostomella oolina												
Epistominella exigua	1	1 05	2	1 42	18	2 99	18	8 33	29	5 45	36	4 09
Fissurina spp			1	0 71	10	1 66	1	0 46	3	0 50	3	0 30
Gavelinopsis translucens											24	2 72
Globocassidulina subglobosa					2	0 33					3	0 39
Gyroidina sp					1	0 17						
Gyroidina altiformis									3	0 50		
Gyroidina orbicularis	1	1 05										
Gyroidina umbonata	1	1 05			4	0 66					3	0 39
Hoeglundina elegans	1	1 05	5	3 55	1	0 17			3	0 50	10	1 11
Hyalinea balthica											3	0 30
Lagena spp					2	0 33			3	0 50		
Lenticulina sp					1	0 17						
Lenticulina peregrina											2	0 28
Melonis barleeanus	1	1 05									3	0 30
Nonionella sp							2	0 93			5	0 61
Nonionella turgida												
Nuttallides pusillus	26	27 37	29	20 57	170	28 19	37	17 13	83	15 35	85	9 63
Nuttallides umbonifera	4	4 21	2	1 42	11	1 82	9	4 17	11	1 98		
Odina spp												
Paratissurina spp					1	0 17						
Polymorphina spp							1	0 46				
Pullenia spp					5	0 83			3	0 50		
Robertina sp									5	0 99		
Robertinoides bradyi												
Sphaeroidina columellaris											1	0 11
Stainforthia fusiformis	1	1 05										
Tolarina sp											3	0 30
Tolarina bradyi	4	4 21	7	4 96	8	1 33	4	1 85	27	4 95	19	2 18
Tolarina pauperata	16	16 84	23	16 31	70	11 61	25	11 57	64	11 88	125	14 23
Uvigerina sp							1	0 46				
Uvigerina mediterranea			3	2 13	1	0 17	3	1 39			6	0 72
Uvigerina peregrina	11	11 58	27	19 15	105	17 41	39	18 06	131	24 26	211	23 91
Uvigerina proboscidea									3	0 50		
Porcellaneous												
Indet					1	0 17	2	0 93	3	0 50	3	0 39
Biloculinella sp							2	0 93	8	1 49		
Biloculinella irregularis	1	1 05										
Cornuspira involvens					2	0 33						
Miliolinella sp									3	0 50	1	0 14
Quinqueloculina seminula												
Quinqueloculina sp 53												
Sigmoilinita sp.												
Spiophtalmidium acutimargo							1	0 46			3	0 30
Triloculina tricarinata												
Non fossilising agglutinated												
Indet	3	3 16	7	4 96	5	0 83	10	4 63	21	3 96	28	3 24
Agglutinated sp 11			2	1 42					3	0 50		
Agglutinated sp 22	3	3 16	11	7 80	3	0 50	13	6 02	32	5 94	19	2 19
Agglutinated sp 29												
Agglutinated sp 46	1	1 05	2	1 42	24	3 98	10	4 63	16	2 97	36	4 12
Adercotryma glomerata					1	0 17			3	0 50	5	0 53
Ammobaculites agglutinans											8	0 91
Cribrostomoides sp												
Cribrostomoides subglobosus	1	1 05	1	0 71			1	0 46			7	0 74
Cystammina argentea	1	1 05									3	0 30
Eggerella sp 128												
Eggerella bradyi					1	0 17						
Eggerella scabra												
Haplophragmoides sp 5			1	0 71	24	3 98			3	0 50		
Haplophragmoides bradyi					3	0 50						
Lagenammina pseudodifflugiformis							1	0 46	3	0 50	9	1 05
Miliammina sp.												
Psammosphaera spp.			1	0 71	2	0 33			3	0 50	25	2 84
Recurvoides spp											4	0 44
Reophax sp	1	1 05							3	0 50		
Reophax bilocularis												
Reophax guttiferus					3	0 50					21	2 40
Reophax incaceus									5	0 99	33	3 74
Reophax scorpiurus							1	0 46			2	0 28
Saccammina spp					1	0 17						
Textularia earlandi					1	0 17					3	0 30
Trochammina sp 1					1	0 17	1	0 46				
Trochammina sp 5												
Trochammina sp.103					14	2 32	1	0 46			5	0 58
Trochammina globigeriniformis	1	1 05			39	6 47	15	6 94	13	2 48	26	2 90
Fossilising agglutinated												
Sigmoilopsis schlumbergeri									3	0 50		
Siphotextularia affinis					1	0 17					3	0 30
Siphotextularia concava												
Textularia sp									3	0 50		
Total live foraminifera	95	100 00	141	100 00	603	100 00	216	100 00	539	100 00	881	100 00
Nbr species	19		19		37		26		31		43	

CHAPITRE 4

Faunes vivantes de foraminifères benthiques à une station de canyon située à 2800 mètres de profondeur dans le Golfe de Gascogne : réponse des faunes à une concentration de matière organique réfractaire.

Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay:
Faunal response to focusing of refractory organic matter.

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Résumé

Une station, située à 2800 mètres de profondeur dans la partie inférieure du canyon de Cap-Ferret (Golfe de Gascogne), a été échantillonnée à trois occasions, en janvier 1999, juin 1999 et avril 2000. A chaque prélèvement, des abondances exceptionnellement élevées d'espèces de foraminifères benthiques endopéliques profonds ont été observées dans les niveaux profonds des sédiments étudiés. Selon nos observations, ces fortes densités de faunes endopéliques profondes ne sont pas directement corrélées aux apports de matière organique labile atteignant l'interface eau-sédiment. Il est plus probable qu'elles soient liées au flux élevé de matière organique résistante et de mauvaise qualité lentement introduite dans les niveaux profonds du sédiment et responsable des successions de gradients redox similaires entre nos échantillonnages. Certaines espèces endopéliques intermédiaires et profondes occupent spécifiquement ces zones de gradient redox. *Melonis barleeanus* vit dans la partie dysoxique du sédiment où des processus de nitrification se produisent. *Globobulimina affinis* apparaît dans des sédiments dysoxiques et anoxiques plus profonds où les concentrations les plus élevées en Fe_{asc} sont enregistrées. Quand elle est présente, *Chilostomella oolina*, est rencontrée dans le sédiment anoxique, associée à une décroissance rapide du contenu en oxydes de Fe (III) et à une intense réduction des oxydes et oxyhydroxydes de Mn (III, IV). Dans la mesure où la plupart des réactions géochimiques sont catalysées par des consortia bactériens hétérotrophes et chimiolithotrophes, les foraminifères endopéliques profonds apparaissent comme des protistes hautement spécialisés capables de se nourrir ou de vivre en symbiose avec des communautés de procaryotes. Les espèces de foraminifères vivant dans la partie superficielle et bien oxygénée du sédiment montrent des réponses faibles, mais néanmoins perceptibles, aux apports saisonniers de phytodétritus liés au bloom de printemps 2000. Durant cette période, nous observons une augmentation modérée de densité d'espèces opportunistes endopéliques superficielles telles que *Bulimina inflata*, *Hoeglundina elegans* et *Epistominella exigua*. Une structure de terrier occupée par une holothurie observée dans une des carottes échantillonnée en avril 2000 a causé un positionnement plus en profondeur des microhabitats des foraminifères benthiques. Cette bioturbation a modifié de façon significative les caractéristiques physico-chimiques du sédiment, provoquant l'approfondissement des gradients redox fondamentaux.

Mots-clés : Canyon ; Foraminifère benthique ; Endofaune profonde ; Microhabitat ; Bactérie ; Gradient redox ; Bioturbation.

Abstract

A 2800 m deep site in the lower part of Cap-Ferret Canyon (Bay of Biscay) was sampled on three occasions in January 1999, June 1999 and April 2000. Exceptionally high abundances of deep infaunal species are observed in the deeper parts of the sediment in all three periods. In our opinion, these high deep infaunal densities are not directly related to labile organic matter reaching the sediment-water interface, but are a response to a massive flux of low quality and resistant organic matter, which is slowly introduced into the deeper parts of the sediment, where it induces a rather stable succession of redox gradients. *Melonis barleeanus* lives in the dysoxic part of the sediment, where nitrification processes take place, whereas *Globobulimina affinis* appears in still deeper dysoxic and anoxic sediments where highest Fe_{asc} concentrations are recorded. *Chilostomella oolina*, when present, is found alive in anoxic sediments, and is associated with a sharp decrease of the content of Fe (III)-oxides and an intensive reduction of Mn (III, IV)-oxides and -oxihydroxides. Because most of the geochemical reactions are catalysed by heterotrophic and chemolithoautotrophic bacterial consortia, deep infaunal foraminifera appear to be highly specialised protozoans, able to feed on, or live in symbiosis with these prokaryotic communities. The foraminiferal taxa living in superficial, oxic sediments, exhibit a very weak, but nevertheless perceptible, response that could be related to phytodetritus deposits in spring 2000. In this period, we observe a moderate density increase of shallow infaunal opportunistic taxa such as *Bulimina inflata*, *Hoeglundina elegans* and *Epistominella exigua*. A burrowing structure occupied by a holothurian, encountered in one of the cores collected in April 2000, may have caused a significantly deeper position of the subsequent redox gradients, as far as a significant modification of the benthic foraminiferal microhabitat patterns is observed.

Keywords: Canyon; Benthic foraminifera; Deep infauna; Microhabitat; Bacteria; Redox gradient; Burrow.

Introduction

In deep-sea environments, the exported organic matter flux, and the oxygenation and redox conditions in the bottom and interstitial waters are generally considered as the major parameters controlling the density, composition and microhabitat of benthic foraminiferal faunas (e.g. Altenbach, 1988; Altenbach and Sarnthein, 1889; Lutze and Thiel, 1989; Mackensen and Douglas, 1989; Rathburn and Corliss, 1994; Jorissen et al., 1995; Rathburn et al., 1996; Fariduddin and Loubere, 1997; Jorissen, 1999a; Schmiedl et al., 2000; Morigi et al., 2001). In a recent study on benthic foraminiferal faunas from a five station (140 – 2000 m) open slope transect from the Bay of Biscay, Fontanier et al. (2002) showed that foraminiferal densities reflect the vertically exported organic matter flux, and thus show a significant decrease with water depth. Foraminiferal standing stocks are high in the relatively eutrophic lower shelf, upper and middle slope environments. Here, foraminifera are generally concentrated at the sediment-water interface, but the first cms of the sediment, where some important redox boundaries are situated, may provide microhabitats for specific foraminiferal taxa. For example, *Melonis barleeanus* generally concentrates in the hypoxic parts of the sediment and still deeper, *Globobulimina affinis* is generally distributed around the zero oxygen level (Fontanier et al., 2002). In the more oligotrophic lower slope environments, benthic foraminiferal density is much lower, and foraminifera are essentially limited to the sediment-water interface, where the scarce trophic resources are concentrated.

Furthermore, foraminiferal faunas respond to seasonal signals. Numerous *in situ* studies show that deep-sea foraminiferal taxa are capable to take rapid advantage of seasonal phytodetritus deposits to the sea floor, and exhibit a density increase close to sediment-water interface during more or less short eutrophic episodes (Gooday, 1988, 1993; Gooday and Lambshead, 1989; Jorissen et al, 1992; Barmawidjaja et al., 1992; Silva et al., 1996; Ohga and Kitazato, 1997; Jannink et al., 1998; Loubere, 1998; Gooday and Rathburn, 1999; Kitazato et al., 2000). Phytoplankton detritus is supposed to consist of easily hydrolysable organic matter, which could sustain metabolic activities of the most opportunistic foraminiferal taxa colonising and reproducing in these compounds once they reach the sea bottom (Gooday, 1988; 1993; Lambshead and Gooday, 1990; Turley et al., 1993). Such opportunistic behaviour was recently confirmed by laboratory experiments, which depict a clear reproductive foraminiferal response to artificial food enrichment of the sediment (Heinz et al., 2001). In a study on the seasonal and inter-annual variability of benthic foraminifera at

a 550 m deep upper slope station in the Bay of Biscay, Fontanier et al. (2003a) suggest that the input of vertically transported phytodetritus deposits provokes a rapid reproductive response of the more opportunistic foraminiferal taxa living in the uppermost sediments (e.g. *Epistominella exigua*). Intermediate and deep infaunal populations that are dependent on the subsequent, deeper, redox fronts in the sediment are much more stable through time, and less affected by phytodetritus deposits.

Canyon environments differ from open slope environments by the sedimentary processes that determine the quantity and quality of inorganic and organic deposits. In open slope settings in temperate latitudes, the organic matter flux consists of seasonal vertical inputs of labile and easily hydrolysable phytodetritus that is directly exported from the surface waters to the sea floor (McCave, 1975; Billett et al, 1983; Lampitt, 1985; Bruland et al., 1989; Auffret et al., 1994; Newton et al., 1994). Resuspension processes induce considerable lateral advection and deposition of reworked organic matter (Verity et al., 2002). In canyons, organic supplies are predominantly induced by downslope transport and/or lateral advection (Van Weering et al., 2002). In this way, important amounts of reworked and/or terrestrial and shallow marine refractory organic matter can be transported to deep-sea environments (Gardner, 1989; Buscail et al., 1990; Gadel et al., 1993; Crémer et al., 1993; 1999; Etcheber et al., 1999; Heussner et al., 1999, Van Weering et al., 2002). A recent study performed by Schmiedl et al. (2000) shows that foraminiferal faunas from a 920 m deep site in the Lacaze-Duthiers Canyon (western Mediterranean Sea) differ strongly from faunas sampled at a 800 m deep open slope station in the Gulf of Lyons. A high lateral advective organic matter flux in the canyon axis induces high organic carbon contents and steep redox gradients within the sediments, which results in high-density faunas characterised by rather important amounts of intermediate and deep infaunal taxa (e.g. *Melonis barleeanus*, *Globobulimina* spp.). In open slope settings, the lower organic matter flux limits foraminiferal faunas to well oxygenated shallow infaunal niches, and restricts the abundance of intermediate and deep infaunal taxa. Only epifaunal and shallow infaunal taxa seem to respond to putative seasonal organic matter flux maxima from the photic zone.

In the lower part of Cap Ferret Canyon, a 2800 m deep station ("I") was sampled on three occasions in January 1999, June 1999 and April 2000, and four multitube cores (including a couple of duplicate cores in April 2000) were reserved for foraminiferal studies. Cap Ferret canyon has been intensively studied in the framework of the ECOMARGE program (Monaco et al., 1999). This canyon actually functions as a trap for resuspended sediment transported along-slope, and constitutes a marked depocenter for organic matter and

fine terrigeneous particles (Heussner et al., 1999; Etcheber et al., 1999). In view of the water depth (2800 m), the organic input at our station I (resulting in 1,35% C_{org} in the topmost sediment) is probably dominated by laterally advected refractory organic matter, with only a minor contribution of vertically transported labile organic matter. However, the spring bloom is a very strong primary production event in the Bay of Biscay (Tréguer et al., 1979; Laborde et al., 1999), and therefore, a weak spring bloom contribution, in terms of labile organic matter (phytodetritus) supply, has to be considered even for our deep canyon environment.

This rather unusual setting, potentially with two strongly contrasting sources of organic matter, raises two important questions:

(1) How does the benthic ecosystem, and the benthic foraminiferal faunas in particular, respond to the dominant input of rather refractory organic material? More specifically, how do the canyon faunas differ from open slope faunas from comparable water depths?

(2) Is there, in spite of the dominance of refractory organic carbon, still a perceptible response to the temporal variability of the probably much weaker vertical flux of labile phytodetritus?

First, we will consider the major sedimentary processes affecting our study area. A major question is whether the lower part of Cap Ferret Canyon can be considered as active, and experiences erosional and/or turbiditic events, or is rather inactive, and serves as a depocenter for laterally advected or downslope transported organic matter.

Next, we will investigate how the sedimentological characteristics affect biogeochemical processes in the upper cm of the sediments and the ecology of benthic foraminiferal faunas. The presence of burrowing macrofauna in one of the duplicate cores collected in April 2000 provides the opportunity to study the impact of deep macrofaunal bioturbation on early diagenetic processes, and indirectly, on the benthic foraminiferal microhabitats.

Study area

Station I (44°49'N, 2°33'W, water depth 2800 m) is situated on a flat part of the northern flank of Cap Ferret Canyon (Fig. 1). It is bathed by bottom waters composed of

Northeastern Atlantic Deep Water (NEADW, T = 2.9°C, S = 34.95 psu) and Antarctic Bottom Water (AABW, T = 2.5°C, S = 34.92 psu) (Durrieu de Madron et al., 1999). Durrieu de Madron et al. (1999) showed that the water flow at a 3000 m deep station, only 5 km away from our site, is oriented along the canyon axis with a mean current velocity of only 6 cm s^{-1}. Bottom waters present low turbidity values (<30 mFTU), indicative of the absence of strong nepheloid layers in the lower canyon and of limited resuspension processes (Durrieu de Madron et al., 1999). The sediments at our station consist of silty muds with less than 30% of carbonates (Hyacinthe et al., 2001).

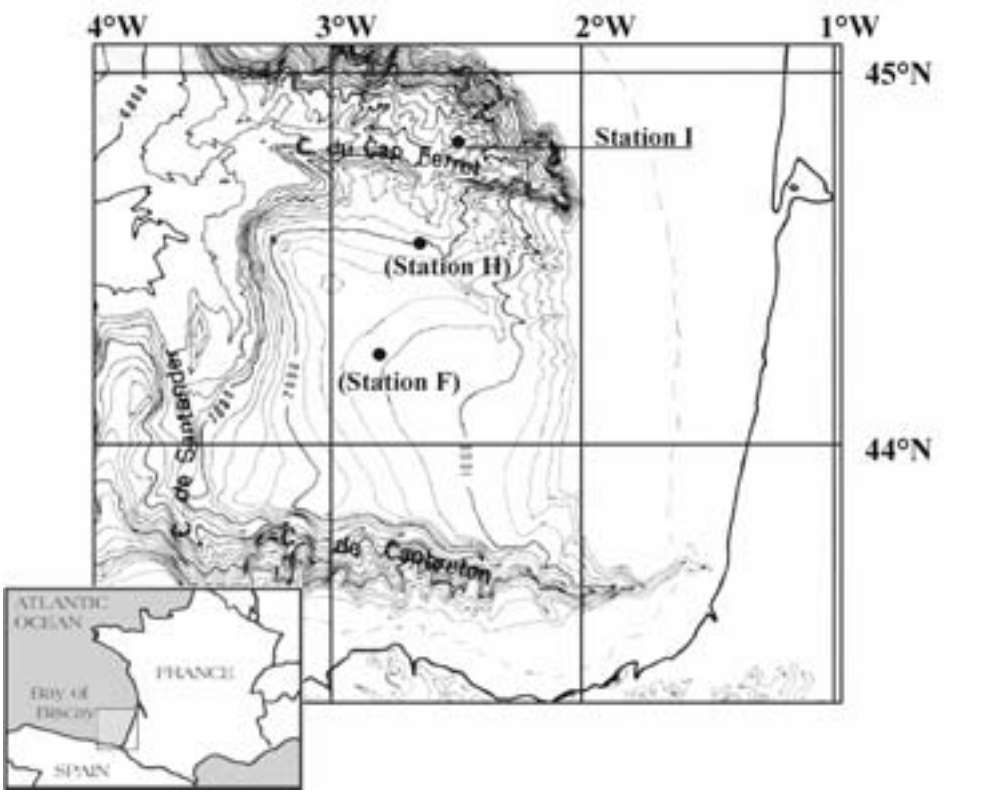

Fig. 1 Study area, bathymetry and geographical position of station I. Stations F and H, discussed in the text, are also presented (Fontanier et al., 2002).

Between 1987 and 1991, the ECOMARGE program studied particle fluxes around Cap Ferret Canyon. In the present high sea-level stand situation, Cap Ferret Canyon is too far away from the continent to be directly fed by riverine sedimentary discharge (Ruch et al., 1993; Castaing et al., 1999). As discussed by Heussner et al. (1999) and Durrieu de Madron et al. (1999), lateral along-slope advection is the dominant particle transport mechanism in the canyon area, whereas sedimentary remobilization by gravity, mass or turbidity flows is

believed to be limited (Crémer et al., 1993; 1999). In the upper and lower parts of the canyon, particulate matter transport is mainly northward, and due to along-slope bottom currents. Suspended particles feeding the canyon preferentially originate from a homogeneous source on the shelf and upper slope (<380 m; Plateau des Landes) south of Cap-Ferret Canyon. A secondary southern source (< 1000m depth) may provide supplementary sediment input to the upper part of the canyon (Radakovitch and Heussner, 1999; Heussner et al., 1999). In the canyon channels, high concentrations of suspended particles move downward along- and/or cross-slope, following a horizontal downstream-decreasing gradient (Heussner et al., 1999). In comparison with the adjacent open slope margin, organic matter concentrates preferentially in the Cap-Ferret depression with an average organic carbon content of about 1.35% for the superficial sediment (Crémer et al., 1999; Etcheber et al., 1999). As far as sediment supplies from shelf and adjacent upper slope that concentrate in canyon depression reach rise or abyssal plain in limited proportion, the Cap-Ferret Canyon is considered as inactive and behaves as a preferential depocenter for organic matter (Etcheber et al., 1999).

Heussner et al. (1999) assumed that the organic matter supply to the seafloor in the Cap-Ferret Canyon consist mainly of reworked and refractory organic matter. However, they concluded also that a small contribution of vertically transported organic matter, originating from primary production in the photic zone, exists. Although Etcheber et al. (1999) show that the quality and quantity of organic carbon in surface sediments do not exhibit important seasonal changes, they do not exclude the possibility that minor amounts of organic matter may originate from the photic zone. Labile compounds may be quickly remineralized at the sediment-water interface or resuspended by bottom currents, and subsequently redeposited in local depressions. According to Sorbe et al. (1999), on the contrary, the pelagos-suprabenthos coupling is rather straightforward: at a 3000 m deep station in the lower part of Cap-Ferret Canyon, suprabenthos shows a clear response to seasonal organic matter inputs from the photic zone during spring bloom events. Isopoda and Amphipoda dominate the suprabenthic faunas, and show a density increase during bloom periods (May 1991).

The spring bloom is supposed to be the strongest primary production seasonal event in the Bay of Biscay (Tréguer et al., 1979; Laborde et al., 1999). Although the precise timing of the phytoplankton bloom is still debated, the spring bloom is thought to last for about two months, beginning in March and ending in May (Tréguer et al, 1979; Fontanier et al., 2003a). Laborde et al. (1999) recorded mean values of 1 mg m^{-3} for maximal Chlorophyll-a concentrations (eutrophic waters) in the surface layer (0-100 m depth) of ECOMARGE stations in May 1990 and in May 1991. Additionally, coccolithophorid blooms may occur in

summer, in association with upwelling cells that develop along the shelf in relation to north-eastern winds blowing along the coast (Heaps, 1980). In the context of the ECOMARGE program, Beaufort and Heussner (1999) showed that direct and rapid input of vertically advected coccolithophore is a dominant component of punctual summer sedimentation events in the lower part of Cap Ferret Canyon.

Materiel and Methods

Station I was sampled in January 1999, June 1999, and April 2000. Cores with an undisturbed sediment-water interface, and with overlying bottom waters, were collected with a classical Barnett multi-tube corer (Barnett et al., 1984). Different cores were used for chemical, faunal and sedimentological analyses.

Geochemical and sedimentological analysis

Details of sampling and sample processing are described by Chaillou et al. (2002). Overlying waters were collected immediately after core recovery for dissolved O_2 measurements, using the Winkler titration method (Strickland and Parsons, 1972). Profiles of pore water O_2 were measured on board with cathode-type mini-electrode (Helder and Bakker, 1985; Revsbech and Jørgensen, 1986). Sediment temperature was maintained stable with an insulating device. Sampling resolution was 0.5 cm from the surface to 4 cm and 1 cm in the lower part of the cores. Pore water was extracted by centrifugation at 5000 rpm for 20 min under inert atmosphere (N_2). The supernatant was filtered (0.2 µm, syringe filter SFCA NALGENE^R purged by N_2), acidified for dissolved metals analysis (HNO_3; s.p.), and frozen for nutrient analysis. Surface sediments from a second core were collected for ^{210}Pb and ^{234}Th analysis.

Porosity was determined from weight loss upon freeze-drying. The freeze-dried solid fraction was homogenised for solid-phase analysis. The maximum sedimentation rates and the thickness of the mixed layer of the sediment were estimated from vertical profiles of excess ^{210}Pb and excess ^{234}Th ($^{210}Pb_{xs}$, $^{234}Th_{xs}$). The activities of radiogenic isotopes, ^{210}Pb (half-life = 22.4 years) and ^{234}Th (half-life = 24.1 days), were determined in freeze-dried samples of about 5 g each. They were sealed in a counting vial and measured by a high-resolution and low-background gamma spectrometer with a semi planar detector for at least 12 hours

(Jouanneau et al., 1988). One of the cores collected in April 2000 was radiographed using a Scopix system, which consists of an X-ray imaging system combined with image analysis software (Migeon et al., 1999). The aim of the X-ray radiography (Fig. 2) was to detect the presence of discrete sedimentary structures in the top 15 cm of the core. In order to evaluate visual changes, a photograph was taken of the same core (Fig. 2). Particle grain sizes were measured with a Malvern Laser Diffraction Particle Sizer (type 2600). This technique was applied to sediment samples belonging to the previously radiographed and photographed core, and allowed the calculation of mean grain sizes (Fig. 2).

Dissolved nitrate ($\Sigma NO_3^- = NO_3^- + NO_2^-$) and ammonia ($NH_4^+$) were analysed by Flow Injection Analysis (FIA) according to standard procedures (Anderson, 1979; Hall and Aller, 1992). Precisions are ± 0.5 µmol l^{-1} for ΣNO_3^- and ± 5% for NH_4^+. Dissolved manganese (Mn^{2+}) was measured by flame atomic absorption spectrometry (Perkin Elmer AA 300). Dissolved iron (Fe^{2+}) was analysed by the ferrozine procedure described by Stookey (1970). The precision for both methods is ± 10%.

In order to extract the most reactive part of Fe (III) phases and all Mn (III, IV) oxides and oxihydroxides, sediment was treated with an ascorbate solution (Kostka and Luther, 1994; Anschutz et al., 1998; Hyacinthe et al., 2001). About 1 g of wet sediment was leached for 24 h with 25 ml of an ascorbate reagent consisting of 50 g of $NaHCO_3$, 50 g sodium citrate and 20 g ascorbic acid in one litre of water with a final pH of 8. In order to analyse Fe and Mn by flame atomic absorption spectrometry, aliquots of centrifuged solution were then diluted to obtain a 0.2 M HCl matrix. The precision estimated from replicates was ± 3% for Mn and ± 7% for Fe. Particulate organic carbon (C-org) and total carbon were measured on freeze-dried samples by combustion in an LECO C-S 125 analyzer. Particulate organic carbon was measured after removal of carbonates with 2 M HCl from 50 mg of powdered sample. The analyses were performed by direct combustion in an induction furnace. The newly formed CO_2 formed was determined quantitatively by infrared absorption. Inorganic carbon is the difference between total carbon and particulate organic carbon. Inorganic carbon was also measured by calcimetry and gave identical results. The precision of these analyses was ± 3 µmol g^{-1}.

Faunal analysis

For faunal analysis, one entire 72 cm² core has been sliced horizontally; usually every 0.25 cm for the first cm of sediment, every half cm between 1 and 4 cm depth, and every cm

between 4 and 10 cm. In April 2000, two replicate cores have been taken from the same multi-tube corer deployment. On board the ship, sediments were stored in 500 cm^3 bottles filled with 95% ethanol containing 1g/l Rose Bengal stain. The samples were shaken for several minutes in order to get a homogeneous mixture. Several weeks after the campaign, samples were sieved through 63 µm and 150 µm mesh screens, and the sieve residues were stored in 95% ethanol. Foraminifera belonging to the >150 µm fraction were sorted from wet (about 50% ethanol) samples, and stored in Chapman slides. Because of the extremely time consuming character, we limited this study of the 63-150µm fraction to the first half cm of the sediment. Our taxonomic framework is outlined in Appendix A.

The use of the rose Bengal staining technique to recognise live foraminifera from dead ones is a cheap and easy method (Walton, 1952; Bernhard, 1988; 2000). However, below the zero oxygen level within the sediment, the degradation of foraminiferal protoplasm may take a considerable period of time after the death of the organism (Corliss and Emerson, 1990); as a consequence, some dead taxa in the deeper anoxic part of the sediment may present a doubtful staining (Bernhard, 1988; 2000; Corliss and Emerson, 1990). We applied our staining criteria (all chambers except the last one stained brightly pink) always very strictly, and compared doubtful individuals with perfectly stained individuals from the same species found in oxic superficial sediment layers, where the staining efficiency is unambiguous. For deep infaunal taxa that usually occupy the anoxic part of the sediment (e.g. *Globobulimina affinis*), the differentiation between live and dead foraminifera was based on the presence of a stained protoplasm body close to the aperture, and the absence of a mosaic-like veil of bacterial degradation at the interior of the test. Non-transparent agglutinated and porcellaneous taxa were crushed in purpose to investigate the test interior. *Glomospira* spp. (*Glomospira charoides* and *Glomospira gordialis)* were not included in the quantitative analyses, because the orange-reddish colour of their test makes it particularly difficult to appreciate whether the organism was alive or dead at the time of sampling. Also fragments of the very fragile arborescent agglutinating foraminiferal fragments (such as *Hyperammina* spp., *Rhizammina* spp., *Bathysiphon* spp.) have not been included, since it is impossible to determine to how many individuals they correspond. Because samples were preserved and sorted in alcohol, many soft-shelled foraminiferal species may have shrunk and may become unrecognisable during picking. Thus, our countings may underestimate soft-shelled foraminiferal group. Faunal counting results are listed in Appendices B and C, for the 63-150 µm and >150 µm fractions, respectively.

In order to get a general idea about the microhabitat patterns, we calculated the Average Living Depth (ALD_x, Jorissen et al., 1995) of the total foraminifera fauna and/or of individual taxa. Following Buzas et al. (1993), we recognise only three different microhabitat categories: shallow, intermediate and deep infaunal taxa. Overall, weighed ALD_{10} values have been calculated for each taxon by integrating the results obtained in the subsequent cores using:

$$\overline{ALD_{10}} = \sum_{C=1,y} \left((ALD_{10})_y \times n_y \right) / N$$

C = Total number of cores, N = Total number of individuals in all cores, ALD_{10}^{y} = Average Living depth for the ten first cm of core y, n_y = number of specimen in the core y.

Results

Sedimentary patterns

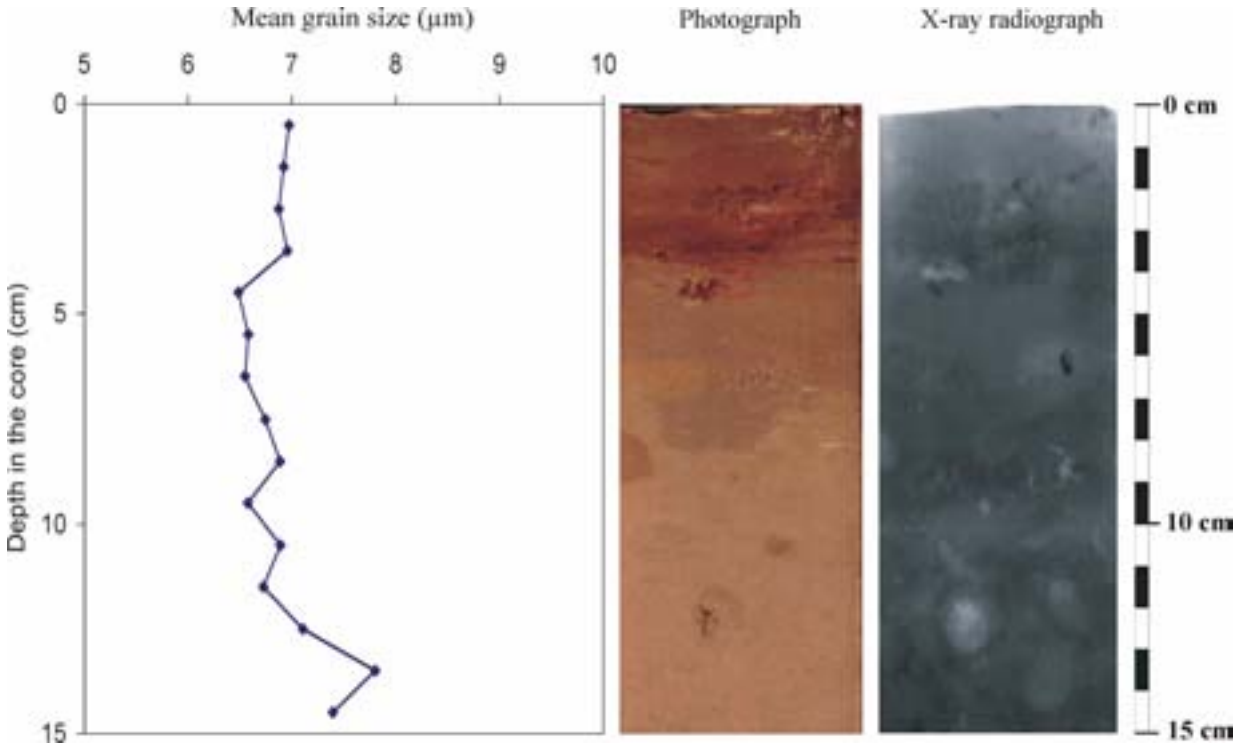

Fig. 2 Photograph and X-ray radiograph of a half core collected in April 2000 at station I. Mean grain size is indicated along the same 15 cm long half-core.

The photographic observation of a 15 cm long vertical section of the core collected in April 2000 allows us to distinguish a vertical succession of four sub-horizontal layers (Fig. 2). The topmost layer is olive-brown and extends down to 2 cm depth. Below, an olive-brown 2 cm thick layer presents discontinuous dark brown sub-horizontal sedimentary micro-horizons. Down to about 7-8 cm depth, a greyish brown layer is present; it exhibits a rather disturbed lower boundary and some brown or brownish-yellow patches. Between 8 and 15 cm depth (the bottom of the core), the sediment is dominantly grey with lighter, ovoid or elongated sub-horizontal patches.

Along the 15 cm long section, the X-Ray radiograph does shows neither clear erosive surfaces, nor graded sediments (Fig. 2). From the sediment-water interface to about 2 cm depth, there is a bright layer with a disturbed lower limit. Below, darker layers incorporate lighter sediment horizons the limits of which are more or less clear (e.g. see the white track at 4 cm depth or the grey patch at 6 cm depth.) and common ovoid or sub-horizontal elongated patches; those latter punctuating structures disturb the homogeneity of the deeper sedimentary layers.

The aforementioned patches probably correspond to burrow infills. In a second core taken in April 2000, we recorded the presence of a live subsphaerical holothurian (of about 3 cm diameter) and a 4 cm long live polychaete between 4 and 7 cm depth in the core. The holothurian belongs to the genus *Molpadia* (Order Apodes, family Molpadidae), an infaunal taxon capable to dig important burrows within the sediment (M. Sibuet, pers. com.; 2002).

The grain size record for the upper 15 cm shows mean values ranging from 6.5 to 7.8 μm (Fig. 2). In the interval extending from 15 to 4 cm depth, a vague fining-up tendency can be distinguished. In the top 4 cm, mean grain size values are rather constant (about 7.0 μm).

Chemical analyses

The absolute values of $^{234}Th_{xs}$ in the topmost sedimentary samples vary significantly between the various sampling periods (January 1999, June 1999, and April 2000) (Fig. 3). In all cores, excess ^{234}Th activity decreases rapidly below the sediment-water interface and reaches the detection limit at about 1 cm depth. The ^{210}Pb excess activity decreases exponentially below the sediment-water interface in all three cores (Fig. 3). In the absence of bioturbation, the downcore $^{210}Pb_{xs}$ profile allows dating of a recent sediment accumulation rate. In the studied sediments, however, where particle mixing by macrofauna will occur, the $^{210}Pb_{xs}$ profile will be modified. In such a case, the $^{210}Pb_{xs}$ profile allows only a maximum

estimate of accumulation rate to be obtained (Silverberg et al., 1986; Thomson et al., 2000). For our cores, these maximum sediment accumulation rates range from 0.033 to 0.046 cm yr^{-1} (33-46 cm ka^{-1}). By combining sedimentation rates with porosity values and the density of particles, the maximum calculated mass accumulation rates range from 17 to 24 mg cm^{-2} yr^{-1}. The organic carbon contents (C-org) of surficial sediments are rather similar (between 1.20 and 1.50 wt%, Fig. 3) for the various sampling periods (January 1999, June 1999, and April 2000). In all cores, the C-org content decreases strongly below the sediment-water interface and reaches ~0.9 wt% at about 4 cm depth. Deeper in the sediment, the C-org content decreases slowly. Exceptionally, in June 1999 the C-org profile shows a slight increase between 4 and 10 cm depth.

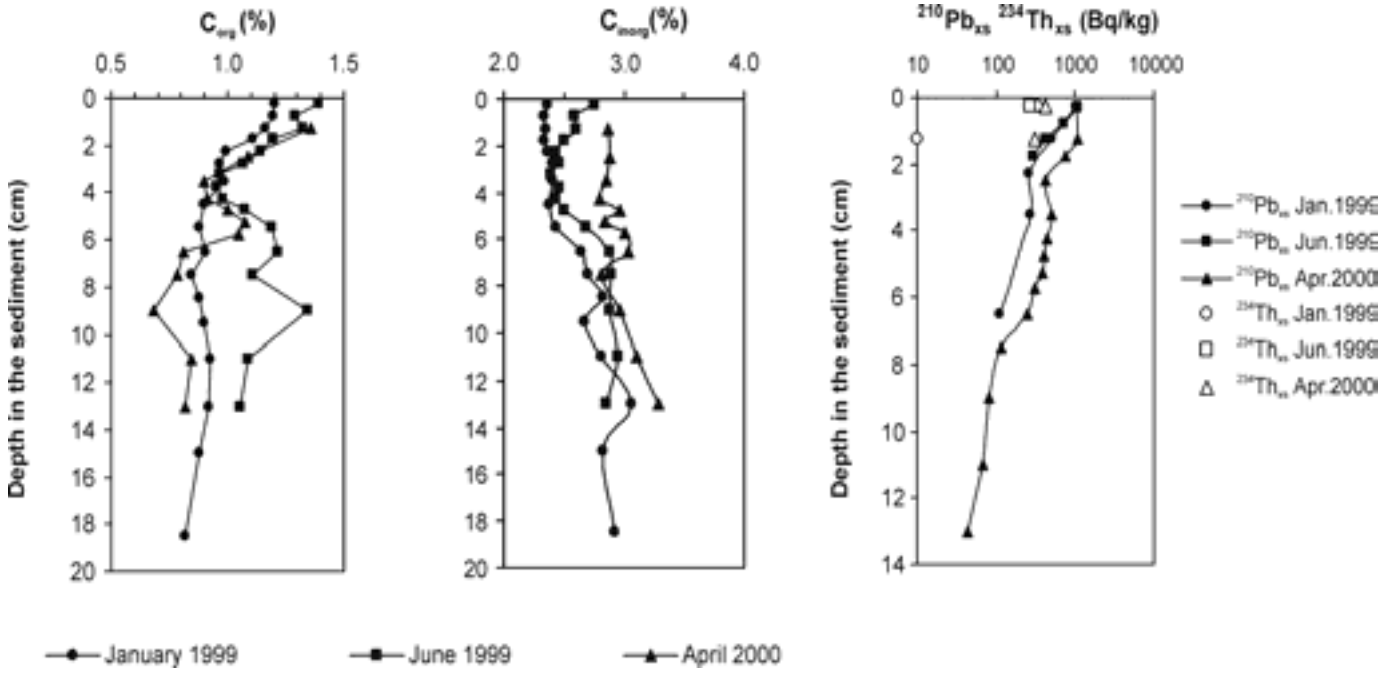

Fig. 3 $^{210}Pb_{xs}$, $^{234}Th_{xs}$ and organic and inorganic carbon content (C-org) vertical profiles for the three sampling periods (January 1999, June 1999 and April 2000).

The O_2 concentrations in the bottom waters and the vertical profiles in the sediment are very similar in January and June 1999 (Fig. 4a and 5a). At the sediment-water interface, O_2 concentrations are close to 240 µmol l^{-1} (5.3 ml l^{-1}) and the oxygen penetration ranges from 4.8 to 5.4 cm depth, with the highest value recorded in January 1999. In April 2000, on the contrary, the O_2 concentration at the sediment-water interface is only 123 µmol l^{-1} (2.7 ml l^{-1}) and the oxygen penetration depth is only 3.8 cm (Fig. 6a).

For all cores, the nitrate concentration ($\Sigma NO_3^- = NO_3^- + NO_2^-$) of the bottom water is close to 20 µmol l^{-1} (Fig. 4a, 5a and 6a). In comparison to bottom waters, interstitial waters of the topmost part of the cores are enriched in ΣNO_3^-. Below, the ΣNO_3^- concentration decreases irregularly and reaches zero below the zero oxygen boundary. However, ΣNO_3^- is present in the anoxic sediment, particularly in January 1999 and April 2000, when ΣNO_3^- concentrations drop to zero far below the O_2-redox boundary (at 8 cm depth). Whereas the concentrations of dissolved NH_4^+ in bottom waters are too low to be detected, they exhibit relatively constant and low values in the oxic topmost layers of all cores (Fig. 4a, 5a and 6a). In January and June 1999, NH_4^+ concentrations increase rapidly below the oxic layer. In April 2000, on the contrary, the NH_4^+ profile is irregular and shows only a slight increase below 4 cm depth. Dissolved manganese (Mn^{2+}) remains undetectable in the oxic part of the sediments (Fig. 4b, 5b and 6b). In the anoxic sediment, the Mn^{2+} concentration increases gently with depth. However, in April 2000 the Mn^{2+} values increase far below the zero redox boundary (at 6 cm depth) (Fig. 4b, 5b and 6b). Dissolved iron (Fe^{2+}) appears directly below the zero oxygen boundary and increases gently downcore in the anoxic interval (Fig. 4b, 5b and 6b).

In January and June 1999, the profiles of particulate manganese extractable by an ascorbate solution (Mn_{asc}) show subsurface maxima just above the zero oxygen boundary. Below the oxic front, the Mn_{asc} content decreases abruptly (Fig. 4b, 5b and 6b). In April 2000, the Mn_{asc} profile does not exhibit a subsurface peak; the first decimetre of sediment is wholly enriched in reactive Mn (mean concentration of 30 µmol g^{-1}). Below 8 cm depth, the Mn_{asc} content decreases to zero (Fig. 6b). The vertical distribution of extractable iron (Fe_{asc}) is almost similar to Mn_{asc} with a subsurface maximum at the zero oxygen boundary just below Mn_{asc} peak and a downcore decrease into the anoxic sediment (Fig. 4b and 5b). In April 2000, the Fe_{asc} profile exhibits a peak between 7 and 10 cm (Fig. 6c).

Live foraminiferal assemblages

In the >150 µm fraction, total foraminiferal densities vary from about 550 (April 2000, core B) to about 240 individuals per 10 cm long, 72 cm² core (January 1999 and April 2000, core A) (Appendix C). In the 63-150 µm fraction, densities vary from about 400 (April 2000, core B) to about 130 individuals in the topmost half cm of a 72 cm² core (January 1999) (Appendix B).

In terms of vertical distribution, density profiles for the >150 µm fraction show a gradual downcore decrease of foraminiferal density in all cores (Fig. 7). This decrease is

particularly well marked in one of the two cores (B) sampled in April 2000, where the faunas in the upper cm are very rich. In the >150 μm fraction, percentages of the perforate foraminiferal group range from 56% in January 1999 to 32% in April 2000 (core B) Percentages of non fossilising agglutinated foraminifera range from 63% in April 2000 (core B) to 39% in January 1999. Porcellaneous and fossilising agglutinated foraminifera always show low percentages (<10%) (Appendix C).

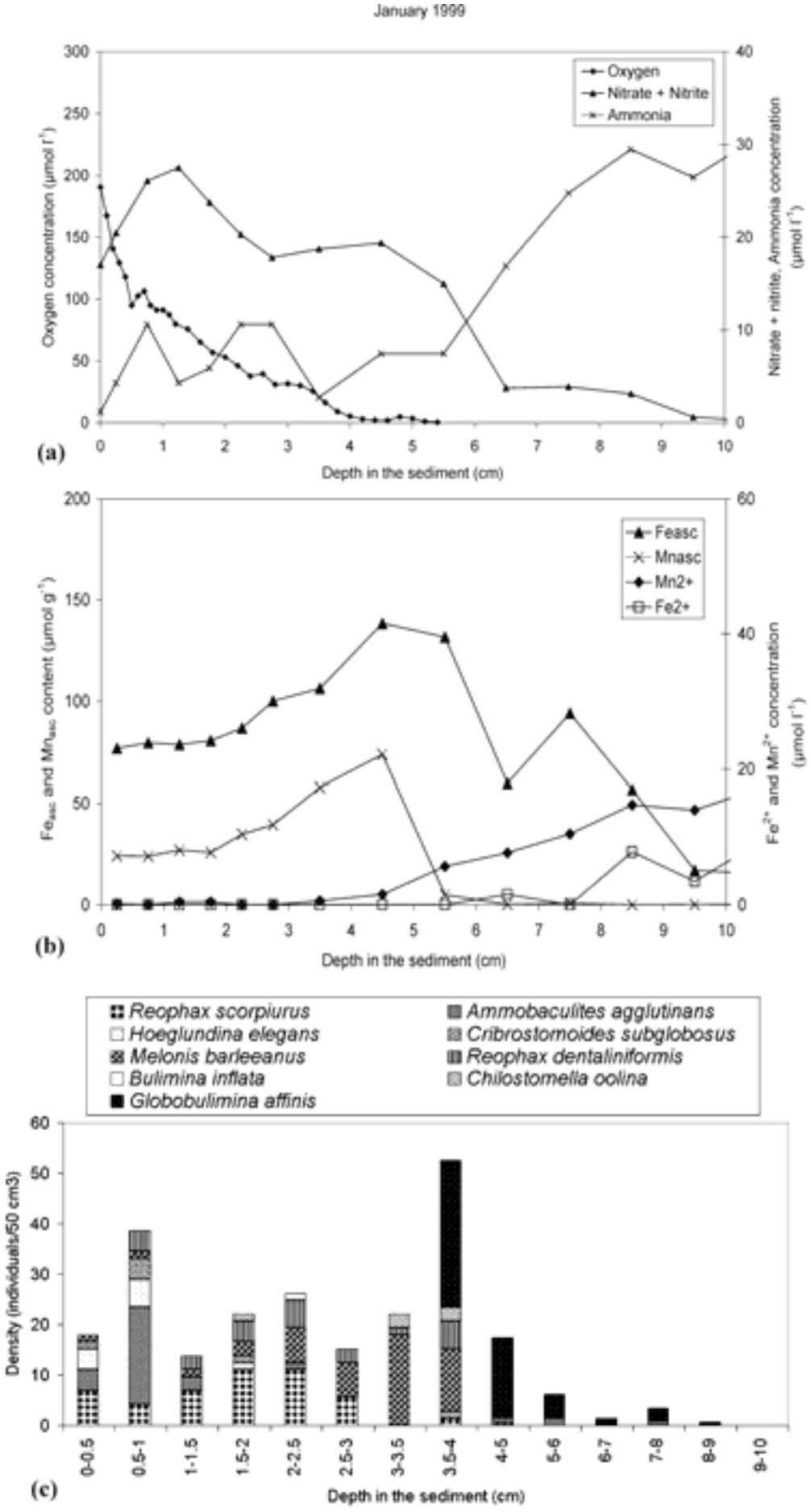
January 1999
Oxygen
Nitrate + Nitrite
Ammonia
Oxygen concentration (µmol l⁻¹)
Nitrate + nitrite, Ammonia concentration (µmol l⁻¹)
Depth in the sediment (cm)
(a)
Feasc
Mnasc
Mn2+
Fe2+
Feasc and Mnasc content (µmol g⁻¹)
Fe2+ and Mn2+ concentration (µmol l⁻¹)
Depth in the sediment (cm)
(b)
Reophax scorpiurus
Hoeglundina elegans
Melonis barleeanus
Bulimina inflata
Globobulimina affinis
Ammobaculites agglutinans
Cribrostomoides subglobosus
Reophax dentaliniformis
Chilostomella oolina
Density (individuals/50 cm3)
0-0.5
0.5-1
1-1.5
1.5-2
2-2.5
2.5-3
3-3.5
3.5-4
4-5
5-6
6-7
7-8
8-9
9-10
Depth in the sediment (cm)
(c)

Fig. 4a-c

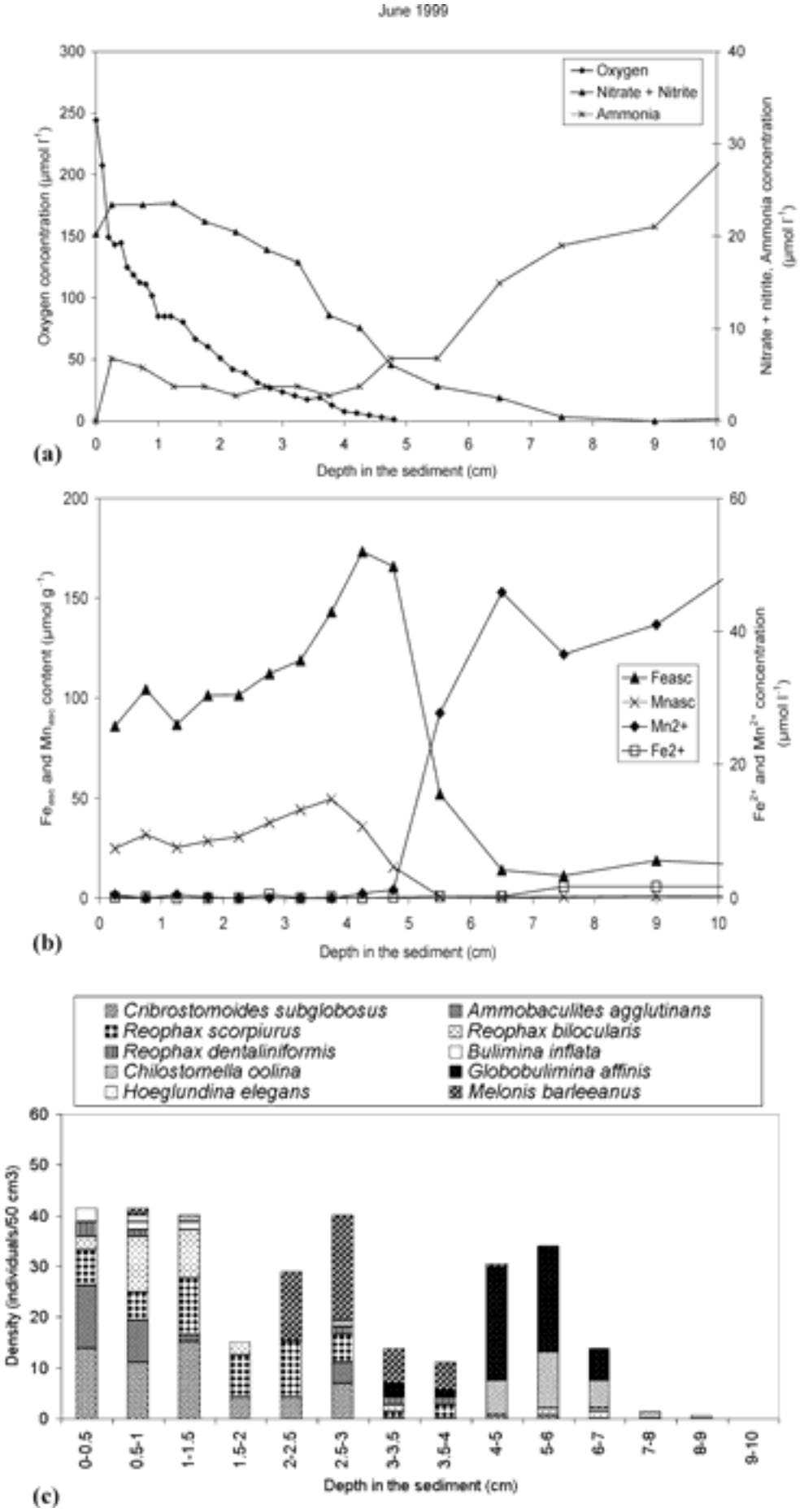
June 1999
Oxygen
Nitrate + Nitrite
Ammonia
Oxygen concentration (µmol l⁻¹)
Nitrate + nitrite, Ammonia concentration (µmol l⁻¹)
Depth in the sediment (cm)
(a)
Feasc
Mnasc
Mn2+
Fe2+
Depth in the sediment (cm)
(b)
Cribrostomoides subglobosus
Ammobaculites agglutinans
Reophax scorpiurus
Reophax bilocularis
Reophax dentaliniformis
Bulimina inflata
Chilostomella oolina
Globobulimina affinis
Hoeglundina elegans
Melonis barleeanus
Density (individuals/50 cm3)
0-0.5
0.5-1
1-1.5
1.5-2
2-2.5
2.5-3
3-3.5
3.5-4
4-5
5-6
6-7
7-8
8-9
9-10
Depth in the sediment (cm)
(c)

Fig. 5a-c

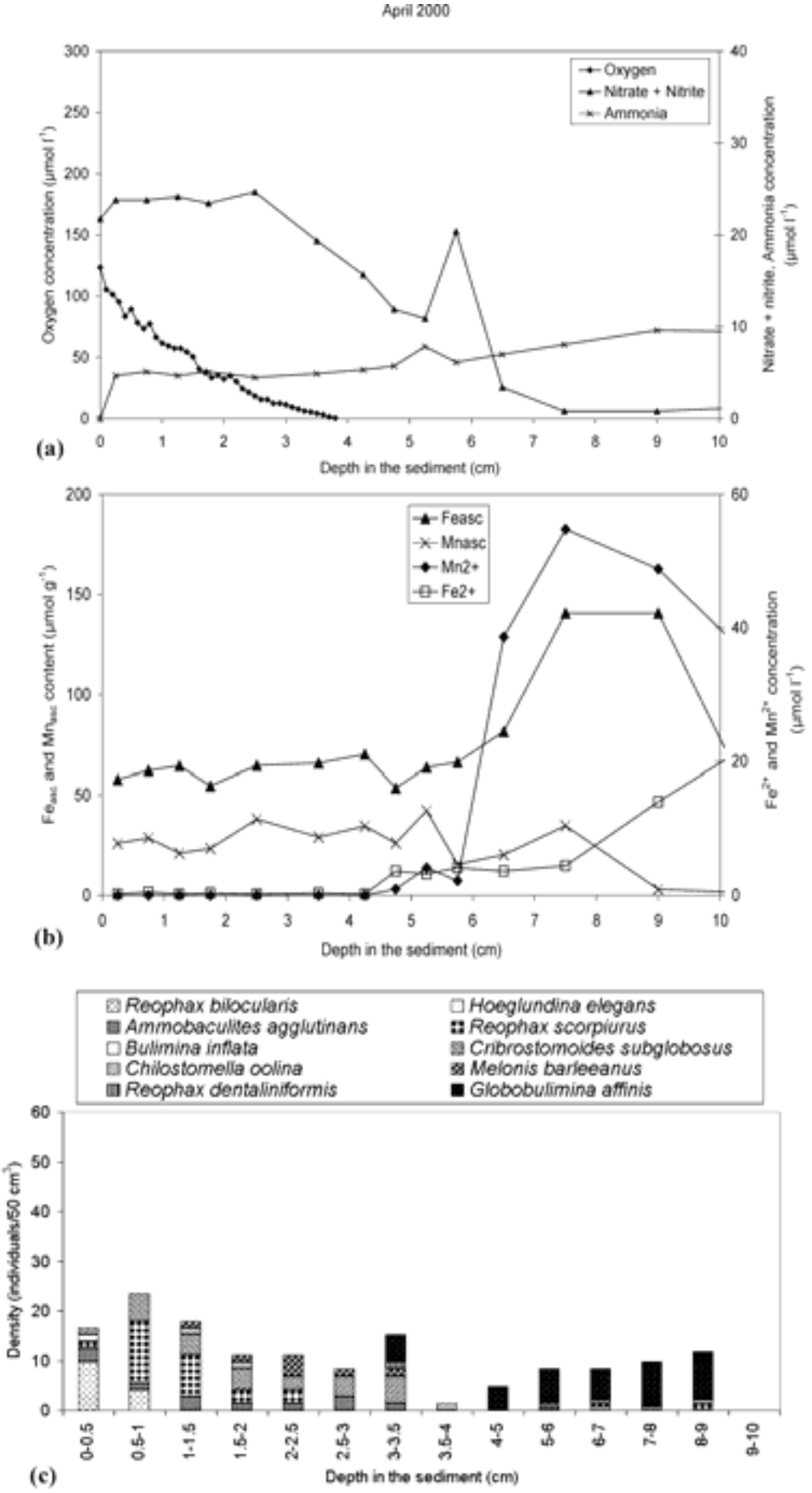
April 2000
Oxygen
Nitrate + Nitrite
Ammonia
Oxygen concentration (µmol l⁻¹)
Nitrate + nitrite, Ammonia concentration (µmol l⁻¹)
Depth in the sediment (cm)
(a)
Feasc
Mnasc
Mn2+
Fe2+
Feasc and Mnasc content (µmol g⁻¹)
Fe2+ and Mn2+ concentration (µmol l⁻¹)
Depth in the sediment (cm)
(b)
Reophax bilocularis
Ammobaculites agglutinans
Bulimina inflata
Chilostomella oolina
Reophax dentaliniformis
Hoeglundina elegans
Reophax scorpiurus
Cribrostomoides subglobosus
Melonis barleeanus
Globobulimina affinis
Density (individuals/50 cm³)
0-0.5
0.5-1
1-1.5
1.5-2
2-2.5
2.5-3
3-3.5
3.5-4
4-5
5-6
6-7
7-8
8-9
9-10
Depth in the sediment (cm)
(c)

Fig.6a-c

Fig. 4; 4a Dissolved oxygen, nitrate + nitrite and ammonia concentrations in a core collected in January 1999; 4b Reduced iron (Fe^{2+}, Mn^{2+}) and iron and manganese oxides oxihydroxides content (Fe_{asc}, Mn_{asc}) in the same core; 4c Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume). Only taxa with a higher than 5% in one of the cores are presented.

Fig. 5; 5a Dissolved oxygen, nitrate + nitrite and ammonia concentrations in a core collected in June 1999; 5b Reduced iron and manganese (Fe^{2+}, Mn^{2+}) and iron and manganese oxides oxihydroxides content (Fe_{asc}, Mn_{asc}) in the same core; 5c Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume). Only taxa with a percentage higher than 5% in one of the cores are presented.

Fig. 6; 6a Dissolved oxygen, nitrate + nitrite and ammonia concentrations in core A collected in April 2000; 6b Reduced iron and manganese (Fe^{2+}, Mn^{2+}) and iron and manganese oxides oxihydroxides content (Fe_{asc}, Mn_{asc}) in the same core; 6c Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm^3 sediment volume). Only taxa with a percentage higher than 5% in one of the cores are presented.

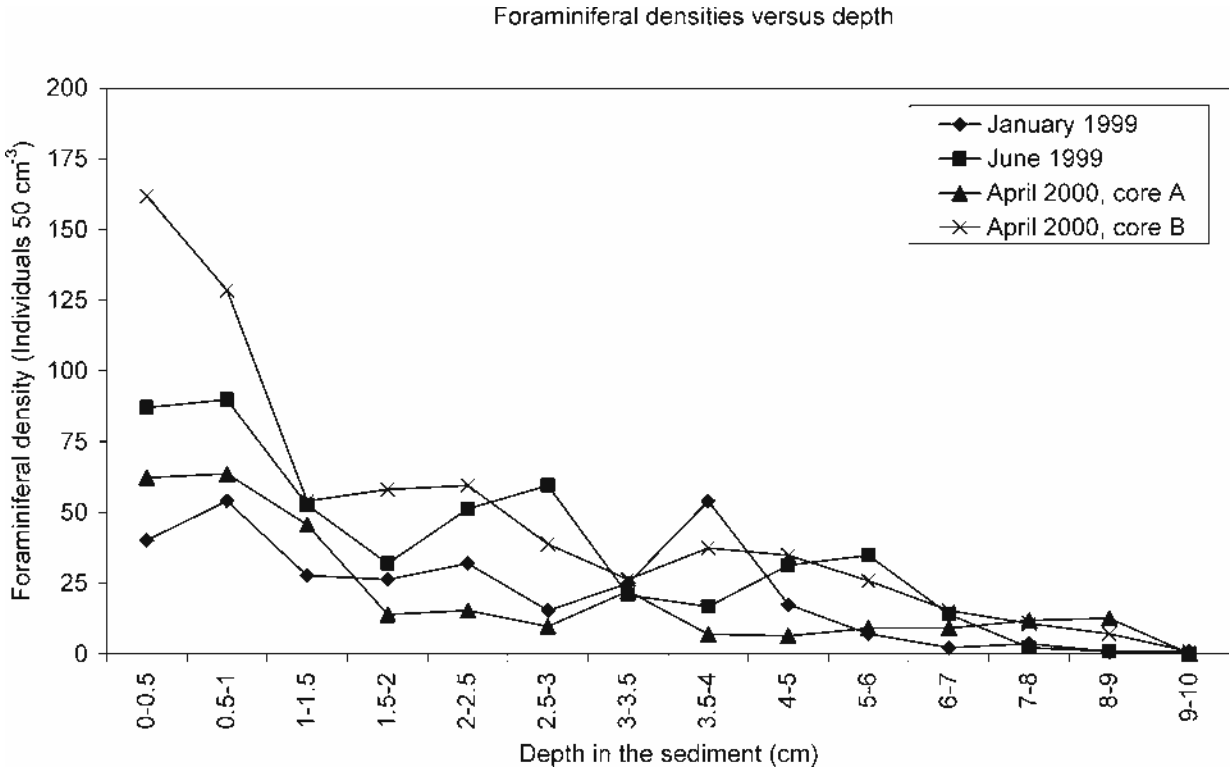

Fig. 7 Vertical profiles of foraminiferal density for the >150 µm fraction for all 4 cores. For each interval, density values are standardised for a 50 cm^3 sediment volume.

The faunal composition of the cores sampled in January 1999, June 1999 and April 2000 (core A) is rather similar (Table 1). The perforate taxa are dominated by *Globobulimina affinis* (18-24%), *Melonis barleeanus* (3-16%) and *Chilostomella oolina* (2-9%). The agglutinated part of the faunas is dominated by *Reophax scorpiurus* (9-14%), *Cribrostomoides subglobosus* (2.5–10%), *Ammobaculites agglutinans* (4-8%) and other *Reophax* species (4-8%). The second core (B) taken in April 2000, in which a holothurian individual was present in its burrow (4-7 cm depth), contains very low numbers of *G. affinis*, and *C. oolina*. This core shows, on the contrary, strongly increased numbers of *Bulimina inflata* and *Hoeglundina elegans*. The agglutinated part of the fauna is rather similar to that found in the other three cores.

In the 63-150 µm fraction of the top half cm, agglutinated non fossilising foraminifera are the major group; their relative contribution varies from 74% in January 1999 to about 45% in April 2000 (both cores) (Appendix B). Percentages of perforate foraminifera range from about 48% in April 2000 (both cores) to 21% in January 1999. Porcellaneous, fossilising agglutinated and soft-shelled foraminifera are minor groups. *Epistominella exigua*, *Cassidulina crassa*, *Gyroidina umbonata*, *Nuttallides pusillus*, and *Pullenia* spp. dominate the perforate group, whereas *Reophax guttiferus*, *Reophax scorpiurus*, *Reophax bilocularis*, *Trochammina globigeriniformis*, *Hippocrepinella* sp. and *Cribrostomoides subglobosus* dominate the non-perforate group (Appendix B).

Taxa (>150µm)	January 1999	June 1999	April 2000, core A	April 2000, core B
Bulimina inflata	0.83	1.21	0.82	4.60
Chilostomella oolina	3.31	9.20	2.06	0.00
Globobulimina affinis	23.97	17.92	23.46	2.02
Hoeglundina elegans	3.31	0.24	0.41	5.51
Melonis barleeanus	15.70	8.72	2.88	4.41
Ammobaculites agglutinans	8.26	4.60	4.52	9.37
Cribrostomoides subglobosus	2.48	10.17	9.64	12.50
Reophax bilocularis	0.00	6.05	4.11	4.60
Reophax dentaliniformis	7.85	1.45	0.41	0.92
Reophax scorpiurus	14.05	9.20	9.46	17.28

Table 1 Relative abundance of dominant taxa in the >150 µm fraction for the four cores.

The vertical distribution of the dominant taxa of the >150 µm fraction is shown in figures 4c, 5c and 6c. ALD_{10} values are represented in Table 2, in which for every taxon a mean, weighed ALD_{10} is given which is based on all cores except core B of April 2000. In

this core, the strongly modified vertical distribution of benthic foraminifera (Fig. 8) is probably caused by active macrofaunal bioturbation. Among the perforate taxa, *G. affinis* (mean weighed ALD_{10} = 5.4 cm) and *C. oolina*. (mean weighed ALD_{10} = 5.0 cm) can be considered as deep infaunal. *M. barleeanus* (mean weighed ALD_{10} = 2.8 cm) and *Pullenia quinqueloba* (mean weighed ALD_{10} = 2.7 cm) occupy intermediate infaunal microhabitats, whereas *Uvigerina peregrina* and *H. elegans* live close to the sediment-water interface. The vertical distribution of agglutinated taxa is much less contrasted. *R. dentaliniformis* and *R. scorpiurus* tend to have infaunal maxima, but many other taxa combine slight surficial maxima with a persistent presence down to a significant depth in the sediment. This rather wide depth range makes it very difficult to attribute microhabitat labels to these taxa.

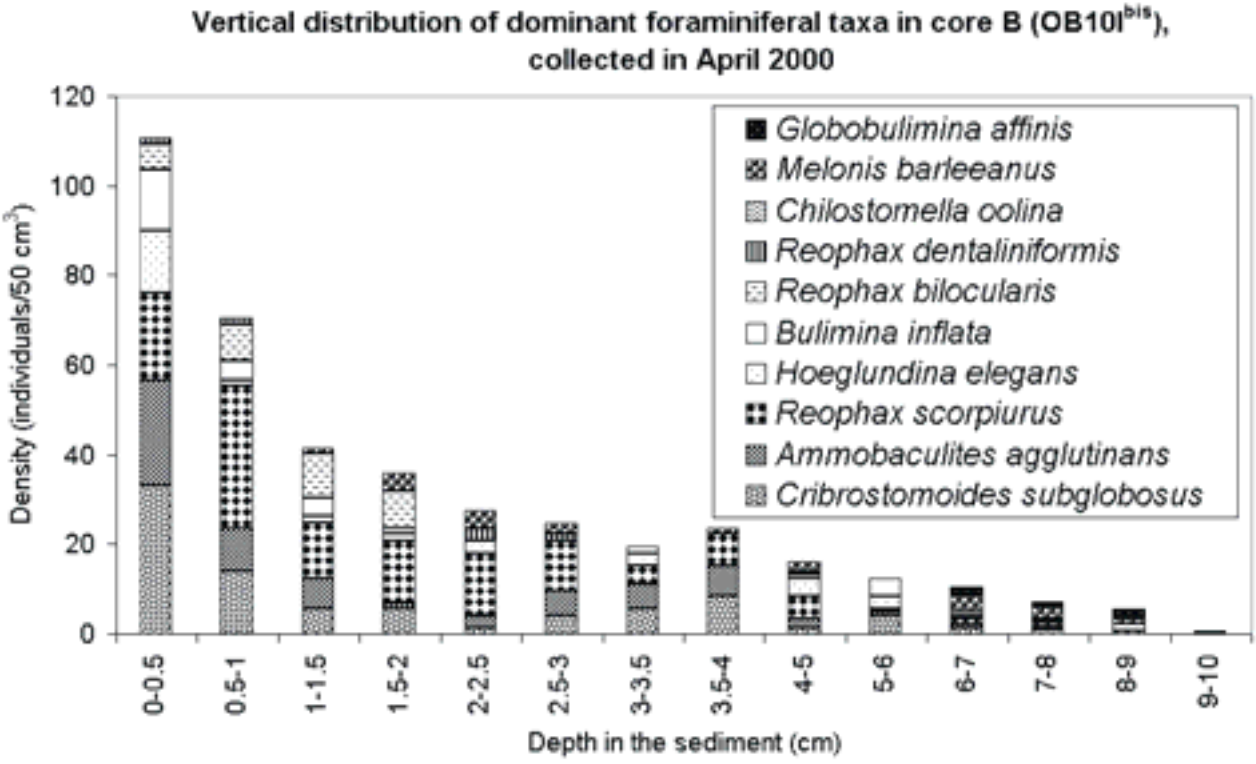

Fig. 8 Foraminiferal distribution (number of individuals >150 µm fraction found in each level, standardized for a 50 cm³ sediment volume) in core B collected in April 2000. Only taxa with a percentage higher than 5% in one of the cores are presented.

Taxa	Cores, ALD_{10}			Average weighed ALD_{10}	Microhabitat
	January 1999	June 1999	April 2000, core A		
Chilostomella oolina	3.68 (7)	5.37 (38)	4.15 (5)	5.01 (50)	DI
Cibicides lobatulus			0.66 (7)	0.66 (7)	SI
Globobulimina affinis	4.69 (58)	5.10 (74)	6.57 (57)	5.42 (189)	DI
Hoeglundina elegans	0.67 (8)			0.67 (8)	SI
Melonis barleeanus	2.93 (38)	2.79 (36)	2.25 (7)	2.81 (81)	II
Pullenia quinqueloba		2.69 (8)		2.69 (8)	II
Uvigerina peregrina	0.35 (12)	0.95 (13)		0.66 (25)	SI
Quinqueloculina seminula	0.68 (5)			0.67 (5)	SI
Quinqueloculina sp.1	1.38 (5)		0.55 (8)	0.87 (13)	SI
Ammobaculites agglutinans	0.78 (20)	0.82 (7)	1.66 (10)	0.98 (49)	SI
Cribrostomoides subglobosus	0.80 (5)	1.37 (42)	1.89 (20)	1.48 (67)	SI/II
Hormosina sp.		0.65 (5)	1.04 (7)	0.88 (12)	SI
Karrerulina sp.		1.21 (9)	0.98 (8)	1.10 (17)	SI/II
Psammosphaera sp.		0.91 (13)	3.40 (5)	2.06 (29)	SI/II
Recurvoides sp.	1.06 (6)	1.26 (13)		1.48 (22)	II
Reophax biloculatis		1.67 (28)	0.35 (10)	1.32 (38)	SI/II
Reophax dentaliniformis	2.24 (19)	1.85 (6)		2.15 (25)	II
Reophax guttiferus		0.51 (9)		0.51 (9)	SI
Reophax scorpiurus	1.67 (34)	1.69 (38)	2.01 (23)	1.87 (189)	II
Total perforate	3.31 (136)	3.93 (191)	4.52 (103)	3.87 (430)	
Total porcellaneous	1.11 (12)	1.66 (7)	0.82 (22)	1.05 (41)	
Total non fossilising agglutinated	1.57 (92)	1.49 (214)	1.80 (118)	1.59 (424)	
Total live foraminifera	2.58 (242)	2.62 (413)	2.87 (243)	2.68 (898)	
Oxygen penetration depth (cm)	5.4	4.8	3.80		

Table 2 Average Living Depth (ALD_{10}) of foraminiferal species and (between parentheses) the number of individuals on which the calculation is based. Only occurrence of ≥ 5 individuals are shown. The grey boxes represent dominant taxa with a relative abundance of ≥ 5% in at least one of the stations. Microhabitat patterns are summarized as Shallow Infaunal (SI), Intermediate Infaunal (II) or Deep infaunal taxa (DI).

Discussion

Sediment transport and mixing

An important question is whether our 2800 m deep lower canyon station is under the influence of erosional and/or turbiditic currents. Such disturbing agents may induce a strong modification of the redox conditions in the underlying and/or remobilized sediments layers (Mulder et al., 2001). Furthermore, recent data for the active Capbreton Canyon suggest that such sediment instability has a profound impact on the benthic foraminiferal faunas (Anschutz et al., 2002). Several successive stages of recolonisation can be recognised and foraminiferal faunas only rarely arrive at a stage of maturity corresponding to a complete ecosystem

recovery (Jorissen et al., 1994; Mulder et al., 2001). The sedimentary structures visible on the photograph and the radiograph of the core collected in April 2000 confirm the sedimentological trends described on the basis of the ECOMARGE results. The vertical succession of four distinct sedimentary faces found in our core is identical to the patterns described for lower canyon cores by Crémer et al., (1999) and Gerino et al. (1999). The lack of graded sediments (X-ray analysis and photograph) and the rather constant grain size (silty clay, mean between 6.5 and 7.8 μm; Fig. 2) do not suggest the presence of turbidites. The $^{234}Th_{xs}$ and $^{210}Pb_{xs}$ profiles lead to the same conclusions. In all our cores, these two radioactive species show a rapid downcore decrease. There are no deeper secondary peaks such as found in a core of Cap Breton canyon with recent turbiditic deposition (Mulder et al., 2001). Only the $^{210}Pb_{xs}$ profile obtained in April 2000 reveals an anomaly between 2.5 and 7.5 cm depth with relatively constant activity (~400 Bq kg^{-1}). This anomaly is probably the result of active sediment downmixing by macrofauna (see below).

Since $^{234}Th_{xs}$ has a short half-life time (24.1 days) with respect to the burial rate resulting from continuous sediment input, the elevated $^{234}Th_{xs}$ values at the sediment-water interface of all cores imply freshly deposited sediments with a total absence of erosional events. This suggests that the bottom current velocity in our study area (about 6 cm s^{-1}) is too weak to cause erosion of the sediment-water interface (Durrieu de Madron et al., 1999). The different $^{234}Th_{xs}$ values in the topmost sediments of the successive cores further suggest short-term variability of sediment supply and/or mixing intensity. The maximum sedimentation rates of 0.033 and 0.046 cm yr^{-1}, based on the $^{210}Pb_{xs}$ profiles, are close to the value of 0.060 cm yr^{-1} found by Radakovitch and Heussner (1999) at a site close to the site I. This very high sedimentation rate suggests a continuous succession of fine-grained, non eroded sediments, caused by continuous deposits of suspended material. The 10 cm long core will probably represent only a few centuries of sedimentation history.

The centimetre-scale ovoid structures visible in the core collected in April 2000 (Fig. 2) are interpreted as cross-sections of macrofaunal burrows. Numerous cores sampled in Cap-Ferret Canyon during the ECOMARGE program exhibit similar bioturbative structures (Gerino et al., 1999). Abandoned burrows are very abundant in subsurface layers (between 5 and 20cm depth). According to Gerino et al. (1999), this intensive bioturbation, linked to high macrofaunal density, reflects the high organic matter supply that characterise non-active canyon environments. According to the same authors, high bioturbating activity would create a rather homogeneous mixed layer on top of the sediment where burrows are permanently

created and reworked (Young et al., 1985; Berger et al., 1979; Mullins et al., 1985; Gerino et al., 1999).

The diagenetic behaviour

Surface sedimentary C_{org} contents for the three cores (January 1999, June 1999, and April 2000) are consistent with the data obtained by Etcheber et al. (1999) in the lower part of the Cap-Ferret canyon (an average of 1.35% at 2500-3000 m water depth) and confirm the organic enrichment of the Cap-Ferret canyon compared to other open slope sedimentary environments in the Bay of Biscay (e.g. sites F and H located at 1200 and 2000 m deep respectively, average C_{org} = 0.70%; unpublished data). Cap-Ferret Canyon can therefore be considered as a marked depocenter for reworked and low quality organic matter resuspended from adjacent open slopes (Etcheber et al., 1999; Heussner et al., 1999). The superficial C_{org} contents of our cores do not show a statistically significant seasonal trend. As at others slope stations studied in the Bay of Biscay (OXYBENT and ECOFER), no significant seasonal variations of abundance (and quality) of organic matter were found (Grémare, pers. com., 2003; Etcheber et al., 1999). Even if very fresh organic matter corresponding to labile phytodetrital marine organic matter may seasonally reach the sediment-water interface, it will be quickly and substantially remineralised in the topmost millimetres of the sediment (Etcheber et al., 1999). This explains why such a short, seasonal C_{org} enrichment in the top of the cores is not detectable in our C_{org} profiles. The C_{org} contents generally decrease by 25-30% from the surface to about 4 cm depth, due to moderate mineralization of the most reactive organic compounds. In the deeper part of the cores, the degradation is probably slower due to the more refractory quality of the remaining organic carbon which is much more resistant to bacterial degradation (Henrich, 1992; Keil et al., 1994). Only in June 1999, we noted a slight local enrichment between 4 and 10 cm. This may correspond to reworked and refractory organic compounds related to past and enhanced suspension/deposition period, or to organic enrichment in an abandoned macrofaunal burrow. Furthermore, we can not exclude that the differences between the two cores sampled at station I are due to spatial variation resulting from minor topographic differences.

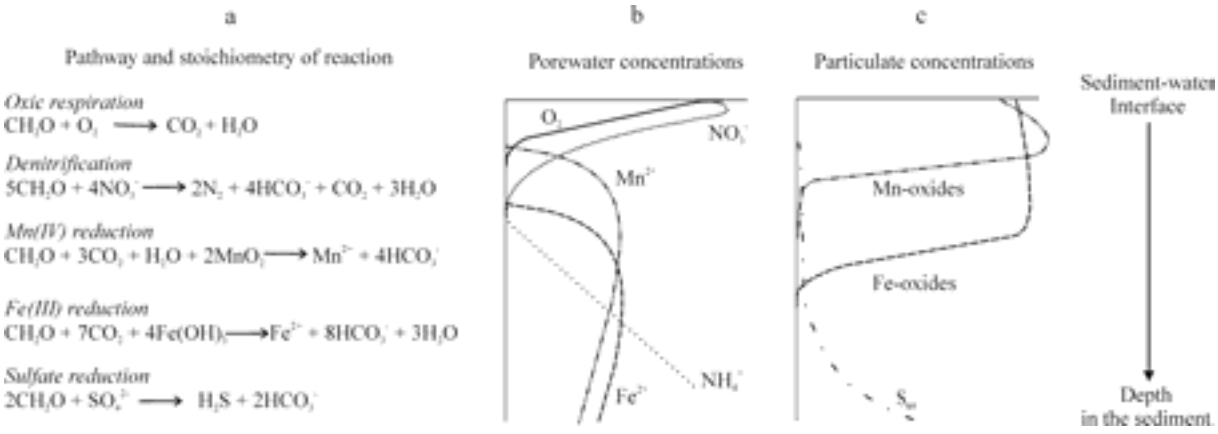

Fig. 9; 9a Vertical distribution of classical bacterially mediated redox reactions for the degradation of sedimentary organic matter in the topmost sediment. Only simple early diagenetic reactions are described. In chemical reaction, organic matter is represented by sucrose molecules (CH_2O); 9b Vertical profiles of main dissolved species in the topmost sediment; 9c Vertical profiles of main particulate phases in the topmost sediment.

It is commonly accepted that the flux of organic matter to the sea floor (either vertical or lateral) governs the distribution of diagenetic species. In all cores, we observe that the dissolved O_2 concentration decreases gradually below the sediment-water interface. Nitrate increases in the top of the oxic layer and then decreases below; it disappears completely in the upper part of the anoxic zone. In relation to the abrupt decrease of Mn- and Fe-oxides and oxihydroxides levels around the zero oxygen boundary, dissolved Mn (Mn^{2+}) and Fe (Fe^{2+}) show remarkable increases in the anoxic sediments. This distribution pattern follows the well-established depth sequence (Fig. 9) resulting from the preferential use of the electron acceptor that yields the highest amount of free energy for the bacterially mediated oxidation of organic matter. Oxygen is reduced near the sediment-water interface, followed by the reduction of nitrate and manganese (Mn_{asc}) in the upper parts of the anoxic zone, and finally by the reduction of reactive iron oxide (Fe_{asc}) (Froelich et al., 1979; Postma and Jakobsen, 1996). All these diagenetic reactions, thermodynamically feasible, are accelerated by an order of magnitude through enzymatic catalysis in living organisms, particularly by prokaryote micro-organisms that use the chemical energy of organic and inorganic compounds for their cell functions (e.g. growth and division, movement, etc.). Whereas many heterotrophic bacteria, that directly use the carbon from the organic matter (both aerobic and anaerobic organisms, such as denitrifying bacteria, Mn- or Fe-reducing bacteria, sulfate-reducing bacteria), are essential for remineralisation, chemolithoautotrophic bacteria play also an important role in

mineral cycling, and particularly in the cycles of N- and S-species (Fenchel et al., 1998; Jørgensen, 2000). These autotrophic organisms, that gain their energy by chemical oxidation, and do not depend on pre-existing organic matter, produce new bacterial biomass that becomes available for the fauna. The process of nitrification, for example, which consists of the oxic conversion of ammonia to nitrate, is brought about by chemolithoautotrophic nitrifying bacteria (Nitrobacteraceae consortia, e.g. *Nitrobacter* sp., *Nitrosomonas* sp., Kaplan, 1993; Jørgensen, 2000, Hensen and Zabel, 2000). Such chemolithoautotrophic metabolisms have also been observed for iron bacteria (*Ferrobacillus* sp., *Shewanella* sp.) which can oxidize Mn^{2+} and Fe^{2+} which diffuse from the anoxic sediment to the more superficial oxic layers (Fenchel et al., 1998; Jørgensen, 2000).

The presence of a living deep infaunal holothurian (*Molpadia* sp.) in the 4-7 cm depth interval in a core (B) collected in April 2000 offers the opportunity to evaluate the short-term impact of macrofaunal bioturbation on the foraminiferal microhabitat distribution. The creation of burrows in hypoxic and/or anoxic part of the sediment may disturb the usual succession of redox zones (Froelich et al., 1979), and may produce partial re-oxygenation of infaunal microenvironments, creating niches for otherwise epifaunal, oxyphilic, taxa. These potential niches are reinforced by the drawdown of labile organic matter, and increased bacterial activity in the burrow walls (Aller, 1982; Aller and Aller, 1986; Gerino et al., 1999). More specifically, the introduction of oxidants into interstitial waters by bio-irrigation, and particularly the O_2 input, may inhibit the anoxic reduction of nitrate (and/or sulphate) and disturb the distribution of metal-oxides and -oxihydroxides (Fe(III), Mn(III, IV)). In the immediate surroundings of the macrofaunal burrows, the classical succession of redox zones will shift to greater depth.

Specific features of the core collected in April 2000

Whereas the dissolved O_2 penetrates to 50 mm in January and June 1999, the depth of the oxic layer is limited to 37 mm in April 2000, when the values in the bottom water are considerably lower (127 µmol l^{-1} compared to 240 µmol l^{-1}). This involves a 60% decrease of the oxygen flux at the sediment-water interface. This oxygen flux value is much lower than that given by Etcheber et al. (1999) and appears to be exceptional.

This temporary decrease in bottom and pore water oxygenation may be explained by a change (quantity and/or quality) of organic carbon input, associated with the spring bloom event, prior to sampling. Although the C_{org} profile exhibits no significant difference with the

two other cores, we think that the increased oxygen consumption is a response to a phytodetritus deposit. Some days or weeks after a depositional event of labile organic matter, which is corroborated by the composition of the benthic foraminiferal fauna (see next chapter), the bottom water oxygen concentration and the oxygen penetration depth into the sediment may still not have recovered from such a short period with a strongly increased oxygen demand. The geochemical response to episodic input of labile organic matter will be amplified in topographic depressions, where the labile organic matter will be concentrated, and the biological oxygen demand will be especially elevated.

Concerning the distribution of the diagenetic species, most geochemical profiles (of the N-, Mn- and Fe-species) show perturbations, particularly between 4 and 8 cm, just as the $^{210}Pb_{xs}$-profile (see above). The presence of a deep infaunal living holothurian (*Molpadia* sp.) in the 4-6 cm depth interval in one of the collected cores in April 2000 suggests a strong potential macrofaunal sediment disturbance at this depth in the sediment. However, we can not exclude that part of the geochemical irregularities is due to sedimentary processes. Furthermore, the classical diagenetic sequence is not exactly respected in this core, where the presence of metal-oxides, far below the oxic layer, allows alternative redox reactions to take place (Hyacinthe et al., 2001).

Faunal characteristics

The benthic foraminiferal faunas of this 2800 m deep station in Cap Ferret Canyon exhibit special characteristics, when compared with deep open-slope faunas. The two deepest stations from an open slope sample transect in the Bay of Biscay (Fontanier et al., 2002) shows that the faunal densities are high at our lower canyon station. Two 72 cm² cores sampled in the open slope stations F (1264 m) and H (1993 m) contain 122 and 179 specimens (>150 µm fraction), respectively, whereas the four cores described in this paper yield between 242 and 554 specimens. Species richness ranging between 27 and 53 at station I is equal or higher than values recorded at station F and H (25 and 27, respectively). This is surprising in view of the much greater water depth and the larger distance from coastal and shelf areas with increased primary production, which should cause a distinctly lower vertical flux of organic matter to the sea floor, and thus, lower diversity foraminiferal fauna. The faunal composition shows even larger differences between the two areas. The relatively poor faunas from the two open slope stations contain about 80% of perforate taxa, and only about 10% of agglutinated taxa. The faunas, which are essentially restricted to the topmost two cm

of sediment, are dominated by the surface dwelling taxa *Uvigerina peregrina* and *Hoeglundina elegans*. Intermediate and deep infaunal taxa are rare at 1264 m (some specimens of *Melonis barleeanus*) and almost totally absent at 1993 m (Fontanier et al., 2002). This poverty of deeper infaunal elements is in accordance with the oligotrophic nature of these sites (Jorissen et al., 1995; Jorissen 1999a). The faunas of our lower slope station "I", on the contrary, are strongly dominated by agglutinated taxa (39-64 %). The cores sampled in January 1999, June 1999 and April 2000 (core A) all show a significant presence of live foraminifera down to 9 cm, and the absence of a perspicuous maximum at the top of the sediment. The perforate component of the fauna shows surprisingly high densities of the intermediate (*M. barleeanus*) and deep infaunal species (*Chilostomella oolina* and *Globobulimina affinis*). These observations agree with a comparative study made by Schmiedl et al. (2000) on foraminiferal faunas from upper slope environments in the Western Mediterranean. In the axis of Lacaze-Duthiers Canyon, foraminiferal density and specific richness values recorded for a 900 m depth station are more elevated than those recorded at an open slope station at an equivalent water depth. Intermediate and deep infaunal taxa (e.g. *M. barleeanus*, *Reophax* spp., *C. oolina*, *G. affinis* and *Globobulimina pseudospinescens*) dominate the "canyon" faunas, and constitute rather stable populations which are adapted to live in the organic-rich sediments of canyon environments (Schmiedl et al., 2000).

Increased percentages of deep infaunal taxa are normally interpreted as indicative of increased organic input and/or low oxygen conditions (Corliss, 1988; Mackensen and Douglas, 1989; Sen Gupta and Machain-Castillo, 1993; Bernhard and Sen Gupta, 1999; Jorissen, 1999b; De Rijk et al., 2000; Morigi et al, 2001). At our 2800 m deep lower canyon station, where bottom water oxygenation are always superior of 123 µmol l^{-1} (2.7 ml l^{-1}), and where the vertical downward flux of labile organic matter should be relatively small, the apparent eutrophicated aspect of the benthic foraminiferal faunas can only be explained by lateral or down-canyon advection of important amounts of refractory organic matter. This idea is supported by the elevated percentages of organic matter found in the superficial and downcore sediments, which have also been recorded in Lacaze-Duthiers Canyon (Schmiedl et al., 2000). As previously discussed, this probably refractory organic matter will bypass the oxic niches at the sediment-water interface, and will be bioturbated into the deeper dysoxic and anoxic sediments layers (Carney, 1989). There, it will be subject to partial degradation by dysaerobic and anaerobic organoheterotrophic bacterial stocks (Fenchel and Finlay, 1995). This slow conversion of refractory organic matter into bacterial biomass opens ecological niches for deep infaunal taxa living in symbiosis with bacteria and/or feeding directly on the

bacterial stocks or on their breakup products (Bernhard and Reimers, 1991; Bernhard, 1993; Bernhard, 1996; Bernhard and Sen Gupta, 1999; Bernhard, 2003). Chemolithoautotrophic bacterial consortia, such as iron or manganese oxidising and nitrifying bacteria, may also take advantage of a particular redox energetic background by converting newly reduced species (Fe^{2+} and Mn^{2+}) into oxidized compounds.

In our three cores unaffected by active deep macrofaunal bioturbation, *M. barleeanus*, *C. oolina* and *G. affinis* generally thrive below 3 cm depth. Such a deep microhabitat is in agreement with numerous studies on the microhabitat characteristics of benthic foraminifera (e.g. Corliss, 1985; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Kitazato, 1994; Rathburn and Corliss, 1994; Jorissen et al., 1995; Rathburn et al., 1996; Jorissen et al., 1998; Kitazato et al., 2000; Schmiedl et al., 2000; Fontanier et al., 2002; 2003a). In order to better understand the precise role of these taxa in the benthic ecosystem, we have compared their vertical distribution with the downcore concentrations of oxygen, nitrate/nitrite (ΣNO_3^-), ammonia (NH_4^+), dissolved metals (Mn^{2+} and Fe^{2+}) and metal-oxides and –oxihydroxides (Mn_{asc} and Fe_{asc}). It should be kept in mind, however, that foraminiferal and geochemical analyses have been performed in two different cores. This may explain small discrepancies, especially in cases of active bioturbation.

Melonis barleeanus appears as an intermediate infaunal species. As already shown by Corliss (1988), Corliss and Emerson (1990), Jorissen et al. (1995; 1998; 1999a) and Fontanier et al. (2002; 2003a), this species mainly lives in the dysoxic part of the sediment. In all of our three unbioturbated cores without active burrows, it settles between 2 and 4 cm depth (Fig. 5c, 6c, 7c), exactly where oxygen values decrease from about 50 to about 5 µmol l-1 and where bacterially mediated nitrification explains the upward increase of nitrate concentrations. These observations confirm the suggestion of Jorissen et al. (1998) of a causative relationship between the microhabitat of *M. barleeanus* and the presence of bacterial consortia. *M. barleeanus* may use bacterial stocks as a direct food source, or entertain symbiotic relationships with chemolithoautotrophic nitrifying bacteria. Such life strategies are envisaged by Lee (1979), Bernhard and Reimers (1991), Thomsen and Altenbach (1993), Bernhard (1993; 1996), Jorissen et al. (1998), Bernhard and Sen Gupta (1999) and Bernhard (2003). Symbiosis between chemosynthetic bacteria and marine benthic organisms is well known (Fisher, 1990, Vacelet et al., 1996; Dubilier et al., 2001). By chemosynthesis, bacteria can fix inorganic carbon and nutrients from interstitial waters and/or from metabolic waste produced by their host. They produce bacteriogenic organic compounds, which can subsequently be used as food by their host (Fisher and Childress, 1986). A foraminiferal host would therefore

no longer need to take up organic matter from its sedimentary biotope and could use dissolved oxygen from interstitial waters to degrade bacteriogenic and internal organic compounds. Conversely, bacterial consortia would take benefit of their host by obtaining a stable environment for growth and reproduction. Another explanation is that *M. barleeanus* may directly use nitrate (and/or nitrite) as an electron acceptor in order to degrade sedimentary or bacteriogenic organic matter (Bernhard and Reimers, 1991; Bernhard, 1993; 1996). *M. barleeanus* is obviously not dependent on freshly deposited labile organic matter here and should therefore not show a direct response to seasonal input of phytodetritus to the ocean floor (Jorissen et al., 1998; Fontanier et al., 2003a).

Chilostomella oolina is only present in fair numbers in the core sampled in June 1999 where the species shows a frequency maximum between 4 and 8 cm core depth. This interval shows oxygen concentrations which descend from about 10 µmol l^{-1} to total anoxia and corresponds to a zone of appearance of reduced species such as NH_4^+, or dissolved Mn^{2+} and Fe^{2+}, and the disappearance of oxidised species, such as ΣNO_3^- and amorphous Mn-oxihydroxides. The *C. oolina* density maximum is rather well correlated with the total reduction of manganese, and with a slight increase of the organic carbon content in the subsurface layers (from 0.95 to 1.22 wt%). This subsurface organic matter peak may correspond to reworked and refractory organic compounds related to a past enhanced suspension/deposition period. We think that *C. oolina* is associated with bacterial consortia involved in the degradation of refractory organic matter in the dysoxic/anoxic parts of the sediment, and may behave as a facultative anaerobe (Bernhard, 1993; 1996). Its occurrence in dysoxic and anoxic sediments has already been discussed (e.g. Rathburn and Corliss, 1994; Rathburn et al., 1996; Fontanier et al., 2002)**.** According to Rathburn and Corliss (1994) and Rathburn et al. (1996), the systematic strict deep infaunal microhabitat of *Chilostomella oolina* is related to subsurface peaks of labile organic matter resulting from turbiditic sedimentation in deep-sea environments. According to the same authors, this labile organic matter would originate from shallow-water and terrestrial sources. In our study, a dependence of labile organic matter input due to turbidite deposition is impossible in view of the previously discussed absence of turbidite sedimentation. According to Fontanier et al. (2002), the deep infaunal niches of *C. oolina* in a 150 m deep shelf-break environment could result from macrofaunal burial of labile organic mater originating from photic zone. At our station, deep macrofaunal burrowing activity may induce the subsurface organic matter enrichment recorded in June 1999, and the co-associated occurrence of *C. oolina*. Nevertheless, it is very improbable that important amounts of labile organic matter are introduced into the sediment.

We think that anaerobic organoheterotrophic bacterial consortia such as Mn-reducing bacteria play an intermediate role, either as food source for *C. oolina* or by converting refractory organic matter into digestible food particles for this deep-dwelling foraminifer. It is surprising, however, that this deep infaunal taxon does not appear in other cores where putative bacterial reduction of metals occurs (January 1999).

In all three cores, *Globobulimina affinis* appears in deep infaunal microhabitats. In January 1999, it has a maximum between 3.5 and 5 cm (where the oxygen concentration descends from 20 to 3 µmol l-1), and extends down to 8 cm. In June 1999, it appears between 4 and 7 cm, in a zone where oxygen concentration decreases from about 10 to 0 µmol l^{-1}; an important part of the fauna inhabits completely anoxic sediments. In the undisturbed core without active burrowing from April 2000 (core A), it appears from 4 to 9 cm depth, in completely anoxic sediments. In the core with active burrowing (B), from April 2000, finally, only small quantities are found from 6 cm downward, below the holothurian burrow. It can not be excluded that in the latter core the main part of the population lives below 10 cm depth, and has not been sampled. The deep infaunal microhabitat of *Globobulimina* spp., close and below the zero oxygen level, is well known (e.g. Corliss, 1985; Mackensen and Douglas, 1989; Corliss, 1991; Jorissen et al., 1995; Jorissen et al., 1998; Schmiedl et al., 2000; Fontanier et al., 2002; Fontanier et al., 2003a). In our study, the different position with respect to the zero oxygen level may be real, but can also be an artefact due to the fact that different cores are used for faunal and chemical analysis. Nevertheless, there is strong evidence that this species is able to live in totally anoxic sediment and must therefore be a facultative anaerobe (Bernhard, 1993; 1996). In all our cores, the density maximum of *G. affinis* coincides with anoxic/dysoxic zones where Fe^{2+} oxidation occurs, suggesting a trophic relation with putative chemolithoautotrophic bacteria involved in this reaction (*Ferrobacillus* sp., *Shewanella* sp.). It may also be envisaged that *G. affinis* lives in symbiosis with these prokaryotic and chemoautotrophic organisms capable of using reduced iron as energy source (Fisher, 1990; Vacelet et al., 1996; Dubilier et al., 2001).

Our present observations support earlier suggestions of a putative strong relationship with major redox boundaries that are associated with heterotrophic (heterotrophs = chemoorganotrophs) bacterial consortia involved in the dysaerobic/anaerobic degradation of refractory organic matter and by the chemolithoautotrophic microbiota. *M. barleeanus*, *G. affinis* and *C. oolina* may behave as highly specialised deep infaunal species which require rather strict and stable bio-redox environments where predation and competition are strongly limited (e.g. Mackensen and Douglas, 1989; Van der Zwaan et al., 1999). If they are

dysaerobic/anaerobic bacteriovores, there should be a more or less complete decoupling between the labile organic matter flux to the sediment-water interface and the behaviour of these deep infaunal taxa. As suggested by Kitazato et al. (2000) and Fontanier et al. (2003a), *M. barleeanus* and *G. affinis* sometimes show a delayed response to phytodetritus deposits in post-bloom periods, when juveniles of both taxa may feed on phytodetrital remains and/or bacterial aerobic consortia in the upper sediment layers after reproduction of the parental individuals in the uppermost niches of the total vertical distributional area of the species.

As discussed before, the benthic foraminiferal faunas appear to be strongly adapted to profit maximally from important supplies of refractory organic matter by downslope or lateral advection, enabled to do so by an intermediate step of bacterial activity. One may ask whether the input and temporal variability of probably much less important quantities of fresh phytodetritus provoke nevertheless a recognisable response of the foraminifera living close to the sediment surface. An important phytoplankton bloom generally occurs in the surface waters of the Bay of Biscay between March and May (Tréguer et al., 1979; Laborde et al., 1999; Fontanier et al., 2003a). Therefore, our cores sampled in April, and in a lesser degree, in June, could represent conditions of increased supply of labile organic matter to the sea floor. The presence of a recent phytodetritus deposit is corroborated by the oxygen concentrations in the core sampled in April 2000. Bottom water oxygen concentration was only 123 µmol l^{-1} (2.7 ml l^{-1}), and the zero oxygen level was already encountered at 3.8 cm, suggesting a period of strongly increased benthic respiration rate immediately prior to sampling.

In general, the foraminiferal faunas close to the sediment surface are surprisingly poor; the usual maximum close to the sediment is even absent in the cores sampled in January, 1999, June 1999 and April 2000 (core A). Only the core with active burrow sampled in April 2000 (core B) exhibits a clear superficial density maximum (Fig. 8). The latter core has by far the richest fauna, which suggests that the surface maximum could indeed be a response to the recent input of labile organic matter. The large differences between the surface faunas found in the two cores sampled in April 2000 suggests very important small scale patchiness due to sea bottom micro-reliefs. Labile organic matter may concentrate in local depressions, thus create ephemeral niches for taxa with an opportunistic tendency (Fontanier et al., 2003a).

When comparing the faunal composition of the core (B) with the surface maximum sampled in April 2000 with that of the three other cores, some striking differences appear. The surface maximum in core B from April 2000 is dominated by three agglutinated taxa (*Cribrostomoides subglobosus, Ammobaculites agglutinans* and *Reophax scorpiurus*)

accompanied by *Bulimina inflata* and *Hoeglundina elegans*. The latter two taxa, which count here for about 10% of the total fauna (55 individuals) are almost absent in the cores sampled in June 1999 and April 2000 (core A), whereas only 8 specimens of *H. elegans* are found in January 1999. Both taxa are shallow infaunal surface dwellers with a moderate opportunistic tendency. Although *H. elegans* is typical of low organic carbon areas (Lutze and Coulbourne, 1984; Corliss, 1985; Corliss and Emerson, 1990; Corliss, 1991; Fontanier et al., 2002; Morigi et al., 2001), De Rijk et al. (2000) argue that *H. elegans* can not thrive under a labile organic matter flux lower than 2.5 g C m^{-2} yr^{-1}. This explains why it is not found in the very oligotrophic waters of the Eastern Mediterranean basins. *B. inflata* appears to prefer slightly more eutrophicated conditions, such as those encountered on the middle slope environments under the very productive surface waters off Cape Blanc, NW Africa (Jorissen et al., 1998, Morigi et al., 2001). The significant increase of these taxa may be a response to the input of fresh organic matter, and subsequent local redistribution by weak bottom currents, during the spring bloom of 2000. The elevated absolute and as well as relative abundances of the three agglutinated taxa (a total of 39.1% of the fauna versus 23.6 to 24.8% in other cores) suggest that they are the most opportunistic components of the agglutinated part of the fauna. This confirms observations of the opportunistic behaviour of these taxa by Linke (1992), Altenbach (1992), and Harloff and Mackensen (1997).

In order to see whether there is a strong response of smaller surface dwelling opportunistic species to the supposed phytodetritus input, we studied the 63-150 µm fraction in the top 0.5 cm of all cores. Again, highest foraminiferal density was found in the top 0.5 cm of the bioturbated core sampled in April 2000 (core B). In this core, the fauna shows elevated percentages of *Cassidulina crassa, Epistominella exigua, Gyroidina umbonata, Nuttallides pusillus* and *Trifarina angulosa*. For several of these taxa, a marked opportunistic life style has been described or suggested (e.g. Gooday, 1988; Gooday and Lambshead, 1989; Jorissen et al, 1992; Silva et al., 1996; Ohga and Kitazato, 1997; Jannink et al.,1998; Loubere, 1998; Jorissen 1999b; Heinz et al., 2001; Gooday and Hughes, 2002; Fontanier et al., 2003a). Together these taxa count for about one third of the fauna, whereas in the probably most oligotrophic conditions represented in the core sampled in January, they count for less than 10% of the total fauna. Nevertheless, the absolute densities of these taxa are relatively low in comparison with the huge frequency peaks of *E. exigua* observed at a 550 m depth open slope station during the 2000 spring bloom (Fontanier et al., 2003a).

We conclude that there is indeed a recognisable but weak foraminiferal response to putative phytodetritus deposit that may be related to the beginning of the 2000 spring bloom.

Such a response would be restricted to the sediment surface of depressional areas where phytodetritus may concentrate. Such areas can easily be missed in studies based on multitube corer samples, where, due to time limits, only a small sediment surface area is studied. As suggested by Thiel et al. (1990), current activity and microtopography may indeed induce a mosaic-like and patchy distribution of phytodetritus at the sea floor. Patchiness is responsible for a certain sea floor heterogeneity and may contribute to the high diversity of deep sea benthic communities (Grassle and Morse-Porteous, 1987; Grassle, 1989; Snelgrove et al., 1994; 1996). However, this episodic faunal response does not change the general aspect of the fauna, which is strongly marked by the permanent input of refractory organic matter by sedimentary processes typical for this lower canyon environment.

In one of the cores collected in April 2000 (core B), a holothurian in life position was encountered between 4 and 7 cm depth. The presence of this large burrowing structure apparently has significantly modified the succession of redox zones, and the accompanying bacterial consortia (Aller and Aller, 1986; Meyers et al., 1987; 1988; Thomsen and Altenbach, 1993; Gerino et al., 1999). In view of their supposed dependence of the redox conditions and/or bacterial consortia, a response of the foraminiferal faunas may be expected. In our case, this response is twofold:

(1) *B. inflata* and *H. elegans*, which are known as shallow infaunal surface dwellers (Corliss, 1985; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Rathburn et al., 1996; Jorissen et al., 1998; Fontanier et al., 2002) reappear between 4 and 7 cm depth, suggesting the creation of oxygenated microenvironments and/or the presence of labile organic carbon deep in the sediment. A very similar faunal response to the presence of deep oxic microenvironments has been found in laboratory experiments (Geslin, pers. com., 2002).

(2) Intermediate and deep infaunal taxa are much less numerous than in all other cores. The intermediate infaunal taxon *M. barleeanus* appears with weak densities that are mainly concentrated from 1.5 to 3 and from 6 to 8 cm, at both sides of the holothurian burrowing structure. The deep infaunal species *G. affinis* appears only in small numbers at 6 cm depth, but it can not be excluded that the main part of the population was situated below 10 cm depth and was consequently not sampled. *C. oolina* is totally absent in this core. These observations suggest the already supposed relationship between deeper infaunal taxa and redox gradients (via bacterial consortia (1) involved in the dysaerobic and anaerobic degradation of organic matter and (2) using energy of redox reactions and inorganic carbon to sustain autotrophic metabolic activities). The burrowing activity of the holothurian would not only introduce

oxidants into the deeper sediments layers, and drag down the succession of redox zones, but it would also cause the introduction of labile organic matter into the sediment (Aller and Aller, 1986; Meyers et al., 1987; 1988; Thomsen and Altenbach, 1993; Gerino et al., 1999). This newly formed niche is apparently colonised by shallow infaunal taxa such as *H. elegans* and *B. inflata*, whereas the normal inhabitants of these deeper sediment layers appear to be less competitive. The normal succession of redox fronts and accompanying bacterial and foraminiferal populations may only be present below the holothurian life structure, from 6 cm downward.

Conclusions

The sedimentary environment of our 2800 m deep lower canyon station is characterised by the rapid accumulation of fine-grained sediments with an important component of refractory organic matter. Quantitatively, the input of labile organic matter from the photic zone is much less important. Benthic foraminiferal faunas show a dual response to these two sources of organic compounds. This response is shown in figure 10, which summarises the relationships between the input of labile and refractory organic matter, bacterially mediated biogeochemical reactions and the foraminiferal response to these processes.

(1) At the sediment-water interface, the flux of labile organic matter is normally too low to sustain important epifaunal/shallow infaunal foraminiferal standing stocks. Only after important phytoplankton blooms, episodic inputs of fresh phytodetritus creates an ephemeral niche for slightly opportunistic shallow infaunal taxa such as *H. elegans* and *B. inflata*.

(2) The continuous input of large amounts of refractory organic matter, which is specific for this canyon environment, causes an intense bacterial activity deeper in the sediment. These bacterial stocks are involved in the dysaerobic/anaerobic breaking up of the refractory organic compounds, and induce a particularly well-established vertical zonation of subsequent redox zones. Chemolithoautotrophic bacterial consortia may take an indirect benefit of redox reactions by oxidizing newly reduced species, and may form consistent labile biomass. Benthic foraminiferal faunas respond to this system by a very strong dominance of intermediate and deep infaunal taxa which are thought to feed directly on bacterial consortia, on their breaking up products, or to live in symbiosis with these bacteria. The vertical zonation of the three principal taxa concerned shows an intriguing correspondence with the precise location of the major biogeochemical gradients. *M. barleeanus* is systematically found in the dysoxic part of the sediment (< 50 µmol/l), in the zone where nitrification by nitrifying

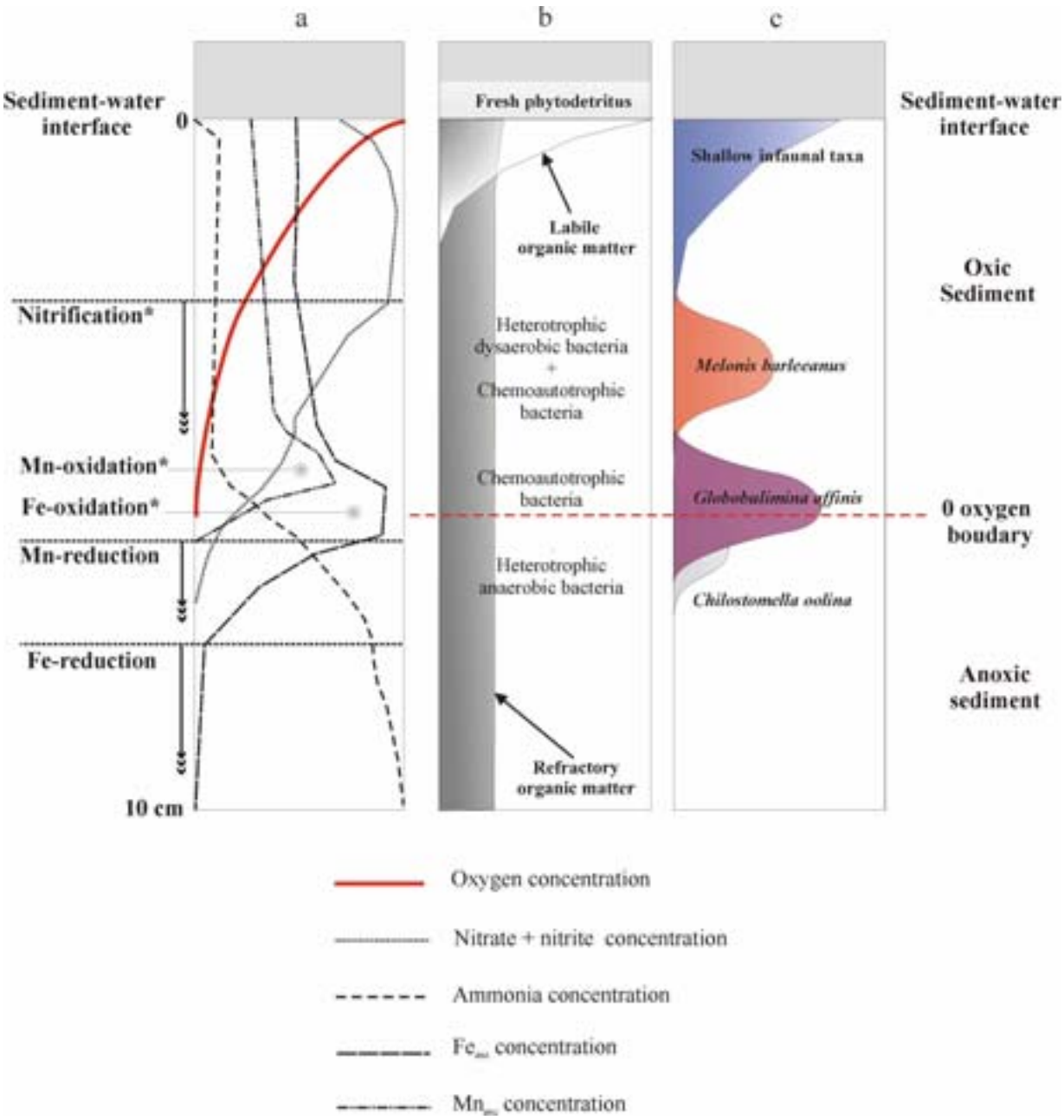

Fig. 10; 10a Principal redox boundaries in the top 10 cm of a virtual core which synthesizes the biogeochemical patterns of cores collected at station I in January or June 1999; 10b Inferred downcore distribution of labile and refractory organic matter as well as deep labile organic carbon produced by bacterial conversion; 10c Vertical distribution and density profiles of shallow infauna (as a unique group), Melonis barleeanus, Chilostomella oolina and Globobulimina affinis are presented.

bacteria occurs. When present, *C. oolina* settles in the anoxic sediment, in a zone where the reduction of Mn_{asc} and Fe_{asc} by putative Mn- and Fe-reducing bacteria is marked. *G. affinis* finally, which lives around as well as below the zero oxygen boundary, shows high densities

in areas of important oxidation of reduced iron components (Fe-oxidizing bacteria). These observations suggest a dependence of the various deeper infaunal taxa of specific bacterial consortia that are associated with chemolithoautotrophic and/or heterotrophic processes.

The peculiar fauna found at this lower canyon station, with its very rich deeper infaunal components poses the problem of the use of these taxa for paleoceanographic reconstructions. Normally, fossil assemblages dominated by these taxa are interpreted as characteristic of eutrophic (important input of labile organic matter) and/or dysoxic conditions. The formation of such an assemblage in a well-oxygenated environment with important focusing of refractory organic matter shows that these taxa should be used for paleoenvironmental analysis with the utmost care.

Acknowledgements

We would like to thank the French national program PROOF (INSU-CNRS) for sponsoring the OXYBENT program. We have special and kind thoughts for the crews and the captains of the Côte de la Manche, our scientific ship during all campaigns. We also thank M. Sibuet, F. Monniot and J.C. Sorbe for the very interesting and helpful discussions we had about macro- and meiofaunal ecology in the Bay of Biscay and elsewhere. We thank very much S. Hess for her help with the identification of some of the foraminiferal taxa. We are grateful to J.M. Jouanneau for providing us access to his data on radioactive elements in our cores. We thank O. Weber for his help in purpose to better understand the X-ray radiography and for providing many of the sedimentological data. We finally thank H. Howa for reviewing our sedimentological analysis.

Appendix A

Species of benthic foraminifera recognized at station I from the Bay of Biscay, with references to plates and figures in the literature on Atlantic and Mediterranean foraminifera.

Appendix B

Census data for live benthic foraminifera in the 63-150 μm size fraction in the first half cm of all 4 cores.
N.B. Numbers are not standardized for sediment volume.

Appendix C

Census data for live benthic foraminifera in the >150 μm size fraction for all 4 cores.
N.B. Numbers are not standardized for sediment volume.

Appendix A

Species	References
Adercotryma glomerata (Brady), 1878	Jones (1994), pl. 34, Figs. 15-18
Ammobaculites agglutinans (d'Orbigny), 1846	Hess (1998), pl. 4, Fig. 4
Bolivina pseudoplicata Heron-Allen & Earland 1930	Schiebel (1992), pl. 8, Fig. 8a-b
Bulimina alazanensis Cushman, 1927	Schiebel (1992), pl. 2, Fig. 5
Bulimina inflata Seguenza, 1862	Van Leeuwen (1989), pl. 8, Fig. 4
Bulimina marginata d'Orbigny, 1826	Hess (1998), Pl. 10, Fig. 7
Cassidulina carinata Silvestri, 1896	Phleger et al.(1953), pl. 9, Figs. 32-37
Cassidulina crassa d'Orbigny, 1839	Jones (1994), pl. 54, Fig. 4 and 5
Chilostomella oolina Schwager, 1878	Jones (1994), pl. 55, Figs. 12-14
Cibicides lobatulus Walker & Jacob, 1798	Jones (1994), pl. 92, Fig. 10
Cibicides wuellerstorfi (Schwager), 1866	Van Leeuwen (1989), pl. 10, Figs. 1-9
Cibicidoides pachydermus (Rzehac), 1886	Jones (1994), pl. 94, Fig. 9
Cibicidoides robertsonianus (Brady), 1881	Van Leeuwen (1989), pl. 9, Figs. 1-3
Cornuspira involvens (Reuss), 1950	Jones (1994), pl. 11, Figs. 1-3
Cribrostomoides subglobosus (Cushman), 1910	Jones (1994), pl. 34, Figs. 8-10
Cribrostomoides wiesneri (Parr), 1950	Jones (1994), pl. 40, Fig. 14 and 15
Eggerella bradyi (Cushman), 1911	Jones (1994), pl. 47, Figs. 4-7
Eggerella scabra (Williamson), 1858	Jones (1994), pl. 47, Figs. 15-17
Epistominella exigua (Bradyi), 1884	Schiebel (1992), pl.5, Fig.9
Globobulimina affinis (d'Orbigny), 1839	Phleger et al.(1953), pl. 6, Fig. 32
Globocassidulina subglobosa (Bradyi), 1881	Jones (1994), pl. 54, Fig.17
Glomospira charoides Jones & Parker, 1860	Phleger et al.(1953), pl. 5, Fig. 1
Glomospira gordialis Jones & Parker, 1860	Phleger et al.(1953), pl. 5, Fig. 2
Gyroidina altiformis Stewart & Stewart, 1930	Jorissen (1987), pl. 1, Fig. 11
Gyroidina orbicularis (sensu Parker, Jones and Brady), 1865	Jones (1994), pl. 115, Fig. 6
Gyroidina umbonata (Silvestri), 1898	Parker (1958), pl. 3, Fig. 19 and 20
Gyroidinoides soldanii (d'Orbigny), 1826	Jones (1994), pl. 107, Fig. 6 and 7
Hoeglundina elegans (d'Orbigny), 1826	Phleger et al.(1953), pl. 9, Fig. 24 and 25
Lagenammina tubulata (Rhumbler), 1931	Hess (1998), pl. 2, Fig. 10
Lenticulina gibba (d'Orbigny), 1839	Hess (1998), pl. 13, Fig. 1
Melonis barleeanus (Williamson), 1858	Van Leeuwen (1989), pl. 13, Fig. 1 and 2
Melonis pompilioides (Fichtel and Moll), 1798	Jones (1994), pl. 109, Fig. 10 and 11
Nonionella turgida (Williamson), 1858	Jones (1994), pl. 109, Figs. 17-19
Nuttallides pusillus (Parr), 1950	Phleger et al.(1953), pl. 9, Fig. 5 and 6
Nuttallides umboniferus (Cushman), 1933	Van Leeuwen (1989), pl. 15, Figs. 11-13; pl. 16, Figs. 1-7
Parafassiruna lateralis (Cushman), 1913	Jones (1994), pl. 56, Fig.17 and 18
Pullenia bulloides (d'Orbigny), 1826	Phleger et al.(1953), pl. 10, Fig. 19
Pullenia quinqueloba (Reuss), 1851	Jones (1994), pl. 84, Fig. 14 and 15
Pyrgo depressa (d'Orbigny), 1826	Jones (1994), pl. 2, Figs. 12, 16 and 17
Pyrgo elongata (d'Orbigny), 1826	Hess (1998), pl. 9, Fig. 5
Pyrgo murrhina (Schwager), 1866	Hess (1998), pl. 9, Fig. 1
Pyrgo subsphaerica d'Orbigny, 1839	Cushman (1929), pl. 18, Fig 1 and 2
Quinqueloculina seminula (Linné), 1758	Jones (1994), pl. 5, Fig. 6
Reophax bilocularis Flint, 1899	Hess (1998), pl. 2, Fig. 13 and 14
Reophax calcareus (Cushman), 1947	Timm (1992), pl. 2, Fig.2a-b
Reophax dentiliniformis Brady, 1881	Jones (1994), pl. 30, Fig. 21 and 22
Reophax gaussicus (Rhumbler), 1913	Jones (1994), pl. 31, Fig. 1 and 2, ?5
Reophax guttiferus Brady, 1881	Jones (1994), pl. 31, Fig. 10-15
Reophax micaceus Eerland 1934	Schiebel (1992), pl. 8, Fig. 7
Reophax nodulosus Brady, 1879	Jones (1994), pl. 31, Figs. 6-9
Reophax scorpiurus Montfort, 1808	Loeblich and Tappan (1988), pl. 44, Figs. 1-3
Reophax spiculifer Brady, 1879	Jones (1994), pl. 31, Fig. 16 and 17
Reophax subfusiformis Eerland, 1933	Schiebel (1992), pl. 8, Fig. 8
Sphaeroidina bulloides Deshayes, 1832	Jones (1994), pl. 84, Figs 1-5, ?6-7
Sigmoilopsis schlumbergeri Silvestri, 1904	Jones (1994), pl. 8, Figs. 1-4
Technitella legumen Norman, 1878	Jones (1994), pl. 25, Figs. 8-10
Technitella melo Norman, 1978	Jones (1994), pl. 25, Fig. 7
Thurammina albicans Brady, 1879	Jones (1994), pl. 37, Fig. 2-7
Trifarina angulosa (Williamson), 1858	Jones (1994), pl. 74, Fig. 17 and 18
Triloculina trigonula (Lamarck), 1804	Jones (1994), pl.3, Fig. 15 and 16
Trochammina globigeriniformis (Parker & Jones), 1865	Timm (1992), pl. 4, Fig. 2a-b
Uvigerina peregrina Cushman, 1923	Van der Zwaan et al. (1986), pl. 1, Figs.1-6

Appendix B

	January 1999		June 1999		April 2000, core A		April 2000, core B	
Taxa	Total	%	Total	%	Total	%	Total	%
Perforate								
Indet					3	1 55		
Ammolindoes sp					1	0 52	1	0 26
Bolivina sp							2	0 52
Bolivina pseudoplicata			7	2.98	4	2 06	9	2 33
Bulimina sp 1	1	0 77	3	1.28	1	0 52	12	3 10
Bulimina alazanensis			2	0.85	1	0 52	2	0 52
Bulimina aculeata	1	0 77	5	2.13	2	1 03	5	1 29
Bulimina marginata			1	0.43	1	0 52	3	0 78
Cassidulina carinata	1	0 77	2	0.85	2	1 03	1	0 26
Cassidulina crassa	1	0 77	7	2.98	19	9 79	26	6 72
Ceratobulimina sp					3	1 55	1	0 26
Cibicides sp.							1	0 26
Cibicides lobatulus	1	0 77			2	1 03	1	0 26
Cibicidoides rohertsonianus							1	0 26
Epistominella exigua	3	2 31	12	5.11	13	6 70	30	7 75
Fissurina sp			1	0.43				
Globocassidulina subglobosa			3	1.28	12	6 19	4	1 03
Gyroidina sp	1	0 77	1	0.43			1	0 26
Gyroidina sp 1	1	0 77	2	0.85				
Gyroidina orbicularis			1	0.43	1	0 52	1	0 26
Gyroidina umbonata	6	4 62	6	2.55	5	2 58	24	6 20
Hoeglundina elegans			4	1 70			1	0 26
Lagena sp					1	0 52	1	0 26
Nonionella sp					3	1 55		
Nuttallides pusillus	1	0 77	22	9.36	8	4 12	27	6 98
Nuttallides umbonifenus							1	0 26
Parafissurina sp	2	1 54					1	0 26
Pullenia sp	1	0 77						
Pullenia sp.1	6	4 62	1	0.43	9	4 64	2	0 52
Pullenia bulloides			1	0.43			1	0 26
Pullenia quinqueloba							1	0 26
Robertinoides sp			2	0.85				
Stainforthia sp					1	0 52	1	0 26
Trifarina angulosa			6	2.55			16	4 13
Uvigerina sp	1	0 77					1	0 26
Uvigerina sp 1							1	0 26
Uvigerina peregrina	1	0 77			3	1 55	4	1 03
Porcellaneous								
Indet					1	0 52		
Cornuspira involvens	1	0 77						
Miliolinella sp					1	0 52	1	0 26
Ophthalmidium sp	3	2 31					1	0 26
Pyrgo sp							1	0 26
Pyrgo elongata							2	0 52
Quinqueloculina sp	1	0 77	4	1.70	4	2 06	23	5 94
Sigmoilina sp			1	0.43			1	0 26
Triloculina sp							1	0 26
Non fossilising agglutinated								
Adercotryma glomerata	8	6 15	4	1 70	4	2 06	4	1 03
Ammobaculites sp.	1	0 77	1	0.43			4	1 03
Cribrostomoides subglobosus			7	2.98	22	11.34	13	3 36
Eggerella bradyi			3	1 28	1	0 52		
Eggerella scabra					1	0 52	2	0 52
Hyperammina sp	4	3 08	34	14 47	10	5 15	37	9 56
Karrerulina sp.			1	0.43	1	0 52		
Psammosphaera sp	1	0 77	5	2 13	3	1 55	1	0 26
Pseudotextularia sp					1	0 52	1	0 26
Recurvoides sp					2	1 03		
Reophax sp			4	1.70	1	0 52		
Reophax sp 3			1	0.43	1	0 52		
Reophax bilocularis	18	13 85	9	3.83	3	1 55	17	4 39
Reophax calcareus	2	1 54						
Reophax dentaloniformis							2	0 52
Reophax guttiferus	36	27 69	28	11.91	13	6 70	24	6 20
Reophax scorpiurus	11	8 46	16	6 81	9	4 64	16	2 88
Spiroplectammina sp	1	0 77			5	2 58	3	0 78
Technitella melo							1	0 26
Trochammina sp			2	0.85				
Trochammina sp 1	2	1 54	2	0 85	3	1 55	2	0 52
Trochamminia globigeriniformis	13	10 00	24	10 21	12	6 19	44	11 37
Fossilising agglutinated								
Sigmoilopsis schlumbergeri							1	0 26
Soft-shelled								
Indet					1	0 52	2	0 52
Total live foraminifera	130	100.00	235	100 00	194	100 00	387	100.00
Nbr species	27		37		39		55	
Ostracoda	6		4		5		2	
Arborescent indet					2			
Glomospira spp	3				4		5	

Appendix C

January 1999																		
Depth	**0-0.25**	**0.25-0.5**	**0.5-0.75**	**0.75-1**	**1-1.5**	**1.5-2**	**2-2.5**	**2.5-3**	**3-3.5**	**3.5-4**	**4-5**	**5-6**	**6-7**	**7-8**	**8-9**	**9-10**	**Total**	**%**
Perforate																		
Indet	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Bulimina inflata	0	0	0	0	0	0	1	0	0	0	0	(1)	0	0	0	0	2	0.83
Chilostomella oolina	0	0	0	0	0	1	0	0	2	2	1	1	0	(1)	0	0	8	3.31
Cibicides wuellerstorfi	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Globobulimina affinis	0	0	0	0	0	0	0	0	0	21	23	7	2	4	1	0	58	23.97
Gyroidina orbicularis	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0	3	1.24
Hoeglundina elegans	1	2	3	1	0	1	0	0	0	0	0	0	0	0	0	0	8	3.31
Melonis barleeanus	0	1	0	1	1	2	5	5	13	9	1	0	0	0	0	0	38	15.70
Nonionella sp	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Parafissurina lateralis	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Pullenia quinqueloba	0	0	0	0	1	0	0	0	0	(1)	0	0	0	0	0	0	2	0.83
Uvigerina sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.41
Uvigerina peregrina	4	5	3	0	0	0	0	0	0	0	0	0	0	0	0	0	12	4.96
Porcellaneous																		
Quinqueloculina seminula	0	1	2	2	0	0	0	0	0	0	0	0	0	0	0	0	5	2.07
Quinqueloculina sp.1	0	0	0	1	3	0	1	0	0	0	0	0	0	0	0	0	5	2.07
Quinqueloculina sp.2	0	0	0	0	1	1		0	0	0	0	0	0	0	0	0	2	0.83
Triloculina trigonula	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Non fossilising agglutinated																		
Indet	0	0	0	1	0	0	2	0	0	0	0	0	0	0	0	0	3	1.24
Agglut. indet sp.B	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
Adercotryma glomerata	0	0	0	0	0	0	0	0	0	0		1	0	0	0	0	1	0.41
Ammobaculites agglutinans	2	1	8	6	2	0	1	0	0	0	0	0	0	0	0	0	20	8.26
Cribrostomoides subglobosus	1	0	2	1	0	1	0	0	0	(1)	0	0	0	0	0	0	6	2.48
Haplophragmoides sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.41
Recurvoides sp.	0	2	0	1	1	2	0	0	0	0	0	0	0	0	0	0	6	2.48
Reophax sp.	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Reophax dentaliniformis	0	0	2	1	2	3	4	2	1	4	0	0	0	0	0	0	19	7.85
Reophax nodulosus	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
Reophax scorpiurus	1	4	2	1	5	8	8	4	0	1	0	0	0	0	0	0	34	14.05
Reophax subfusiformis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0.41
Total live foraminifera	11	18	23	16	20	19	23	11	18	39	25	10	3	5	1	1	242	100.00
Nbr species	6	9	8	9	11	8	7	3	5	7	3	4	1	2	1	1	27	
Ostracoda	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	
Arborescent indet	6	15	10	16	14	10	7	3	8	0	3	0	3	0	0	0	95	

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Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	Total	%
Perforate																		
Indet.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Bulimina inflata	1	1	1	0	1	0	0	0	0	0	0	0	(1)	0	0	0	5	1.21
Chilostomella oolina	0	0	0	0	1	0	0	1	0	0	10	16	8	2	0	0	38	9.20
Cibicides lobatulus	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Globobulimina affinis	0	0	0	0	0	0	0	0	2	1	32	30	9	0	0	0	74	17.92
Gyroidina sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
Gyroidina orbicularis	0	0	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.48
Gyroidinoides soldanii	1	0	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	2	0.48
Hoeglundina elegans	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Melonis barleeanus	0	0	0	1	0	0	10	15	5	4	1	0	0	0	0	0	36	8.62
Nonionella atlantica	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Parafissurina lateralis	1	0	0	0	0	0	0	(1)	0	0	0	0	0	0	0	0	2	0.48
Pullenia bulloides	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
Pullenia quinqueloba	0	0	0	0	0	0	2	5	1	0	0	0	0	0	0	0	8	1.94
Robertina sp.	0	0	0	0	0	0	0	4	0	0	0	0	0	0	0	0	4	0.97
Robertinoides sp.	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Uvigerina peregrina	2	1	3	1	4	1	1	0	0	0	0	0	0	0	0	0	13	3.15
Porcellaneous																		
Comuspira involvens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0.24
Pyrgo depressa	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0.48
Pyrgo elongata	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.24
Pyrgo murrhina	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Quinqueloculina seminula	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Quinqueloculina sp.1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Triloculina sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Triloculina trigonula	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Non fossilising agglutinated																		
Indet.	2	1	0	0	0	0	0	0	1	1	0	0	0	0	0	0	5	1.21
Agglut. sp.C	0	0	0	0	0	2	2	0	0	0	0	0	0	0	0	0	4	0.97
Adercotryma glomerata	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
Ammobaculites agglutinans	6	3	4	2	1	0	0	3	0	0	0	0	0	0	0	0	19	4.60
Cribrostomoides subglobosus	6	4	5	3	11	3	3	5	0	0	1	1	0	0	0	0	42	10.17
Cribrostomoides wiesneri	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.24
Cystammina sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
Eggerella bradyi	1	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	4	0.97
Haplophragmoides sp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.24
Hippocrepinella sp.	1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.48
Hormosina sp.	1	0	3	0	1	0	0	0	0	0	0	0	0	0	0	0	5	1.21
Karrerulina sp.	0	2	2	1	0	2	2	0	0	(1)	0	0	0	0	0	0	10	2.42
Psammosphaera sp.	6	4	1	1	0	2	1	1	1	0	0	(1)	0	(1)	0	0	19	4.60
Recurvoides sp.	0	1	1	5	1	3	2	0	0	0	0	0	0	0	0	0	13	3.15
Reophax sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Reophax sp.3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Reophax biloculanis	2	0	0	8	7	2	0	0	1	0	0	2	2	0	(1)	0	25	6.05
Reophax calcareus	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Reophax dentaliniformis	1	1	0	1	0	0	0	1	1	1	0	0	0	0	0	0	6	1.45
Reophax gaussicus	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	0	3	0.73
Reophax guttiferus	2	1	5	1	0	0	0	0	0	0	0	0	0	0	0	0	9	2.18
Reophax micaceus	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.24
Reophax scorpiurus	2	3	3	1	8	6	8	4	1	2	0	0	0	0	0	0	38	9.20
Technitella legumen	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Technitella melo	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.24
Fossilising agglutinated																		
Sigmoilopsis schlumbergeri	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0.24
Total live foraminifera	37	26	36	29	38	23	37	43	15	12	45	50	20	3	1	0	413	100.00
Nbr species	16	14	18	14	12	9	15	13	9	7	5	5	4	2	1	0	49	
Glomospira spp.	0	1	0	1	1	2	1	4	3	2	4	4	3	3	1	0	30	
Ostracoda	0	1	0	0	0	1	0	0	0	0	0	1	0	0	0	0	3	
Arborescent indet.	1	10	27	19	18	12	13	5	11	0	0	0	0	0	0	0	116	

April 2000, core A																		
Depth	0-0 25	0.25-0 5	0.5-0 75	0.75-1	1-1 5	1 5-2	2-2.5	2 5-3	3-3 5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina alazanensis	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Bulimina inflata	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	(1)	0	2	0.82
Chilostomella oolina	0	0	0	0	**1**	1	0	0	0	1	0	0	**1**	1	0	0	5	2.06
Cibicides lobatulus	2	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	7	2 88
Cibicides wuellerstorfi	2	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.23
Cibicidoides robertsonianus	0	**1**	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	2	0.82
Fissurina sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Fissurina sp.1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.41
Globobulimina affinis	0	0	0	0	0	0	0	0	**4**	0	**7**	10	9	13	14	0	57	23.46
Gyroidina altiformis	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Gyroidina orbicularis	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Gyroidinoides soldanii	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Hoeglundina elegans	0	0	0	0	0	0	0	0	0	0	0	0	**1**	0	0	0	1	0 41
Lagena sp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Melonis barleeanus	0	0	0	0	**1**	1	3	1	1	0	0	0	0	0	0	0	7	2 88
Melonis pompilioides	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Nonionella atlantica	0	**1**	0	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0 82
Parafissurina lateralis	0	0	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	1	0.41
Pullenia quinqueloba	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0 41
Pullenia sp.1	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0 82
Robertinoides sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Sphaeroidina bulloides	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1	0.41
Uvigerina sp.	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.41
Uvigerina peregrina	0	0	0	0	0	0	**1**	0	0	0	0	0	(1)	0	0	0	2	0.82
Porcellaneous																		
Cornuspira involvens	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0 41
Pyrgo sp.	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	0 41
Pyrgo depressa	1	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0 82
Pyrgo elongata	0	**1**	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	1 23
Pyrgo subsphaerica	1	**1**	1	0	**1**	0	0	0	0	0	0	0	0	0	0	0	4	1 65
Quinqueloculina seminula	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Quinqueloculina sp.1	2	3	0	2	**1**	0	0	0	0	0	0	0	0	0	0	0	8	3.29
Quinqueloculina sp.2	0	0	0	1	**1**	0	0	0	0	0	0	0	0	0	0	0	2	0.82
Non fossilising agglutinated																		
Indet.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Agglut. sp.C	2	0	1	1	3	0	0	0	0	0	0	0	0	1	0	0	8	3.29
Adercotryma glomerata	0	0	0	0	**1**	0	0	0	3	0	0	0	0	0	0	0	4	1 65
Ammobaculites agglutinans	0	2	1	0	2	1	**1**	2	1	0	0	(1)	0	0	0	0	**11**	**4 53**
Cribrostomoides sp.	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Cribrostomoides subglobosus	1	0	2	2	3	3	2	3	**4**	0	0	(1)	0	0	0	0	21	8 64
Haplophragmoides sp	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0 41
Hippocrepinella sp	0	**1**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Hormosina sp.	1	0	0	1	5	0	0	0	(1)	0	0	0	0	0	0	0	8	3.29
Karrerulina sp.	0	**1**	3	1	2	0	**1**	0	0	0	0	0	0	0	0	0	8	3 29
Psammosphaera sp.	1	0	1	0	**1**	0	0	0	0	0	0	0	0	2	0	0	5	2.06
Recurvoides sp.	0	0	0	2	**1**	1	0	0	0	0	0	0	0	0	0	0	4	1.65
Reophax sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	(1)	0	2	0.82
Reophax sp.3	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0.82
Reophax bilocularis	5	2	2	1	0	0	0	0	0	0	0	0	0	0	0	0	10	4.12
Reophax dentaliniformis	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
Reophax gaussicus	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	2	0.82
Reophax guttiferus	1	**1**	1	0	0	0	0	0	0	0	0	0	0	0	0	0	3	1.23
Reophax nodulosus	0	0	0	0	**1**	0	0	0	0	0	0	0	0	0	0	0	1	0 41
Reophax scorpiurus	1	0	3	6	6	2	2	0	0	0	0	0	**1**	0	2	0	23	9 47
Reophax spiculifer	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.41
Trochammina sp.	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	1	0.41
Total live foraminifera	24	**21**	20	26	33	10	11	7	16	5	9	13	13	17	18	0	243	100.00
Nbr species	16	17	13	14	18	7	7	**4**	7	4	2	5	4	**4**	4	0	53	
Glomospira spp.	0	0	3	2	7	4	11	8	10	3	**4**	7	3	**4**	0	0	66	
Ostracoda	3	**1**	2	1		1	0	0	0	0	0	0	0	0	0	0	8	
Arborescent indet	4	11	28	62	84	41	8	33	14	3	0	1	0	0	0	0	289	

April 2000, core B																		
Depth	0-0.25	0.25-0.5	0.5-0.75	0.75-1	1-1.5	1.5-2	2-2.5	2.5-3	3-3.5	3.5-4	4-5	5-6	6-7	7-8	8-9	9-10	**Total**	**%**
Perforate																		
Bulimina alazanensis	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	2	0.37
Bulimina inflata	8	2	3	0	3	1	0	0	0	0	1	6	1	0	0	0	25	4.60
Cibicides wuellerstorfi	1	0	4	0	0	0	0	2	0	0	0	0	(1)	0	0	0	8	1.47
Cibicidoides robertsonianus	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	3	0.55
Fissurina sp	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.18
Globobulimina affinis	0	0	0	0	0	0	0	0	0	0	0	0	3	4	3	1	11	2.02
Gyroidina sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.18
Gyroidina altiformis	1	0	0	0	0	0	0	0	0	0	(1)	0	0	0	0	0	2	0.37
Gyroidina orbicularis	0	0	0	1	0	1	1	0	0	0	(1)	0	0	0	0	0	4	0.74
Gyroidinoides soldanii	0	1	0	0	2	0	0	0	0	0	0	(1)	0	0	0	0	4	0.74
Hoeglundina elegans	6	4	0	1	1	1	2	0	2	0	6	4	1	0	2	0	30	5.51
Lenticulina gibba	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0.18
Melonis barleeanus	0	0	0	0	1	3	3	2	0	1	3	0	5	4	2	0	24	4.41
Melonis pompilioides	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.18
Nonionella atlantica	1	0	0	0	(1)	0	0	0	0	0	0	0	0	0	0	0	2	0.37
Pullenia sp.	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0.18
Pullenia bulloides	3	1	1	0	0	(1)	0	0	0	0	0	0	0	(1)	0	0	7	1.29
Pullenia quinqueloba	0	1	0	0	0	0	6	0	0	1	3	5	0	0	0	0	16	2.94
Pullenia sp 1	0	0	1	0	0	1	0	2	0	1	4	2	0	0	0	0	11	2.02
Robertina sp.	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Uvigerina peregrina	4	4	2	1	0	0	1	1	0	1	1	2	1	0	0	0	18	3.31
Porcellaneous																		
Indet	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0.18
Comuspira sp.	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	2	0.37
Comuspira involvens	0	0	0	0	0	0	0	0	1	0	0	1	0	0	0	0	2	0.37
Ophtalmidium sp.	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Pyrgo elongata	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	2	0.37
Pyrgo murrhina	0	1	0	0	0	0	1	0	0	1	0	0	0	0	0	0	3	0.55
Pyrgo subsphaerica	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Quinqueloculina seminula	0	1	0	3	0	0	0	0	0	0	0	2	0	0	0	0	6	1.10
Quinqueloculina sp 1	0	0	0	0	0	0	1	0	1	0	0	0	0	0	0	0	2	0.37
Quinqueloculina sp 2	1	0	1	3	0	0	0	0	0	0	0	0	0	0	0	0	5	0.92
Non fossilising agglutinated																		
Indet	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	5	0.92
Agglut. sp.C	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0.55
Ammobaculites agglutinans	14	3	5	2	5	1	2	4	4	5	3	1	1	1	0	0	51	9.38
Cribrostomoides sp.	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0.18
Cribrostomoides subglobosus	14	10	5	5	4	4	1	3	4	6	2	6	2	1	1	0	68	12.50
Cribrostomoides wiesneri	0	0	0	0	0	0	0	1	0	1	2	0	0	1	0	0	5	0.92
Eggerella bradyi	0	0	1	0	0	1	0	0	0	0	0	0	0	0	0	0	2	0.37
Haplophragmoides sp.	0	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0	3	0.55
Hippocrepinella sp.	3	0	1	2	1	0	0	0	0	0	0	0	0	0	0	0	7	1.29
Hormosina sp.	0	1	1	0	1	7	4	0	1	1	3	0	0	0	0	0	19	3.49
Karrerulina sp.	1	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	3	0.55
Lagenammina tubulata	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0.18
Psammosphaera sp	0	0	0	0	0	1	0	1	0	1	3	1	0	1	0	0	8	1.47
Recurvoides sp.	1	2	0	2	1	1	0	1	1	2	0	0	0	0	2	0	13	2.39
Reophax sp	2	1	3	0	0	0	2	0	0	0	1	1	0	0	0	0	10	1.84
Reophax bilocularis	1	3	4	2	7	6	0	0	1	0	1	0	0	0	0	0	25	4.60
Reophax dentaliniformis	1	0	0	1	0	0	2	1	0	0	0	0	0	0	0	0	5	0.92
Reophax guttiferus	1	1	1	4	2	0	0	2	0	0	1	0	0	0	0	0	12	2.21
Reophax scorpiurus	10	4	15	8	9	10	10	8	3	5	7	1	2	2	0	0	94	17.28
Thurammina albicans	0	0	0	0	0	0	1	0	1	1	0	0	0	0	0	0	3	0.55
Trochammina sp.	0	0	0	0	0	0	1	0	0	0	1	1	0	1	0	0	4	0.74
Fossilizing agglutinated																		
Sigmoilopsis schlumbergeri	0	0	0	0	0	0	0	0	0	0	2	1	1	0	0	0	4	0.74
Total live foraminifera	76	41	54	39	39	42	43	28	19	27	50	37	22	16	10	1	544	100.00
Nbr species	20	16	19	16	14	13	15	9	8	10	18	14	11	5	4	1	51	
Glomospira spp	3	3	3	1	6	3	10	8	9	12	13	15	15	19	6	0	126	
Ostracoda	1	1	2	1	3	1	1	0	0	0	0	0	0	0	0	0	10	
Arborescent indet	3	5	6	8	22	50	49	8	7	8	0	5	2	1	0	0	174	

CHAPITRE 5

Une révision du genre *Globobulimina* Cushman, 1927 : Aspects écologiques, composition isotopique ($\delta^{18}O$ et $\delta^{13}C$) et applications paléo-océanographiques.

A review of the genus GLOBOBULIMINA Cushman, 1927: Ecological aspects, isotopic composition ($\delta^{13}C$ and $\delta^{18}O$) and paleo-oceanographic applications.

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Résumé

Dans ce papier, nous présentons une revision des connaissances concernant le genre de foraminifère *Globobulimina*. Nous utilisons des données du Golfe de Gascogne et au large de Cape Blanc pour compléter et préciser les caractéristiques écologiques et isotopiques ($\delta^{13}C$ and $\delta^{18}O$) de ce taxon. Le genre *Globobulimina* est une espèce eurybathe qui s'étale depuis la plate-forme jusque dans les environnements abyssaux. Grâce à des adaptations métaboliques supputées (microaérophilie, processus anérobies alternatifs, symbiose), il peut occuper des microhabitats appauvris en oxygène voire anoxiques. C'est pourquoi, il vit préférentiellement autour et dessous la « limite oxygène zéro » comme une espèce endopélique très spécialisée. Là, il lui est possible de trouver différentes sources de carbone organique nécessaires à l'entretien son activité métabolique, principalement des détritus organiques enfouis en profondeur et en voie de décomposition ou de la biomasse bactérienne. Dans le Golfe de Gascogne et au large de Cap Blanc, la profondeur de la « limite oxygène zéro » résulte d'un ensemble composite de facteurs abiotiques parmi lesquels le flux exporté de carbone organique depuis les eaux de surface est un paramètre majeur. A partir des données mondiales, il apparaît que les fortes densités de *Globobulimina* sont généralement enregistrées dans les sédiments où des flux élevés de matière organique sont enregistrés. C'est le cas d'environnements eutrophes plus ou moins profonds ainsi que les environnements de canyon. En terme de dynamique de population, les études in situ et expérimentales suggèrent que dans le Golfe de Gascogne *Globobulimina* présente un cycle de vie plus long qu'une année. Il ne se comporte pas comme une espèce opportuniste et montre des taux bas d'assimilation du carbone. Des densités élevées de *Globobulimina* enregistrées dans certains environnements très bien oxygénés suggèrent que l'interprétation des assemblages fossiles où *Globobulimina* est dominant comme indicatives de paléo-environnements sous-oxygénés n'est pas pertinente. Dans le Golfe de Gascogne, la signature $\delta^{13}C$ de *Globobulimina* reflète son microhabitat endopélique profond. Le $\Delta\delta^{13}C$ entre *Globobulimina* et l'espèce endopélique peu profonde *Uvigerina peregrina* pourrait être un outil pertinent de reconstruction des paléo-profiles de $\delta^{13}C$ du carbone inorganique dissous dans les eaux porales. En outre, dans la mesure où *Globobulimina* biomineralise son test avec un écart faible et constant par rapport à la calcite à l'équilibre avec le $\delta^{18}O_{e.c}$ de l'eau de fond, sa signature isotopique $\delta^{18}O$ peut être utilisée pour construire ou complèter des charpentes chronostratigraphiques isotopiques utilisées pour les études paléo-océanographiques.

Mots-Clés: *Globobulimina*; Microhabitat; Densité; Signatures isotopiques; Flux exporté de carbone organique; Oxygenation de l'eau de fond; Limite oxygène zéro; dynamique saisonnière; Applications paléo-océanographique.

Abstract

In this paper, we present a critical review of the present knowledge about the foraminiferal genus *Globobulimina*. We use data from the Bay of Biscay and from off Cape Blanc to complete and refine our knowledge of the ecological and isotopic ($\delta^{13}C$ and $\delta^{18}O$) patterns of this taxon. The genus *Globobulimina* is an eurybathyal taxon that spreads from shelf to abyssal environments. Thanks to putative metabolic adaptations (microaerophilic, alternative anaerobic pathways, symbiosis), it can occupy strongly oxygen depleted or even anoxic microhabitats. The genus preferentially lives around and below the zero oxygen boundary as a highly specialized infaunal taxon. In this microenvironment, it may find different organic carbon sources necessary to perform its metabolic activity, mainly organic phytodetritus in bacterial conversion and/or bacterial biomass. In the Bay of Biscay and off Cape Blanc, zero oxygen boundary depth results from a composite set of abiotic factors among which the exported organic carbon flux from the surface waters appears to be the major controlling parameter. An overview of recently published distributional data suggests that high standing stocks of *Globobulimina* are commonly recorded in sediments exposed to important vertical and/or lateral fluxes of organic matter. This is the case in more or less eutrophic environments as well as in passive canyon settings. In terms of population dynamics, in situ and experimental studies suggest that *Globobulimina* from the Bay of Biscay presents a life cycle longer than 1 year. It exhibits slow rates of organic matter assimilation and can certainly not be considered as an opportunistic taxon. High densities (and percentages) of *Globobulimina*, that are recorded in some well-oxygenated environments, suggest that fossil assemblages in which *Globobulimina* is a dominant taxon can not be considered straightforward as indicative of oxygen depleted environments. In the Bay of Biscay, the $\delta^{13}C$ of *Globobulimina* generally reflects its deep infaunal microhabitat. The $\Delta\delta^{13}C$ between *Globobulimina* and the shallow infaunal *Uvigerina peregrina* could be used to reconstruct the paleo-profile of dissolved inorganic carbon $\delta^{13}C$ in the pore water, and to gain insight in the fate of organic matter introduced into the sediment. Furthermore, since *Globobulimina* biomineralises its test with a rather constant and low offset to calcite in

equilibrium with bottom water $\delta^{18}O_{e.c.}$, its $\delta^{18}O$ signature can be used to construct or complete isotopic frameworks for paleoceanographic studies.

Keywords: *Globobulimina*; Microhabitat; Density; Isotopic signatures; Exported organic carbon flux; Bottom water oxygenation; Zero oxygen boundary; Seasonal dynamics; Paleo-oceanographic applications.

Introduction

Our knowledge of the ecological tolerances and limitations of deep-sea heterotrophic benthic foraminifera (FORAMINIFERA, GRANORETICULOSA, PROTOCTISTA) has been consistently improved by the last two decades of ecological studies on live foraminiferal communities. Corliss (1985) was the first to show that live benthic foraminiferal faunas from well-oxygenated deep-sea environments are not restricted to very shallow infaunal or epifaunal niches, but can spread down to several centimetres down below the sediment-water interface. Whereas some foraminiferal taxa occupy strictly superficial and well-oxygenated microhabitats at the sediment-water interface and in the topmost sediment, other species can thrive in dysoxic, suboxic and even anoxic niches, until several decimetres depth within the sediment. Numerous subsequent studies (e.g. Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Rathburn and Corliss, 1994; Kitazato, 1994; Jorissen et al., 1995; Jorissen et al., 1998; Kitazato et al., 2000; Licari et al., 2003) confirmed the presence of a vertical succession of distinct microhabitats in the sediment, for oxygen depleted as well as well-oxygenated environments. These observations show that live benthic foraminiferal faunas sampled in the first cm of the sediment do not necessarily reflect the total live foraminiferal assemblage. In situ and laboratory ecological studies also demonstrated that the density, composition and microhabitat of benthic foraminiferal faunas are controlled by various environmental variables among which the organic carbon flux from the surface waters to the seafloor and the dissolved oxygen concentration at and below the sediment-water interface are preponderant (e.g. Altenbach and Sarnthein, 1989; Loubere et al., 1993; Jorissen et al., 1995; Fariduddin and Loubere, 1997; Jorissen et al., 1998; Licari et al., 2003). The vertical organic matter flux to the seafloor consists mainly of labile phytoplankton aggregates that are rapidly consumed in the top sediment. The heterogeneous distribution of phytodetrital organic matter aggregates at the sediment-water interface may also be responsible for small-

scale spatial patchiness of benthic foraminiferal faunas (Fontanier et al., 2003a). Shallow infaunal and epifaunal opportunistic foraminiferal taxa are able to respond to phytodetritus patches by feeding on them and by rapid reproduction (e.g. Gooday, 1988; Altenbach and Sarnthein, 1989; Barmawidjaja et al., 1992; Silva et al., 1996; Kitazato et al., 2000; Heinz et al., 2001; 2002; Ernst, 2002). Species living in deeper sediment layers may benefit from altered phytodetritrus introduced into the sediment by bioturbation (e.g. Jorissen et al., 1995; Schmiedl et al., 2000; Kitazato et al., 2000). As shown by Jorissen et al. (1995) in their TROX-model, the foraminiferal microhabitat and the faunal composition would be food-controlled in oligotrophic settings, where benthic foraminiferal taxa would be restricted to surficial microhabitats where most of the scarce phytodetrital organic compounds are degraded. In more mesotrophic conditions, foraminiferal taxa could live in deeper infaunal niches where more or less altered phytodetritus should be available and which should still contain oxygen. In eutrophic conditions, the foraminiferal vertical distribution and species composition would be oxygen-controlled, since most of the foraminiferal faunas could only live in the very shallow oxygenated sediment. In extremely eutrophic conditions, with strongly hypoxic upper sediments, only foraminiferal taxa resistant to low oxygen conditions would be able to survive. The impact of bottom and pore water oxygenation on foraminiferal faunas was reviewed by Sen Gupta and Machain-Castillo (1993) and Bernhard and Sen Gupta (1999), who listed deep-sea foraminiferal taxa able to survive in oxygen depleted environments (e.g. *Bolivina*, *Bulimina*, *Globobulimina*). Some Other species are able to live in hypoxic conditions but are excluded by episodic anoxia (e.g. Alve and Bernhard, 1995; Moodley and Hess, 1992). Under prolonged anoxia, no foraminifera can survive (Bernhard et Reimers, 1991).

In view of the available ecological observations and assumptions, the deep infaunal genus *Globobulimina* is a very intriguing taxon. It is a dominant component of benthic foraminiferal assemblages from many oceanic slope environments, where it is able to live in oxygen-depleted microhabitats deeper in the sediment (e.g. Corliss, 1985; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Corliss, 1991; Jorissen et al., 1998; Schmiedl et al., 2000). The ecology of this genus and, more specifically, its role in suboxic and/or anoxic microenvironments and in benthic trophic chains is still poorly understood. The advantages of episodically or permanently living in the adverse conditions found deeper in the sediment are still unclear. Since most benthic foraminifera are considered as aerobic and heterotrophic organisms, they will need oxygen and labile organic compounds to perform their metabolic activity (growth, biomineralisation and reproduction). Therefore, if foraminifera occupying

deeper infaunal microhabitats, such as *Globobulimina*, are active, they must present still unknown adaptations to survive under the adverse conditions prevailing in deeper sediments. The conditions around the zero oxygen boundary are characterised by oxygen depletion and organic matter dominated by refractory components. Alternatively, if deep infaunal foraminiferal taxa are inactive (in dormancy, diapause, quiescence), they must perform a major part of their life functions (reproduction, feeding, growth) elsewhere, under more favorable conditions. However, until now, very few observations seem to indicate that this is the case.

Globobulimina forms also an important part of dead/fossil foraminiferal assemblages from slope environments. Traditionally, the genus is considered as a taxon typical of oxygen-depleted environments (e.g. Mullineaux et Lohmann, 1981; Baas et al., 1998). Recent data, however, show that low oxygenation in bottom waters is not a prerequisite for high percentages of *Globobulimina* (e.g. Schmiedl et al., 2000 ; Fontanier et al., 2003c). These observations put the long-claimed relationship between *Globobulimina* and low oxygen conditions into question.

Globobulimina lives, and probably calcifies in the deeper, suboxic or anoxic part of the sediment column. Its stable isotopic composition ($\delta^{13}C$) mirrors the composition of the interstitial waters. Its $\delta^{18}O$ signature is close to calcite in equilibrium with bottom waters (e.g. McCorkle et al., 1990; 1997). Therefore, the isotopic signature of *Globobulimina* may be useful to give insight into past $\delta^{13}C$ profiles within the sediment and the $\delta^{18}O$ of bottom waters.

In view of the important role of *Globobulimina* in many slope faunas, and the potential paleoceanographic applications, we decided to critically review the available knowledge on this still poorly understood benthic foraminiferal taxon, and complete this knowledge with our own observations from the Bay of Biscay (NE Atlantic) and from off Cape Blanc (NW Africa). In this paper, we will subsequently:

1) Review the taxonomy of recent representatives of *Globobulimina*, on the basis of our own as well as literature evidence. We will raise morphological arguments to considerably diminish the species names (about twelve) used in literature.
2) Give a literature-based overview of the geographical distribution of recent *Globobulimina,* completed with our own data, and try to describe preferred ecological

conditions for this genus. We will also consider the scarce data on the temporal variability of *Globobulimina* populations.

3) Discuss the ecological strategies, which allow this taxon to be one the most successful foraminifera in the deep infaunal niche. We will focus on time series studies as well as on laboratory experiments.
4) Discuss the stable isotopic composition of *Globobulimina*; we will especially focus on interspecific $\delta^{13}C$ differences with more superficially living taxa, and discuss the potential applicability of these differences in paleoceanographic studies.

Study areas and Methodology

Study areas

In this paper, we propose to use additional data about foraminiferal faunas from two study areas that where earlier described by Jorissen et al (1998) and Fontanier et al. (2002, 2003a, 2003b, 2003c).

The first study area consists of a 5-station transect off Cape Blanc (Northwest Africa) (Fig. 1). This is one of the most productive areas in the world's oceans, with primary production values reaching 325 g C/m²/yr. Jorissen et al. (1998) present a study about the live foraminiferal faunas along this bathymetric transect, which spreads from 1195 to 3010 m depth along the open slope (Table 1). The samples were taken in March 1994 with a multitube corer. At the time of sampling, bottom water oxygenation was higher than 164 µmol/l. More precise information about the hydrography and the primary production patterns of this study area is given by Jorissen et al. (1998). The second study area corresponds to a set of seven open-slope and canyon stations ranging from 140 to 2800 m depth in the Bay of Biscay (north eastern Atlantic Ocean). They were sampled between October 1997 and April 2001 in purpose to study the ecology of live benthic foraminiferal faunas (Table 1; Fig. 2). The Bay of Biscay is a semi-enclosed mesotrophic basin marked by seasonal spring and autumn blooms (e.g. Laborde et al., 1999; Fontanier et al., 2003a). Water masses filling the basin are well oxygenated (>140 µmol/l) (Ogawa and Tauzin, 1973; our data see Table 1). Our study area and most stations (without station C) to which we refer in this review have been described earlier in recent papers dealing with live foraminiferal faunas from the Bay of Biscay (Fontanier et al., 2002; 2003a; 2003b; 2003c). Only station C (235 metres depth) is newly

studied in this paper. This is an upper slope station, which is situated on the northern flank of Cap-Breton canyon, in the North Atlantic Central Waters. It was sampled in October 1997 (Table 1)**.** Table 1 presents the main characteristics of all stations discussed in this paper.

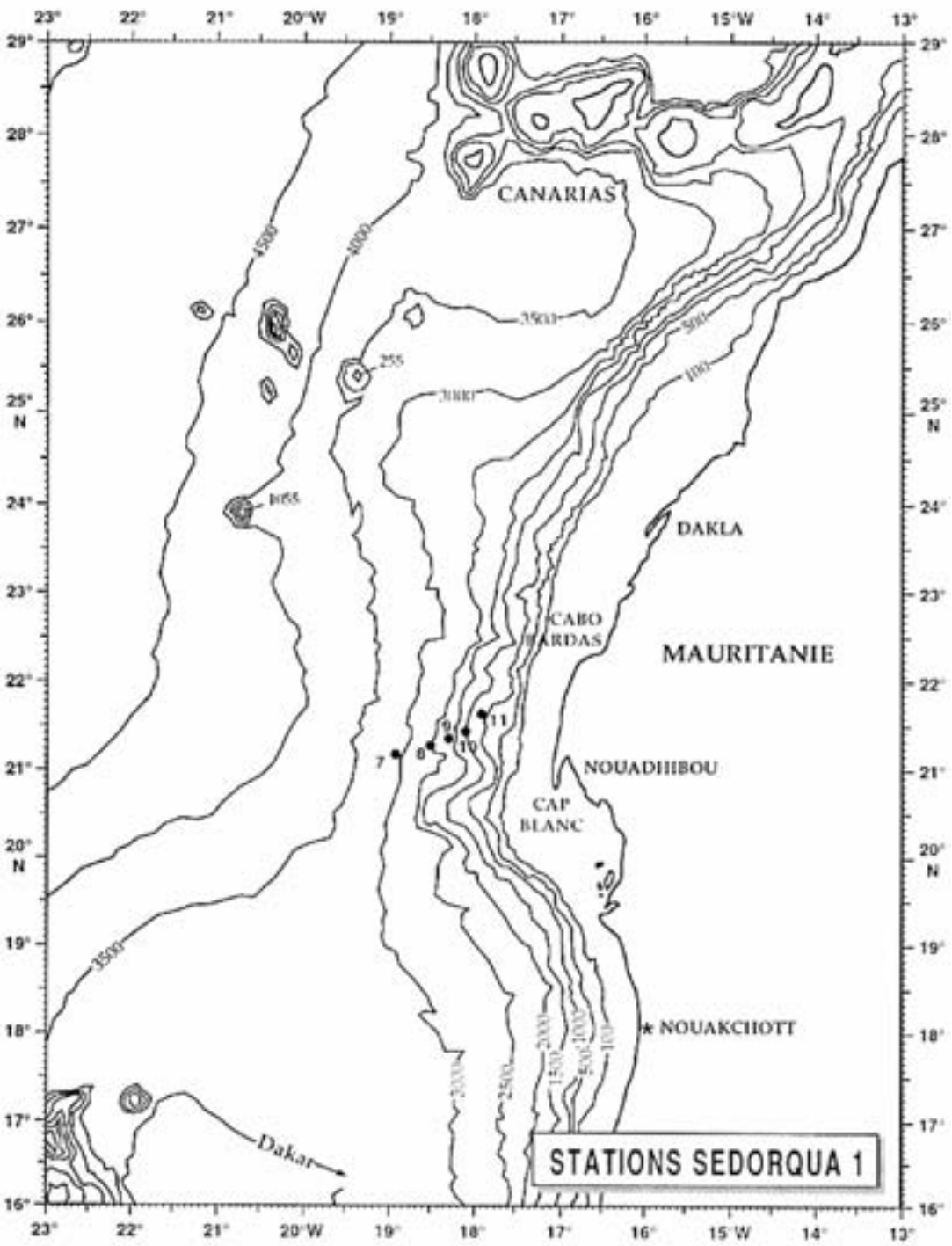


Fig. 1 Study area, bathymetry and geographical position of 5 stations off Cape Blanc (NW Africa)

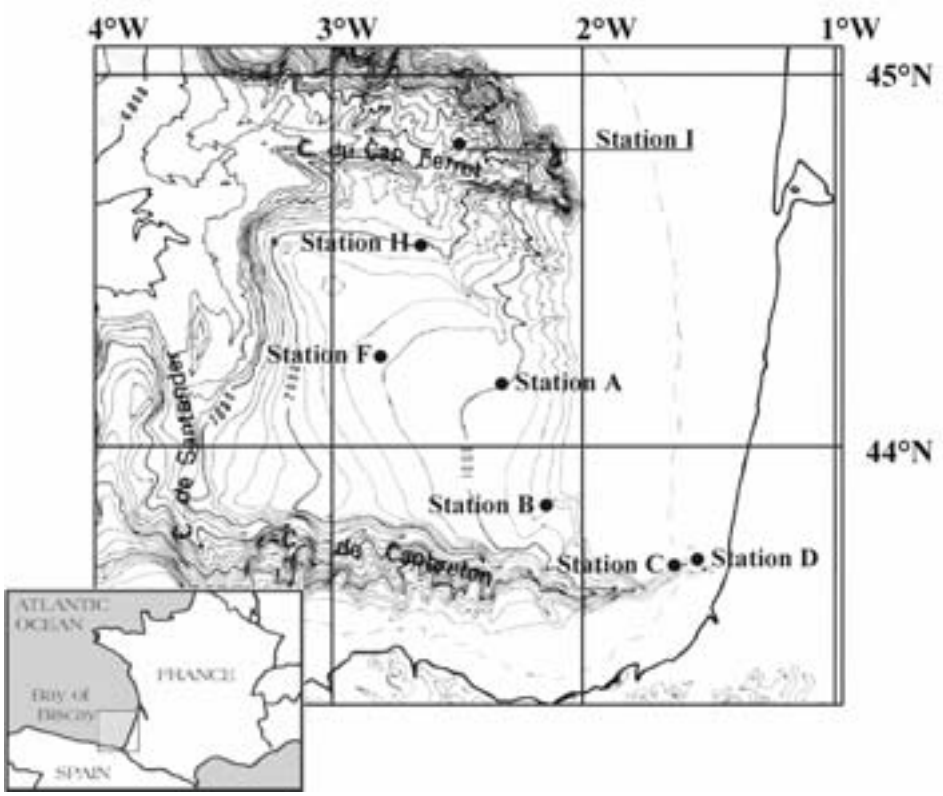


Fig. 2 Study area, bathymetry and geographical position of 7 stations in the Bay of Biscay (NE Atlantic).

Material and Methods

Our faunistic and chemical analyses are based on cores sampled with a Barnett multi-tube corer (Barnett et al., 1984), which allows sampling of first decimetres of the sediment, the overlying bottom waters, and an undisturbed sediment-water interface.

Off Cape Blanc, cores were collected in March 1994. Details about chemical analysis are given by Jorissen et al. (1998). In this paper, we will focus on oxygenation values of bottom and pore waters and the organic carbon content in the surface sediments. For faunistic analysis, one core at each station was sectioned in 0.5 cm slices down to 4 cm and 1 cm slices below, down to 10 cm deep. Only foraminifera belonging to the >150 μm fraction were investigated. We used rose-Bengal coloration in order to discriminate live from dead foraminifera. In the Bay of Biscay, cores were collected between October 1997 and April 2001. Chaillou et al. (2002) present details about sampling and conditioning for chemical analyses. In this paper, we will concentrate on dissolved oxygen concentration and organic carbon content (C-org %).

Station	Depth (m)	Latitude	longitude	Sampling Date	Cruises	Cores	Temperature (°C)	Salinity (PSU)	Bottom water oxygenation (µmol/l)	Zero oxygen boundary (mm)
Off Cape Blanc										
11	1195	21°28'80N	17°57'20W	Mar-94	1	1	ND	ND	164	11
10	1525	21°25'00N	18°04'20W	Mar-94	1	1	ND	ND	191.5	10
9	2005	21°19'70N	18°15'10W	Mar-94	1	1	ND	ND	198	23
8	2530	21°14'80N	18°27'50W	Mar-94	1	1	ND	ND	200	29
7	3010	21°11'40N	18°51'50W	Mar-94	1	1	ND	ND	218	26
Bay of Bicay										
D	140	43°41'93N	1°34'10W	Oct-97	1	1	12.5	35.50	220	8
C	235	43°40'08N	1°38'87W	Oct-97	1	1	12.0	35.60	225	12
B	~550	43°49'98N	2°23'04W	Oct-97 -- Apr-00	10	15*	11.0	35.60	205-221	17-26
A	~1000	44°09'78N	2°20'27W	Oct-97 -- Apr-01	10	12*	9.5	35.75	138-201	8-36
F	1264	44°17'10N	2°44'95W	Jan-98	1	1	8.0	35.50	211	63
H	1993	44°17'10N	2°44'95W	Oct-98	1	1	4.0	35.00	263	60
I	~2800	44°49'46N	2°33'78W	Jan-99 -- Apr-00	3	4*	2.9	34.95	147-253	38-54

Station	Depth (m)	Primary production (gC/m²/year)	Jz (gC/m²/year)	Surficial sediment organic content (%)	Foraminiferal density (/100 cm²) (>150 µm)	Globobulimina spp. density (/100 cm²) (>150 µm)
Off Cape Blanc						
11	1195	185	6.2	2.4	1907	35
10	1525	200	5.5	1.9	543	38
9	2005	230	5.2	2.0	400	37
8	2530	235	4.4	1.1	660	124
7	3010	200	3.2	0.5	528	29
Bay of Bicay						
D	140	150	31.4	2.3	2763	17
C	235	150	19.6	2.0	3008	29
B	~550	150	9.3	1.8	795 +/-96	51 +/-7
A	~1000	150	5.6	1.5	611 +/-87	30 +/-15
F	1264	150	4.6	0.7	169	1
H	1993	150	3.2	0.7	249	7
I	~2800	150	2.5	1.4	416 +/-79	88 +/-8

Table 1 Main characteristics of stations studied off Cape Blanc (NW Africa) and in the Bay of Biscay. In the Bay of Biscay, temperature and salinity data come from Ogawa and Tauzin (1973), Durrieu de Madron et al. (1999) and CTD measurements performed during PROTAGO program (February 2003). For both study areas, Jz represents the exported organic carbon flux calculated according to the formula proposed by Berger et Wefer (1990) and improved by Herguera (1992). The asterisk indicates that duplicate cores are available; 5 replicates at station B and 2 at station A. Globobulimina spp. and total foraminiferal fauna densities are also given (individuals/100 cm²).

The methodology of faunistic analysis is described in Fontanier et al. (2002; 2003a; 2003b; 2003c). For faunal analysis, at least one entire 72 cm^2 core was sliced horizontally for each station, usually every 0.25 cm for the first cm of sediment, every half cm between 1 and 4 cm depth, and every cm between 4 and 10 cm. Foraminifera belonging to the >150 µm fraction were studied along the 10 cm long cores for each core. At station B (550 m depth), A

(1000 m depth) and I (2800 m depth), several cores were collected from 1997 to 2001, in order to investigate the seasonal and interannual variability of live foraminiferal faunas (Table 1) (Fontanier et al., 2003a; 2003b, 2003c). At those three stations, the 63-150 µm size fraction was investigated in the first half cm of each core. For all cores, we followed the sediment storage and preparation methods as described by Fontanier et al. (2002).

We use rose-Bengal coloration to identify living foraminiferal specimens. The reliability of rose Bengal for the recognition of living foraminifera was critically discussed by Bernhard (1988, 2000) and is still debated. Rose Bengal (rose Bengal, C.I. 779; $C_{20}H_2O_5I_4Cl_4Na_2$; solubility in water 36.25%; solubility in alcohol 7.53%) is a biological terminal staining primarily used in bacterial and cytoplasm studies (Conn and Darrow, 1946; Walton, 1952). It is a very practical technique since it is cheap and can be used for large samplings studies where long-term storage of material is necessary (Walton, 1952). For this reason most recent ecological studies based of numerous samplings of deep-sea foraminiferal faunas use this technique to separate live benthic foraminifera from the dead ones. A disadvantage of the method is that foraminifera in necrosis stages may still be stained (although weakly) by rose Bengal (Bernhard, 1988; Hannah and Rogerson, 1997). Douglas et al. (1978) suggested that particularly in anaerobic environments, protoplasm decay may be a slow process. Corliss et Emerson (1990) calculated that the maximum degradation (half-life) times for benthic foraminiferal protoplasm could range from 2 to 80 years for taxa living in deep and anoxic sediments. In view of this evidence, it is clear that recently dead deep infaunal foraminiferal, preserved in anoxic sediments may present an unreliable coloration. A comparison of living foraminifera determined by the ATP method and foraminifera stained by rose Bengal showed that the overestimation of living foraminifera by the rose Bengal method is maximal below the level of detectable oxygen (Bernhard, 1992). This suggests that deep infaunal foraminifera could remain stainable for a considerable time after their death. In the samples from both our study areas (Bay of Biscay and off Cape Blanc), very often a wide range of staining intensities can be observed. We suppose that the most intensively stained individuals were alive at the time of sampling, whereas more dully stained tests correspond to dead individuals, in a state of slow decomposition. Therefore, we use very strict criteria of coloration for the identification of live deep infaunal individuals. These are:

1. The presence of a corpus of protoplasm corpus close to the aperture, with a dark red to flashing pink coloration.
2. The absence of a rose Bengal stained mosaic-like bacterial veil within the test.

3. The absence of larger perforation holes or fractures in the test.
4. The absence of nematodes (or other meiofaunal organisms) within the test

We will compare isotopic measurements performed on individuals belonging to two different taxa (*Globobulimina* spp., *Uvigerina peregrina*) from open-slope stations in the Bay of Biscay (D, B, A, F and H). The stable isotopic composition of live (stained) benthic foraminifera was determined with a Finnigan MAT 251 isotope ratio gas mass spectrometer directly coupled to an automated carbonate preparation device (Kiel I) and calibrated via NBS 19 to the PDB scale. All measurements were performed in the Alfred Wegener Institute (AWI, Germany). The number of *Globobulimina* specimens analyzed in a single measurement varied from 3 to 20. The number of *Uvigerina peregrina* analyzed for a single measurement varied from 10 to 20 individuals. All values are given in δ–notation versus VPDB (Vienna Pee Dee Belemnite) (Table 2). The overall precision of the measurements based on repeated analysis of an internal laboratory standard (Solnhofen limestone) over a one-year-period was better than ±0.08 and ±0.06‰ for oxygen and carbon, respectively.

For stations from the Bay of Biscay, we calculated dissolved inorganic carbon $\delta^{13}C$ in bottom water (= $\delta^{13}C_{DIC}$) using Kroopnick's equation linking apparent oxygen utilization in bottom water (*AOU*) to $\delta^{13}C_{DIC}$ (Kroopnick, 1985) (Table 2):

$$\delta^{13}C_{DIC} = 1.54 - 0.0074 \times AOU$$

AOU is defined as the difference between the saturated dissolved oxygen concentration in the bottom water and the measured dissolved oxygen concentration ($O_2(meas.)$):

$$AOU = O_2(sat) - O_2(meas.)$$

Bottom water $\delta^{18}Ow$ of the different water masses in the Bay of Biscay was calculated using a North Atlantic mixing equation $\delta^{18}O/S$ with a slope of 0.61 and a zero salinity water $\delta^{18}Ow$ of -21‰ (according to Craig and Gordon, 1965). As a first approximation, we suppose that Mediterranean Waters (MW) in our study area are intensively mixed with the surrounding water masses (NACW and NADW). Thus, bottom water $\delta^{18}Ow$ at station A is calculated following the North Atlantic mixing equation. $\delta^{18}O$ of calcite in equilibrium with

bottom water at a given temperature T (°K) (= δ^{18}Oe.c.) can be calculated with the following equation:

$$\delta^{18}Oe.c.(SMOW) = \left(e^{((2.78\times10^3 / T^2)-(2.89/10^3))} \times \left(\delta^{18}Ow + 1000\right)\right) - 1000,$$

where δ^{18}Ow is the oxygen isotopic composition of bottom water on the SMOW scale. This equation is derived from the expression for the calcite-water fractionation factor determined by O'Neil et al. (1969), incorporating a revised estimate of the CO_2-water fractionation factor (1.0412 rather than 1.0407) as discussed by Friedman and O'Neil (1977). The SMOW-PDB conversion is calculated according the equation (2) (Friedman and O'Neil, 1977):

$$\delta^{18}O(PDB) = \left(0.97006 \times \delta^{18}O(SMOW)\right) - 29.94$$

Station (depth)	*Globobulimina* spp.		*Uvigerina peregrina*		Bottom water	
	$\ddot{o}^{13}C$	^{18}O	$\ddot{o}^{13}C$	^{18}O	$\ddot{o}^{13}C_{DIC}$ (PDB)	δ^{18}Oe.c. (PDB)
Station D (140 m)	-2.16 +/- 0.20	1.83 +/- 0.00	-1.78	1.66	1.20	1.47
Station B (550 m)	-1.55 +/- 0.03	2.03 +/- 0.03	-1.28 +/- 0.04	1.67 +/- 0.04	1.08 +/- 0.01	1.90
Station A (1000 m)	-1.16	2.23	-0.87 +/- 0.03	1.91 +/- 0.03	0.89	2.36
Station F (1264 m)	-1.32	2.57	-0.61 +/- 0.03	2.21 +/- 0.03	0.93	2.58
Station H (1993 m)	-2.28	3.43	-0.63	3.03	1.09	3.30
Station B (550 m)						
Oct-97	-1.52	1.98	-1.60 +/- 0.09	1.69 +/- 0.03	1.11	1.90
Jan-98	-1.58	2.13	-1.38	1.74	1.10	1.90
Jun-98	-1.68	1.84	-1.15	1.63	1.07	1.90
Jul-98	-1.78	1.99	-1.20	1.55	1.04	1.90
Oct-98	-1.49	1.94	-1.38 +/- 0.03	1.27 +/- 0.04	1.02	1.90
Dec-98	-1.40	2.06	-1.13 +/- 0.05	1.78 +/- 0.03	1.07	1.90
Jan-99	-1.53	1.92	-1.32	1.59	1.13	1.90
Apr-99	-1.61	2.14	-1.11	1.75	1.04	1.90
Apr-99 bis	-1.37	2.14	-1.24	1.84	1.04	1.90
Jun-99	-1.54	2.11	-1.05	1.83	1.10	1.90
Jun-99 bis	-1.49	2.00	-1.30	1.77	1.10	1.90
Apr-00	-1.49	2.09	-1.24	1.78	1.14	1.90
Apr-00 bis	-1.69	2.07	-1.19	1.78	1.14	1.90

Table 2 Isotopic data for Globobulimina spp. and Uvigerina peregrina in the Bay of Biscay. Standard errors are calculated when several measurements are available at a same station (along the bathymetric transect), or when several measurements are available in the same core at station B. Bottom water isotopic signatures are also given (see methodological part for details).

In this review, we use the dissolved oxygen concentration nomenclature defined by Tyson and Pearson (1991):

- Oxic >2 ml/l
- Dysoxic 0.2-2.0 ml/l
- Suboxic 0-0.2 ml/l
- Anoxic 0 ml/l

The more general physiological or ecological term "hypoxia" indicates a degree of oxygen depletion that would induce a severe stress on marine organisms, without necessarily implying a specific threshold value (Tyson and Pearson, 1991).

Taxonomic observations

The actual taxonomic classification of Foraminifera (class FORAMINIFERA, phylum GRANULORETICULOSA, kingdom PROTOCTISTA) is exclusively based on morphological features of the test (e.g. Loeblich and Tappan, 1988; Sen Gupta, 1999). The identification of foraminiferal species, genera, families and higher categories depends on major criteria such as wall structure, test microstructure, chemical composition and/or on more precise features such as chamber arrangement or aperture. A potential problem of such a classification based on morphology is the potential underestimation of genetic diversity present in a single morphological category, traditionally considered as a species. On the contrary, two or three morphologically distinct forms may also belong to the same biological species due to di/trimorphism resulting from the alternation of sexual and asexual generations. Thanks to recent advances in genetics (e.g. Pawlowski, 2000), a foraminiferal classification based on the genotype is now becoming available, although practical applications are still limited. In this paper, we use a traditional morphology-based approach in order to reconsider the taxonomy of the genus *Globobulimina*. For its suprageneric position we follow Loeblich and Tappan (1988) and the revision by Sen Gupta (1999). Table 3 describes the diagnostic description of *Globobulimina* according to Cushman (1927) and Sen Gupta (1999).

Order BULIMINIDA. Test of low-Mg calcite; wall bilamellar, perforate, multichambered, with trochospiral, triserial, biserial or uniserial chamber arrangement; aperture in many advanced forms with internal toothplate.

Superfamily BULIMINACEA Jones, 1875. Test high trochospiral throughout, or modified to biserial or uniserial in later part. Aperture interiomarginal, loop-shaped, with internal toothplate; wall optically radial.

Family BULIMINADEA Jones, 1875. Test triserial.

Genus *GLOBOBULIMINA* Cushman, 1927. "Test globular to ovate, chambers triserially arranged, strongly overlapping earlier ones; wall calcareous, thin, finely perforate, radial in structure, surface smooth; aperture loop-shaped, with tendency to become terminal, tooth plate doubly folded pillar-like trough joined apertural border at one side, upper part with projecting fanlike tip, lower portion extending into chamber cavity as arched trough, then curving forward, free shank coalescing with free border of aperture, lower part of tooth plate touching projected tip tooth plate of proceeding chamber."

Table 3. The classification of the genus Globobulimina according to Sen Gupta (1999). The original description of the genus Globobulimina was by Cushman (1927); the description presented here is taken from Loeblich and Tappan (1988)

On the basis of a morphological analysis of our material from the shelf edge to lower bathyal environments in the Bay of Biscay and from off Cap Blanc (NW Africa), and a comparison with *Globobulimina* species figured in the recent literature, we propose here a new taxonomic framework for this complex species, in which we recognise two main morphogroups, which we tentatively consider as two different species. It is important to realise that our taxonomic framework is exclusively based on morphology and that genetic analysis will have to confirm our tentative species concept. Furthermore, our taxonomy is mainly based on adult specimens. The distinction between our two species may be very difficult or even impossible for some juvenile specimens. In our division into two morphospecies, we insist on conservative characteristics, which we suppose to be unrelated to the alternation of microspheric and megalospheric generations, such as the form of the apertural structures, and the general aspect of the wall.

- The first morpho-species is characterised by three main features:
  1. A prominent toothplate that sticks out from a rather pointed aperture
  2. The near absence of striation on the wall surface
  3. Megalospheric individuals have a clear drop-like shape.

For reasons of anteriority, the species name *G. pyrula* seems best adapted to this morphogroup and is retained for the species as a whole. Within this species we can distinguish three morphotypes:

A. The megalospheric morphotype, that is inflated, rounded or even a bit acuminated; at the initial end chambers are involute, smooth, and have very slightly marked sutures. This morphotype corresponds rather well to *Globobulimina pyrula* (d'Orbigny, 1846) and will be considered as the "forma typica" (Pl. 1, fig. A, B; Pl. 3, fig. A).

B. The second morphotype is represented by individuals that have the same droplike overall shape, but are provided with spines at the basal end. It has been described in the literature as *Globobulimina pyrula* var. *pseudospinescens* Emiliani 1949. We propose to use the name informally and will indicate it as "forma pseudospinescens" (Pl. 1, fig. C, D; Pl. 3, fig. B).

C. The third morphotype is the microspheric form, with a small first chamber leading to a pointed initial end. No specific name was found in the literature for this morphotype. So, we will indicate it as "forma microsphera" (Pl. 1, Fig. E).

- The second morpho-species is characterised by:
  1. A more "flattened" aperture with a toothplate that does not stick out.
  2. Very marked striations on the wall
  3. Deeper sutures between the chambers
  4. The global shape in megalospheric specimens is more tapered.

Again, for reasons of anteriority, the name of *Globobulimina affinis* (d'Orbigny, 1839) seems best adapted for this morphogroup, although it represents the relatively rare microspheric morphotype. We distinguish two morphotypes, who correspond to the megalospheric and microspheric generations. The first one, the megalospheric morphotype, is very close to Uchio's description of *Globobulimina hoeglundi* (1960) with a test that is more or less elongated in function of the growth stage, with several visible whorls, and with a rounded to slightly pointed initial end without any ornamentation. We will call it "forma hoeglundi" (Pl. 1, fig. F, G, I; Pl. 2, fig. A-G; Pl. 3, fig. C, D, F**)**. The second morphotype is a microsphere. The chambers of the last whorl are very much inflated, with a very pointed initial end; there are four visible whorls. This microspheric morphotype corresponds rather well to the description of *G. affinis,* which for reasons of anteriority is retained for the species group as a whole (Pl. A, Fig. H, E).

An interesting observation is the different reaction to coloration with Rose Bengal of our two morphospecies. Whereas *G. pyrula* shows a bright pink coloration, *G. affinis* systemally stains dark red-orange in our samples. Of course this observation can not be a

relevant criteria to discriminate between the two species and should be used with the utmost reserve. In the recent literature, about nine different species names have been used for these two morpho-species of *Globubulimina*. An overview of the morphological characteristics of these taxa is given in Table 4.

Species	description
Holotypes corresponding to our *G. pyrula*	
pyrula (d'Orbigny), 1846	test oval, smooth, last whorl overlapping 7/8 of the test, comma-shaped raised aperture
auriculata (Bailey), 1851	shell ellipsoidal, smooth, sutures not very disctinct, aperture has an ear shaped appendix
pacifica Cushman, 1927	test subglobular, involute, broad toothplate
turgida (Bailey), 1851	shell ovoidal, several small dentate projections at the basis, tests much inflated, aperture with a raised
pseudospinescens (Emiliani), 1949	distinct from *pyrula* by the presence of a few spines at the basis
Holotypes corresponding to our *G. affinis*	
affinis (d'Orbigny), 1839	test oblong, four visible whorls, aperture with a comma-shape
pupoides (d'Orbigny), 1846	test oblong, smooth, four visible whorls
ovata (d'Orbigny), 1846	test oval, smooth, tapered, four visible whorls
hoeglundi Uchio, 1960	test fusiform, sutures depressed, last chamber extends half way back to the apical end
Holotypes corresponding to other species belonging to the genus *Praeoglobobulimina*	
spinescens (Brady), 1884	close to *G.pyrula* but the broad initial end is covered with spines
spinifera (Cushman), 1927	test broadly fusiform, initial end pointed and bases of the chambers scarcely spinose
barbata (Cushman), 1927	test oval, sutures distinct, early portion covered with spines

Table 4. Overview of different species names of Globobulimina used in the recent literature

Three other species, *G. spinifera*, *G. barbata*, *G. spinescens*, appear to belong to the genus *Praeoglobobulimina,* and do not belong to our two morphospecies. As far as possible, we have integrated recent citations in the synonymy of our two species (Table 5). Unfortunately, only a limited number of recent authors published pictures and/or detailed descriptions of *Globobulimina* species in living faunas (Ingle et al., 1980; Miller and Lohman, 1982; Corliss, 1985; Corliss, 1991; Goldstein and Corliss, 1994; Bernard et al 2001), or in thanatocoenoses (Den Dulk et al., 1998; Quinterno and Gardner, 1987) or presented a more or less complete reference list (Kitazato et al., 2000; Schmiedl et al., 2000, de Rijk et al., 2000;

Fontanier et al., 2002), allowing a critical judgement of the taxonomic status of their material. Incomplete descriptions limit the use of many recent papers for our taxonomic purpose.

Globobulimina pyrula (d'Orbigny) forma typica
1846 *Bulimina pyrula* d'Orbigny, p.185, tab.XI, fig.9-10.
1851 *Bulimina auriculata* Bailey, p.12, pl., figs. 25-27.
1927 *Globobulimina pacifica* Cushman, p.67, pl.14, fig.12.
1958 *Globobulimina? sp.* Parker, partim, p 262, pl.2, fig.28 (not 26, 27).
1982 *Globobulimina sp.,* Miller and Lohman, pl.1, fig.8.
1982 *Globobulimina pacifica* Cushman, Matoba and Yamaguchi, p.1045, pl.2, fig.8.
Globobulimina pyrula (d'Orbigny) forma pseudospinescens
1949 *Bulimina pyrula* d'Orbigny var.*pseudospinescens* Emiliani, p.9, pl.2, figs.24-25.
1958 *Globobulimina pseudospinesens* (Emiliani), Parker, pars , p 262, pl.2, fig.26 (not 27, 28).
1994 *Globobulimina pacifica* Cushman; Goldstein and Corliss, fig.1B.
1998 *Globobulimina spp,* den Dulk et al., pars, plate II, fig 10 (not 11, 12).
Globobulimina pyrula (d'Orbigny) forma microsphera
1951 *Bulimina turgida* Bailey, p.12, pl., figs.28-31.
1958 *Globobulimina pseudospinesens* (Emiliani), Parker, pars, p 262, pl.2, fig.27 (not 26, 28).
1998 *Globobulimina spp,* Den Dulk et al., pars, plate II, fig 11 (not 10, 12).
2001 *Globobulimina sp.,* Bernhard et al., fig.4H.
Globobulimina affinis (d'Orbigny) forma hoeglundi
1846 *Bulimina* d'Orbigny, p.184, tab.XI, fig.13-14.
1846 *Bulimina pupoides* d'Orbigny, p.185, tab.XI, fig.11-12.
1953 *Globobulimina affinis* (d'Orbigny), Phleger et al., pl.6, fig.32.
1958 *Globobulimina affinis* (d'Orbigny), Parker, p 262, pl.2, fig.24-25.
1960 *Globobulimina hoeglundi* Uchio, p.64, pl.6, figs.7-8.
1980 *Globobulimina affinis* (d'Orbigny), Ingle et al., pl.4, figs.10-11.
1982 *Globobulimina sp.,* Miller and Lohman, pl.1., fig.5.
1982 *Globobulimina affinis* (d'Orbigny). Matoba and Yamaguchi, p.1044, pl.2, fig.5-7.
1985 *Globobulimina affinis* (d'Orbigny). Corliss , p.436, pl.1, fig.8.
1991 *Globobulimina affinis* (d'Orbigny). Corliss, pl.II, fig15.
Globobulimina affinis (d'Orbigny) forma typica
1839 *Bulimina affinis* d'Orbigny, p.105, pl., fig.25-26.
1998 *Globobulimina spp.* den Dulk et al., pars, plate II, fig.12 (not 10, 11).

Table 5. Synonymy of the various morphotypes of G. pyrula and G. affinis

Plate 1

A. *Globobulimina pyrula* forma typica, station D (140 m deep)
B. Aperture of *G. pyrula* forma typica, station D (140 m deep)
C. *Globobulimina pyrula* forma pseudospinescens, station C (235 m deep)
D. Aperture of *G. pyrula* forma pseudospinescens, station C (235 m deep)
E. *Globobulimina pyrula* forma microsphera, station C (235 m deep)
F. *Globobulimina affinis* forma hoeglundi, station B (550 m deep)
G. *Globobulimina affinis* forma hoeglundi, station B (550 m depth)
H. *Globobulimina affinis* forma typica, station B (550 m depth)
I. Aperture of *Globobulimina affinis* forma hoeglundi, station B (550 m deep)

Plate 2

A. *Globobulimina affinis* forma hoeglundi, station A (1000 m deep)
B. *G. affinis* forma hoeglundi, station A (1000 m deep)
C. *G. affinis* forma hoeglundi, station I (2750 m deep)
D. *G. affinis* forma hoeglundi, station I (2750 m deep)
E. *G. affinis* forma hoeglundi, station I (2750 m deep)
F. Aperture of *G. affinis* forma hoeglundi, station I (2750 m deep)
G. Poral dispersion of *G. affinis* forma hoeglundi, station I (2750 m deep)

Plate 3

A. *Globobulimina pyrula* forma typica (Cape Blanc, 1195 m)
B. *Globobulimina pyrula* forma pseudospinescens (Cape Blanc, 1195 m)
C. *Globobulimina affinis* forma hoeglundi (Cape Blanc, 1195 m)
D. *G. affinis* forma hoeglundi (Cape Blanc, 1195 m)
E. *Globobulimina affinis* forma typica (Cape Blanc, 1195 m)
F. Pore pattern of *G. affinis* forma hoeglundi, detail of Fig. 3C (Cape Blanc, 1195 m)

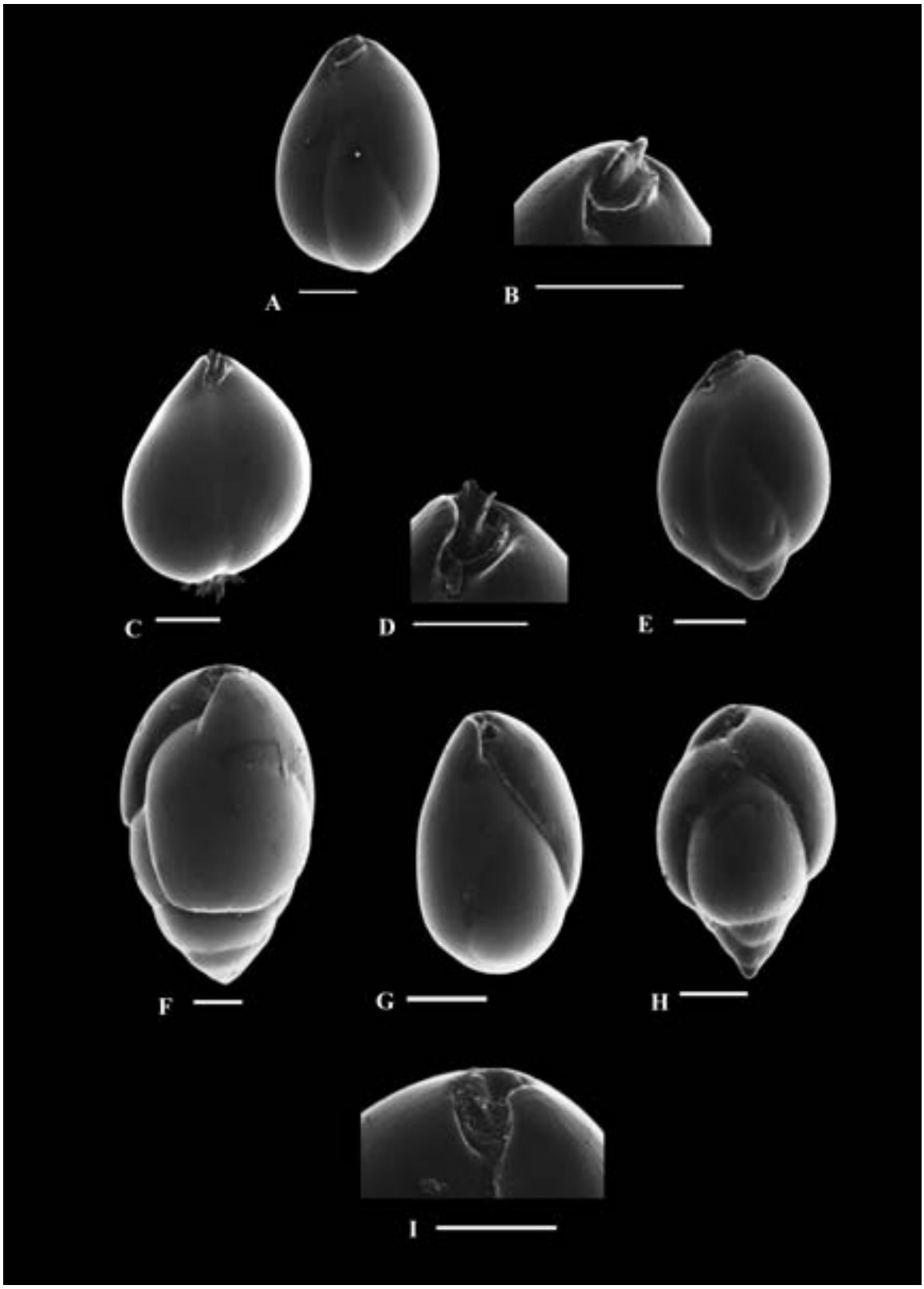


PLATE 1

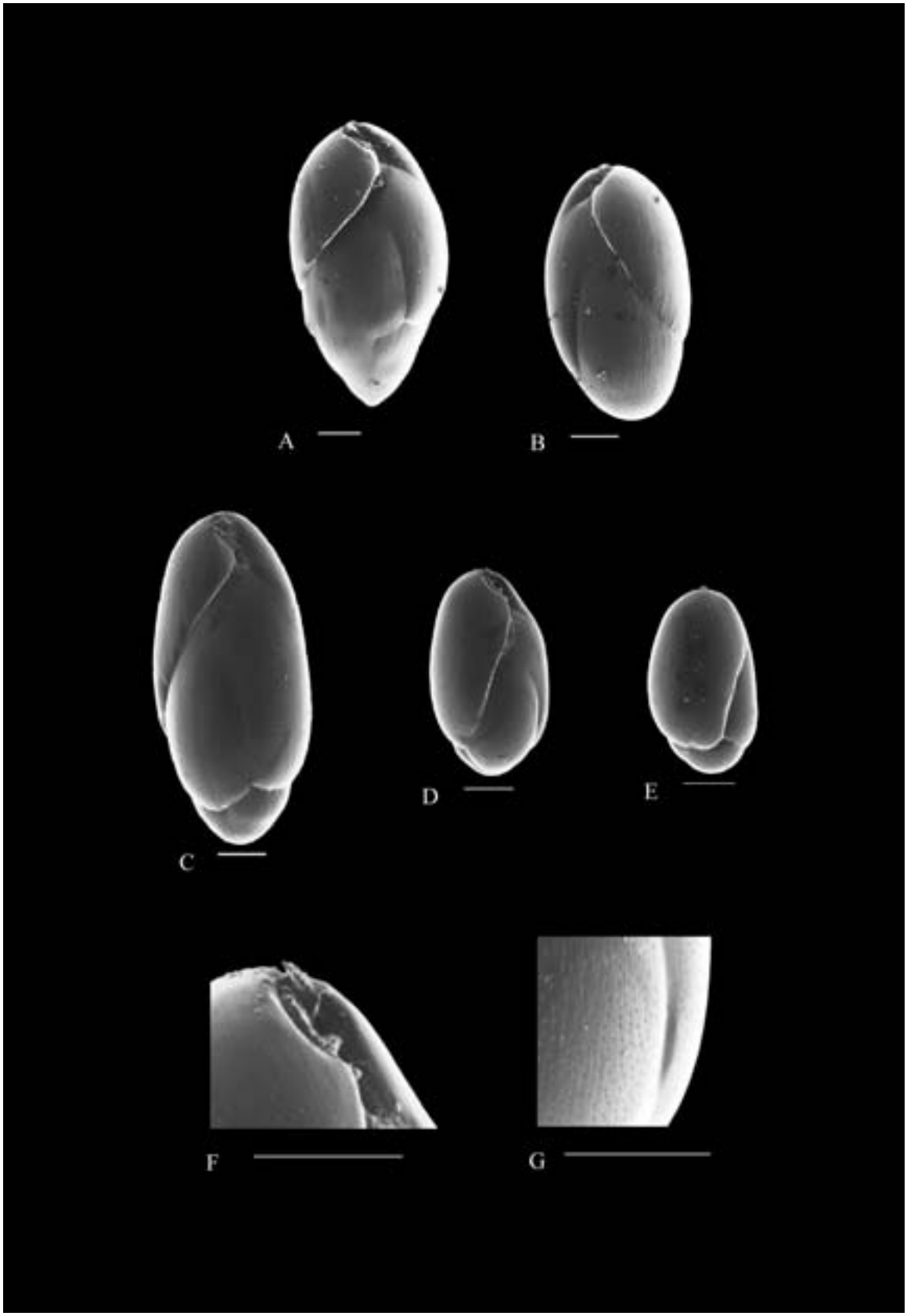


TABLE 2

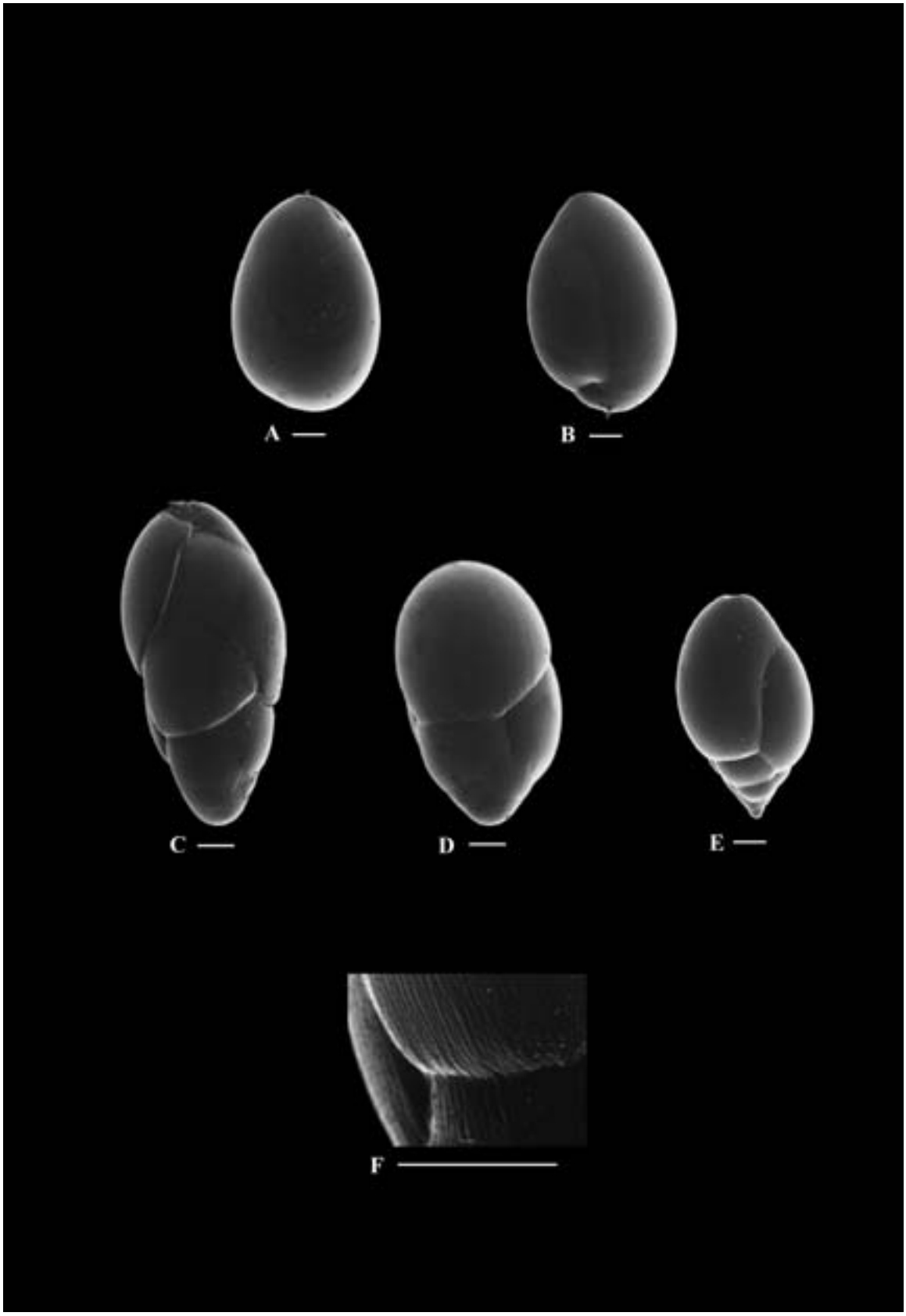


TABLE 3

Geographical distribution

Literature data

Table 5 presents the main recent studies in which the genus *Globobulimina* has been recorded in the live foraminiferal fauna or in the surface sediment thanathocoenoses. This table suggests that *Globobulimina* occurs in a very wide range of marine environments, from inner shelf to abyssal plains (e.g. Corliss, 1985, Rathburn and Corliss, 1994). The genus occurs in sedimentary environments as variable as fjords (e.g. Alve et Bernhard, 1995) or hydrothermal vents (Sen Gupta et Aharon, 1994). It can dominate faunas collected in well-oxygenated environments (e.g. Corliss, 1985, Corliss and Emerson, 1990; Corliss, 1991; Corliss and van Weering, 1993; McCorkle et al., 1997; Jorissen et al., 1998; Schmiedl et al., 2000; Gooday et al., 2001) as well as foraminiferal assemblages sampled in oxygen-depleted environments (e.g. Phleger and Soutar, 1973; Douglas and Heitman, 1979; Douglas and Mackensen, 1989; Bernhard, 1992; Corliss and Silva, 1993; Sen Gupta and Machain Castillo, 1993; Silva et al., 1996; Bernhard and Sen Gupta, 1999; Gooday et al., 2000). It may occur with high relative frequencies in canyon settings (Jorissen et al., 1994, Schmiedl et al., 2000) as well as in open slope environments (e.g. Corliss and Emerson, 1990; Corliss, 1990). Also Sen Gupta and Machain-Castillo (1993), who present a review of benthic foraminifera in oxygen-poor habitats, show the wide depth range of *Globobulimina*. These authors remind that *Globobulimina pacifica,* that they consider typical of eastern North Pacific oxygen-minimum waters, is an eurybathyal taxon, since it is present from neritic to abyssal environments along the North American Pacific margin (Culver and Buzas, 1985; 1986; 1987). When considered together, the large variability of environments represented by the cited studies show the difficulty to define precise ecological preferences and/or limitations for the genus *Globobulimina*.

Table 5 References and corresponding study areas (and characteristics) where the genus Globobulimina and related species are recorded in live foraminiferal faunas or in surficial sediment thanathocoenoses. r-B = rose Bengal staining, ATP = ATP identification, ND = No data (see after).

Reference	Study area	Comments
Licari et al. (2003)	Guinea Basin, tropical east Atlantic	Open slope
Licari et al. (2003)	Angola basin, tropical east Atlantic	Open slope under high primary production, ocean upwelling
Fontanier et al. (2002)	Bay of Biscay, north eastern Atlantic Ocean	Outer shelf and open slope under moderate primary production
Fontanier et al. (2003a)	Bay of Biscay, north eastern Atlantic Ocean	Open slope under moderate primary production
Fontanier et al. (2003b)	Bay of Biscay, north eastern Atlantic Ocean	Canyon
Fontanier et al. (2003c)	Bay of Biscay, north eastern Atlantic Ocean	Open slope under moderate primary production
Kurbjeweit et al. (2002)	Northern Arabian Sea, Indian Ocean	Open slope under high primary production
Kurbjeweit et al. (2002)	Northern Arabian Sea, Indian Ocean	Open slope under high primary production
Jannink et al. (2001)	South eastern Leventine Basin, eastern Mediterranean Sea	Outer shelf
Bernhard et al. (2001)	Monterey Bay, Californian margin, eastern Pacific Ocean	Cold seep
Bernhard et al. (2001)	Monterey Bay, Californian margin, eastern Pacific Ocean	Cold seep
Gooday et al. (2001)	North Carolina slope, northwest Atlantic Ocean	Open slope
Gooday et al. (2001)	North Carolina slope, northwest Atlantic Ocean	Open slope
Rathburn et al. (2000)	Northern californian margin, eastern Pacific Ocean	Cold methane seep
Rathburn et al. (2000)	Northern californian margin, eastern Pacific Ocean	Cold methane seep
Rathburn et al. (2000)	Northern californian margin, eastern Pacific Ocean	Cold methane seep
Rathburn et al. (2000)	Northern californian margin, eastern Pacific Ocean	Cold methane seep
Schmiedl et al. (2000)	Gulf of Lions, western Mediterranean Sea	Canyon
Schmiedl et al. (2000)	Gulf of Lions, western Mediterranean Sea	Open slope
Kitazato et al. (2000)	Sagami Bay, off Japon, western Pacific Ocean	Open slope under high primary production
Gooday et al. (2000)	Oman margin, Northern Arabian Sea, Indian Ocean	Open slope under high primary production
De Stigter et al. (1998)	Adriatic Sea, western mediterranean sea	Outer shelf and open slope
De Stigter et al. (1998)	Adriatic Sea, western mediterranean sea	Open slope
De Stigter et al. (1998)	Adriatic Sea, western mediterranean sea	Open slope
Jannink et al. (1998)	Pakistan continental margin, Northern Arabian Sea, Indian Ocean	Open slope under high primary production, strong coastal upwelling
Jorissen et al. (1998)	North western Africa, off Cape Blanc, eastern Atlantic Ocean	Open slope under high primary production , strong coastal upwelling
Jorissen et al. (1998)	North western Africa, off Cape Blanc, eastern Atlantic Ocean	Open slope under high primary production, strong coastal upwelling
Ohga and Kitazato (1997)	Sagami Bay, off Japon, western Pacific Ocean	Open slope under high primary production
McCorkle et al. (1997)	North Carolina slope, northwest Atlantic Ocean	Open slope
McCorkle et al. (1997)	North Carolina slope, northwest Atlantic Ocean	Open slope
McCorkle et al. (1997)	North Carolina slope, northwest Atlantic Ocean	Open slope
McCorkle et al. (1997)	North Carolina slope, northwest Atlantic Ocean	Open slope
McCorkle et al. (1997)	North Carolina slope, northwest Atlantic Ocean	Open slope
McCorkle et al. (1997)	California continental slope, eastern Pacific Ocean	Open slope
McCorkle et al. (1997)	California continental slope, eastern Pacific Ocean	Open slope
McCorkle et al. (1997)	California continental slope, eastern Pacific Ocean	Open slope
Bernhard et al. (1997)	Santa Barbara basin, Californian Borderland, eastern Pacific Ocean	Nearshore basin with a strong OMZ
Jorissen et al. (1995)	Adriatic Sea, western mediterranean sea	Outer shelf and open slope
Alve et Bernhard (1995)	Inner Oslofjord, Norway	Fjord
Kitazato (1994)	Sagami Bay, off Japon, western Pacific Ocean	Open slope under high primary production
Rathburn and Corliss (1994)	Sulu Sea, western Pacific Ocean	Silled marginal basin
Jorissen et al. (1994)	New Jersey submarine Canyon, north western Atlantic Ocean	Canyon
Sen Gupta et Aharon (1994)	The Green Canyon, Gulf of Mexico, western Atlantic Ocean	Hydrocarbon vents
Goldstein and Corliss (1994)	San Pedro Basin, Californian Borderland, eastern Pacific Ocean	Inner borderland basin
Corliss and Silva (1993); Silva et al. (1996)	San Pedro Basin, Californian Borderland, eastern Pacific Ocean	Inner borderland basin
Corliss and Silva (1993); Silva et al. (1996)	San Pedro Basin, Californian Borderland, eastern Pacific Ocean	Inner borderland basin
Corliss and Silva (1993); Silva et al. (1996)	San Pedro Basin, Californian Borderland, eastern Pacific Ocean	Inner borderland basin
Hunt and Corliss (1993)	Canadian Arctic Archipelago	No comment
Corliss and van Weering (1993)	Skagerrak basin, eastern part of the North Sea	Basin
Corliss and van Weering (1993)	Skagerrak basin, eastern part of the North Sea	Basin
Corliss and van Weering (1993)	Skagerrak basin, eastern part of the North Sea	Basin
Corliss and van Weering (1993)	Skagerrak basin, eastern part of the North Sea	Basin
Bernhard (1992)	Central California continetal slope an rise, eastern Pacific Ocean	Open slope
Bernhard (1992)	Central California continetal slope an rise, eastern Pacific Ocean	Open slope and rise
Corliss and Emerson (1990) and Corliss (1991)	Gulf of Maine, western north Atlantic Ocean	Open slope
Corliss and Emerson (1990) and Corliss (1991)	Nova Scotia Margin, western north Atlantic Ocean	Open slope
Mackensen and Douglas (1989)	Santa Monica Basin, Californian Borderland, eastern Pacific ocean	Inner borderland basin
Mackensen and Douglas(1989)	Santa Catalina Basin, Californian Borderland, eastern Pacific ocean	Outer borderland basin
Corliss (1985)	Eastern United States continental rise, western north Atlantic Ocean	Continetal rise
Lutze and Coulbourn (1984)	Continental margin of North western Africa, Atlantic Ocean	High productivity area, open slope
Lutze and Coulbourn (1984)	Continental margin of North western Africa, Atlantic Ocean	High productivity area, open slope
Lutze and Coulbourn (1984)	Continental margin of North western Africa, Atlantic Ocean	High productivity area, open slope
Lutze and Coulbourn (1984)	Continental margin of North western Africa, Atlantic Ocean	High productivity area, open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Shelf edge and open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Shelf edge and open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Shelf edge and open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Ingle (1980)	Southern Peru-Chile Trench, southeastern Pacific Ocean	Open slope
Douglas and Heitman (1979)	Offshore basins, Californian Borderland, Pacific ocean	Outer borderland basins
Douglas and Heitman (1979)	Offshore basins, Californian Borderland, Pacific ocean	Outer borderland basin floor
Douglas and Heitman (1979)	Nearshore basins, California borderland, Pacific ocean	Inner borderland basins
Douglas and Heitman (1979)	Nearshore basins, California borderland, Pacific ocean	Inner borderland basin floor
Phleger and Soutar (1973)	Santa Barbara basin, Californian Borderland, Pacific Ocean	Basin
Morigi et al. (2002)	North western Africa, off Cape Blanc, eastern Atlantic Ocean	Open slope under high primary production, strong coastal upwelling
Morigi et al. (2002)	North western Africa, off Cape Blanc, eastern Atlantic Ocean	Open slope under high primary production, strong coastal upwelling
De Rijk et al. (2000)	Alboran Sea, transect off North Algeria and Southern Spain, western Mediterranean Sea	No comment
De Rijk et al. (1999); De Rijk et al. (2000)	Off North Algeria, western Mediterranean Sea	No comment
De Rijk et al. (1999); De Rijk et al. (2000)	Alboran Sea, off Southern Spain, western Mediterranean Sea	No comment
Quintero and Gardner (1987)	Northern Californian continental margin adjacent to Russian River, eastern Pacific Ocean	Outer shelf and open slope, seasonal upwelling
Quintero and Gardner (1987)	Northern californian continental margin adjacent to Russian River, eastern Pacific Ocean	Open slope, seasonal upwelling
Mullins et al. (1985)	Off central californian coasts, Pacific Ocean	Open slope under high primary production, strong coastal upwelling
Miller and Lohmann (1982)	Southeast of Cape Cod, western north Atlantic	Open slope
Miller and Lohmann (1982)	Southeast of Cape Cod, western north Atlantic	Rise
Pujos-Lamy (1973)	Bay of Biscay, north eastern Atlantic Ocean	Open slope under moderate productivity
Pujos-Lamy (1973)	Bay of Biscay, north eastern Atlantic Ocean	Open slope under moderate productivity

Table 5

Reference	Species	Method	Depth range
Licari et al. (2003)	*Globobulimina pacifica*	r-B	1341 m
Licari et al. (2003)	*Globobulimina pacifica*	r-B	1301 m
Fontanier et al. (2002)	*Globobulimina* spp.	r-B	150-1960 m
Fontanier et al. (2003a)	*Globobulimina* spp.	r-B	550 m
Fontanier et al. (2003b)	*Globobulimina* spp.	r-B	2750 m
Fontanier et al. (2003c)	*Globobulimina* spp.	r-B	1000 m
Kurbeveet et al. (2002)	*Globobulimina affinis*, *Globobulimina pacifica*, *Globobulimina turgida*	r-B	1917-4073 m
Kurbeveet et al. (2002)	*Globobulimina affinis*	r-B	2243 m
Jannink et al. (2001)	*Globobulimina pacifica*	r-B	120 m
Bernhard et al. (2001)	*Globobulimina* spp.	r-B, ATP	906 m
Bernhard et al. (2001)	*Praeglobobulimina spinescens*	r-B, ATP	1003 m
Gooday et al. (2001)	*Globobulimina auriculata*	r-B	850 m
Gooday et al. (2001)	*Globobulimina pyrula*	r-B	850 m
Rathburn et al. (2000)	*Globobulimina pacifica*	r-B	500 m
Rathburn et al. (2000)	*Globobulimina spinifera*	r-B	500 m
Rathburn et al. (2000)	*Globobulimina pacifica*	r-B	500 m
Rathburn et al. (2000)	*Globobulimina spinifera*	r-B	500 m
Schmiedl et al. (2000)	*Globobulimina affinis*/*Globobulimina pseudopsinescens*	r-B	920 m
Schmiedl et al. (2000)	*Globobulimina* spp.	r-B	800 m
Kitazato et al. (2000)	*Globobulimina affinis*	r-B	1430 m
Gooday et al. (2000)	*Globobulimina* sp.	r-B	412 m
De Stigter et al. (1998)	*Globobulimina pyrula*	r-B	146 m
De Stigter et al. (1998)	*Globobulimina pyrula*	r-B	398 m
De Stigter et al. (1998)	*Globobulimina pyrula*	r-B	487 m
Jannink et al. (1998)	*G. affinis*, *G. pacifica*	r-B	556-1226 m
Jorissen et al. (1998)	*Globobulimina pyrula*	r-B	1200-3010 m
Jorissen et al. (1998)	*Globobulimina pyrula*	r-B	2530 m
Ohga and Kitazato (1997)	*Globobulimina* spp.	r-B	1450 m
McCorkle et al. (1997)	*Globobulimina affinis*	r-B	337 m
McCorkle et al. (1997)	*Globobulimina affinis*	r-B	577 m
McCorkle et al. (1997)	*Globobulimina affinis*	r-B	720 m
McCorkle et al. (1997)	*Globobulimina affinis*	r-B	825 m
McCorkle et al. (1997)	*Globobulimina affinis*	r-B	1470 m
McCorkle et al. (1997)	*Globobulimina pacifica*	r-B	786 m
McCorkle et al. (1997)	*Globobulimina pacifica*	r-B	998 m
McCorkle et al. (1997)	*Globobulimina pacifica*	r-B	3705 m
Bernhard et al. (1997)	*Globobulimina pacifica*	r-B	431 and 522 m
Jorissen et al. (1995)	*Globobulimina pacifica*	r-B	146-578 m
Alve et Bernhard (1995)	*Globobulimina auriculata*	ATP	71 m
Kitazato (1994)	*Globobulimina affinis*	r-B	1445 m
Rathburn and Corliss (1994)	*Globobulimina* spp.	r-B	4515 m
Jorissen et al. (1994)	*Globobulimina affinis*	r-B	1567-2386 m
Sen Gupta et Aharon (1994)	*Globobulimina* sp.	r-B	584 m
Goldstein and Corliss (1994)	*Globobulimina pacifica*	determined as live under microscop	710 m
Corliss and Silva (1993), Silva et al. (1996)	*Globobulimina pacifica*	r-B	720 m
Corliss and Silva (1993), Silva et al. (1996)	*Globobulimina hoeglundi*	r-B	720 m
Corliss and Silva (1993), Silva et al. (1996)	*Globobulimina barbata*	r-B	720 m
Hunt and Corliss (1993)	?*Globobulimina* sp.	r-B	330 m
Corliss and van Weering (1993)	*Globulimina auriculata* (= *G. turgida*)	r-B	74 m
Corliss and van Weering (1993)	*Globulimina auriculata* (= *G. turgida*)	r-B	210 m
Corliss and van Weering (1993)	*Globulimina auriculata* (= *G. turgida*)	r-B	530 m
Corliss and van Weering (1993)	*Globulimina auriculata* (= *G. turgida*)	r-B	621 m
Bernhard (1992)	*Globobulimina pacifica*	ATP	786 and 998 m
Bernhard (1992)	*Globobulimina pacifica*	ATP	1864, 3344 and 3728 m
Corliss and Emerson (1990) and Corliss (1991)	*Globobulimina affinis*	r-B	202 m
Corliss and Emerson (1990) and Corliss (1991)	*Globobulimina affinis*	r-B	1575 and 2225 m
Mackensen and Douglas (1989)	*Globobulimina pacifica*, *Globobulimina hoeglundi*	r-B	529 m
Mackensen and Douglas(1989)	*Globobulimina pacifica*, *Globobulimina hoeglundi*, *Globobulimina spinifera*	r-B	895 m
Corliss (1985)	*Globobulimina affinis*	r-B	3000 m
Lutze and Coulbourn (1984)	*Globobulimina hoeglundi*	r-B	1751 m
Lutze and Coulbourn (1984)	*Globobulimina turgida*	r-B	731 m
Lutze and Coulbourn (1984)	*Globobulimina* sp.324	r-B	167 m
Lutze and Coulbourn (1984)	*Globobulimina* sp.	r-B	157 m
Ingle (1980)	*Globobulimina ovula*	r-B	135-1948 m
Ingle (1980)	*Globobulimina ovata*	r-B	142-1242 m
Ingle (1980)	*Globobulimina pacifica*	r-B	142-962 m
Ingle (1980)	*Globobulimina auriculata*	r-B	200 m
Ingle (1980)	*Globobulimina affinis*	r-B	274-1948 m
Ingle (1980)	*Bulimina pyrula spinescens*	r-B	800-2568 m
Ingle (1980)	*Globobulimina affinis*	r-B	800-1948 m
Ingle (1980)	*Globobulimina pyrula*	r-B	800-962 m
Ingle (1980)	*Globobulimina pupoides*	r-B	962-1948 m
Ingle (1980)	*Bulimina barbata*	r-B	1800-2634 m
Douglas and Heitman (1979)	*Globobulimina spinifera*	r-B	300-1900 m
Douglas and Heitman (1979)	*Globobulimina hoeglundi*	r-B	1200-1900 m
Douglas and Heitman (1979)	*Globobulimina pacifica*	r-B	85-450 m
Douglas and Heitman (1979)	*Globobulimina affinis*, *Globobulimina hoeglundi*	r-B	550-950 m
Phleger and Soutar (1973)	*G. hoeglundi*	r-B	575 m
Morigi et al. (2002)	*Globobulimina affinis*	Thanatocoenosis	506-1000 m
Morigi et al. (2002)	*Globobulimina affinis*	Thanatocoenosis	1000-3010 m
De Rijk et al. (2000)	*Globobulimina* spp.	Thanatocoenosis	210-2594 m
De Rijk et al. (1999); De Rijk et al. (2000)	*Globobulimina* spp.	Thanatocoenosis	936 m
De Rijk et al. (1999); De Rijk et al. (2000)	*Globobulimina* spp.	Thanatocoenosis	2594 m
Quinterno and Gardner (1987)	*Globobulimina* spp.	Thanatocoenosis	90-450 m
Quinterno and Gardner (1987)	*Globobulimina* spp.	Thanatocoenosis	500-1300 m
Mullins et al. (1985)	*Globobulimina*/*Praeglobobulimina*	Thanatocoenosis	~1000 m
Miller and Lohmann (1982)	*Globobulimina* spp. (including *Globobulimina affinis*)	Thanatocoenosis	352-505 m
Miller and Lohmann (1982)	*Globobulimina* spp.	Thanatocoenosis	2500-3580 m
Pujos-Lamy (1973)	*Praeglobobulimina turgida*	Thanatocoenosis	250-500 m
Pujos-Lamy (1973)	*Globobulimina ovata*, *Globobulimina* sp.2	Thanatocoenosis	1900-2500 m

Table 5

Reference	Percentage*	Bottom water oxygenation	C-org content
Licari et al. (2003)	~2%	208.5 µmol/l	ND
Licari et al. (2003)	~2%	189.5	ND
Fontanier et al. (2002)	Between 0.6 and 26.5%	196-263 µmol/l	Between 0.7 and 2.3%
Fontanier et al. (2003a)	Between 2.3 and 15.3%	208-221 µmol/l	~1.8%
Fontanier et al. (2003b)	Between 17.9 and 24.0%	240-123 µmol/l	~1.4%
Fontanier et al. (2003c)	Between 0.2 and 26.5%	138-201 µmol/l	~1.5%
Kurbeweit et al. (2002)	-	>1 ml/l (below the Oxygen Minimum Zone)	>0.6%
Kurbeweit et al. (2002)	~8%	>1 ml/l (below the Oxygen Minimum Zone)	>1%
Jannink et al. (2001)	< 5%	From oxygen depleted to well oxygenated bottom waters	ND
Bernhard et al. (2001)	~8%	ND	ND
Bernhard et al. (2001)	<1%	ND	ND
Gooday et al. (2001)	Between 64.9 and 77.7 %	4.5 ml/l	1.70%
Gooday et al. (2001)	1.36%	4.5 ml/l	1.70%
Rathburn et al. (2000)	3.60%	0.6-1 ml/l	ND
Rathburn et al. (2000)	< 1%	0.6-1 ml/l	ND
Rathburn et al. (2000)	1.70%	0.6-1 ml/l	ND
Rathburn et al. (2000)	< 1%	0.6-1 ml/l	ND
Schmiedl et al. (2000)	~10%	4.2 ml/l	0.90%
Schmiedl et al. (2000)	< 1%	4.2 ml/l	0.60%
Kitazato et al. (2000)	Between 1.5 and 68.5%	~1.1 ml/l	Between 2.8 and 3.5%
Gooday et al. (2000)	Between 20.4 and 22.3%	0.13 ml/l (in the Oxygen Minimum Zone)	4.90%
De Stigter et al. (1998)	< 5%	ND	ND
De Stigter et al. (1998)	< 5%	ND	ND
De Stigter et al. (1998)	< 5%	ND	ND
Jannink et al. (1998)	< 10%	< 40 µmol/l (from the core and to the lower edge of the Oxygen Minimum Zone)	ND
Jorissen et al. (1998)	Between 2 and 20%	3.67-4.68 ml/l	Between 0.5 and 2.4%
Jorissen et al. (1998)	20%	4.46 ml/	1.10%
Ohga and Kitazato (1997)	Present	1 ml/l (in the deeper part of the Oxygen Minimum Zone)	???
McCorkle et al. (1997)	Dominant	186 µmol/l	ND
McCorkle et al. (1997)	Dominant	239 µmol/l	ND
McCorkle et al. (1997)	Dominant	259 µmol/l	ND
McCorkle et al. (1997)	Dominant	260 µmol/l	ND
McCorkle et al. (1997)	Rare	276 µmol/l	ND
McCorkle et al. (1997)	Dominant	12 µmol/l (in the Oxygen Minimum Zone)	ND
McCorkle et al. (1997)	Present	20 µmol/l (in the Oxygen Minimum Zone)	ND
McCorkle et al. (1997)	Dominant	129 µmol/l	ND
Bernhard et al. (1997)	< 1%	15.4 and 3.5 µmol/l (at the upper edge of the Oxygen Minimum Zone)	Between 3.5 and 8.0%**
Jorissen et al. (1995)	Present	Putatively well oxygenated bottom waters	ND
Alve et Bernhard (1995)	~5%	ND	ND
Kitazato (1994)	~8%	~1.3 ml/l	ND
Rathburn and Corliss (1994)	~5%	53.6 µmol/l	0.74%
Jorissen et al. (1994)	Between 4 and 20 %	Putatively well-oxygenated bottom waters	ND
Sen Gupta et Aharon (1994)	< 1%	3.3-4.5 ml/l	ND
Goldstein and Corliss (1994)	ND	<15 µmol/l	~3%
Corliss and Silva (1993); Silva et al. (1996)	24-42%	2.5-16 µmol/l	~3%
Corliss and Silva (1993); Silva et al. (1996)	< 5%	2.5-16 µmol/l	~3%
Corliss and Silva (1993); Silva et al. (1996)	< 1%	2.5-16 µmol/l	~3%
Hunt and Corliss (1993)	Rare	ND	Between 2 and 3%
Corliss and van Weering (1993)	Rare	130-175 µmol/l	1.50%
Corliss and van Weering (1993)	Dominant (~20%)	190-225 µmol/l	Between 1 and 1.5%
Corliss and van Weering (1993)	Present	50-215 µmol/l	2%
Corliss and van Weering (1993)	Rare	200-250 µmol/l	2.50%
Bernhard (1992)	Dominant	12.6-21.3 µmol/l (in the Oxygen Minimum Zone)	Between ~3 and ~4.5%
Bernhard (1992)	Present	72.4-129.2 µmol/l (below the Oxygen Minimum Zone)	Between ~1.5% and ~3%
Corliss and Emerson (1990) and Corliss (1991)	Between 53 and 63 %	Putatively well-oxygenated bottom waters	4.20%
Corliss and Emerson (1990) and Corliss (1991)	Between 21 and 45 %	Putatively well-oxygenated bottom waters	Between 0.5 and 2.0%
Mackensen and Douglas (1989)	~15 %	<0.2 ml/l	Between 2.0 and 3.0%
Mackensen and Douglas (1989)	~51%	0.2-0.5 ml/l	~5%
Corliss (1985)	~23%	Putatively well-oxygenated bottom waters	ND
Lutze and Coulbourn (1984)	Present	~5 ml/l	ND
Lutze and Coulbourn (1984)	Present	2-3 ml/l	ND
Lutze and Coulbourn (1984)	Present	2-3 ml/l	ND
Lutze and Coulbourn (1984)	Present	2-3 ml/l	ND
Ingle (1980)	<3%	~1-5 ml/l (in and below the Oxygen Minimum Zone)	Between 0.54 and 2.67%
Ingle (1980)	<2%	~1-5 ml/l (in and below the Oxygen Minimum Zone)	Between 0.54 and 2.30%
Ingle (1980)	<2%	~1-5 ml/l (in and below the Oxygen Minimum Zone)	Between 0.54 and 2.30%
Ingle (1980)	<1%	~1 ml/l (in the Oxygen Minimum Zone)	0.54%
Ingle (1980)	<2%	~1-5 ml/l (in and below the Oxygen Minimum Zone)	Between 0.64 and 2.67%
Ingle (1980)	<3%	~3-4 ml/l	Between 1.13 and 2.67%
Ingle (1980)	<2%	~3-4 ml/l	Between 1.13 and 2.68%
Ingle (1980)	<0.5%	~3 ml/l	Between 1.16 and 1.37%
Ingle (1980)	<1%	~3-4 ml/l	Between 1.13 and 2.67%
Ingle (1980)	<5%	~3-4 ml/l	Between 1.13 and 2.59%
Douglas and Heitman (1979)	Present	Between 0.1 and 1.1 ml/l	Between 1 and 6%
Douglas and Heitman (1979)	Present	Between 0.25 and 0.5 ml/l	Between 5 and 8%
Douglas and Heitman (1979)	Dominant	Between 0.5 and 3 ml/l (in the Oxygen Minimum Zone)	Between 1 and 3%
Douglas and Heitman (1979)	Present	Between 0.08 and 0.9 ml/l	Between 6 and 9%
Prieger and Soutar (1973)	Dominant	~0. 1ml/l	ND
Morigi et al. (2002)	5-9%	<3 ml/l	ND
Morigi et al. (2002)	~5%	>4.6 ml/l	ND
De Rijk et al. (2000)	Present or dominant	ND	ND
De Rijk et al. (1999); De Rijk et al. (2000)	~8%	ND	~1.0%
De Rijk et al. (1999); De Rijk et al. (2000)	~11%	ND	~1.4%
Quinterno and Gardner (1987)	~10%	Putatively well-oxygenated bottom waters	ND
Quinterno and Gardner (1987)	~15%	<0.5 ml/l (at the lower edge of the Oxygen Minimum Zone)	ND
Mullins et al. (1985)	~40%	<0.5 ml/l (at the lower edge of the Oxygen Minimum Zone)	ND
Miller and Lohmann (1982)	Dominant	3 ml/l (in the Oxygen Minimum Zone)	Between 0.2 and 0.6%
Miller and Lohmann (1982)	Present	6 ml/l	~0.5%
Pujos-Lamy (1973)	<10%	Putatively well-oxygenated bottom waters	ND
Pujos-Lamy (1973)	<10%	Putatively well-oxygenated bottom waters	ND

Table 5

Our data sets

Off Cape Blanc, *Globobulimina* is present in all sampled stations, from 1195 to 3010 m depth. Both *Globobulimina affinis* and *Globobulimina pyrula* are present. The joint percentages of these two species, which were not separated by Jorissen et al. (1995) varies from 1.9% at station 11 (1195 m deep) to 18.7% at station 8 (2530 m deep), where bottom water oxygenation is 200 µmol/l. In terms of density, standing stocks of *Globobulimina* range from 20 to 84 individuals per core (from 29 to 124 individuals/100 cm²) (Table 1; Fig 3a). The highest density is found at station 8 (2530 m deep) whereas the lowest is recorded at station 7 (3010 m deep). At the shallower station (station 11) where the organic carbon content in the sediment (2.43%) and the estimated exported organic carbon flux (6.15 gC/m²/year) are maximal, the standing stock of *Globobulimina* is only 35 individuals/100 cm² (Table 1).

In the Bay of Biscay, *Globobulimina* is present from the outer shelf (Station D, 150 m) to lower bathyal environment (station I, 2800 m depth). *Globobulimina affinis* is dominant in the lower and upper slope stations (from 550 m to 2800 m depth) whereas *Globobulimina pyrula* preferentially occurs on the outer shelf (140 m depth) and on the upper slope (between 235 and 550 m depth). Mean percentages of *Globobulimina* range from 1.0 to 6.8% in the total live foraminiferal faunas (>150 µm) at upper slope stations (C, B and A). *Globobulimina* presents its highest percentage at the 3000 m deep canyon station I (~21.8%) that is characterised by important focussing of refractory organic matter (Fontanier et al., 2003c). Surprisingly, this taxon is rare at the shallowest station D (150m) where the exported carbon matter flux and organic carbon content in surficial sediments are maximal. In open slope mesobathyal environments (stations H and F), *Globobulimina* is present in very low percentages. In terms of density, the standing stocks at the upper slope stations (C, B and A) range from 21 to 37 individuals per core (29-51 individuals/100 cm²). *Globobulimina* presents its highest standing stocks at the canyon station I (63 individuals per core; 88 individuals/100cm²) (Table 1; Fig 3b).

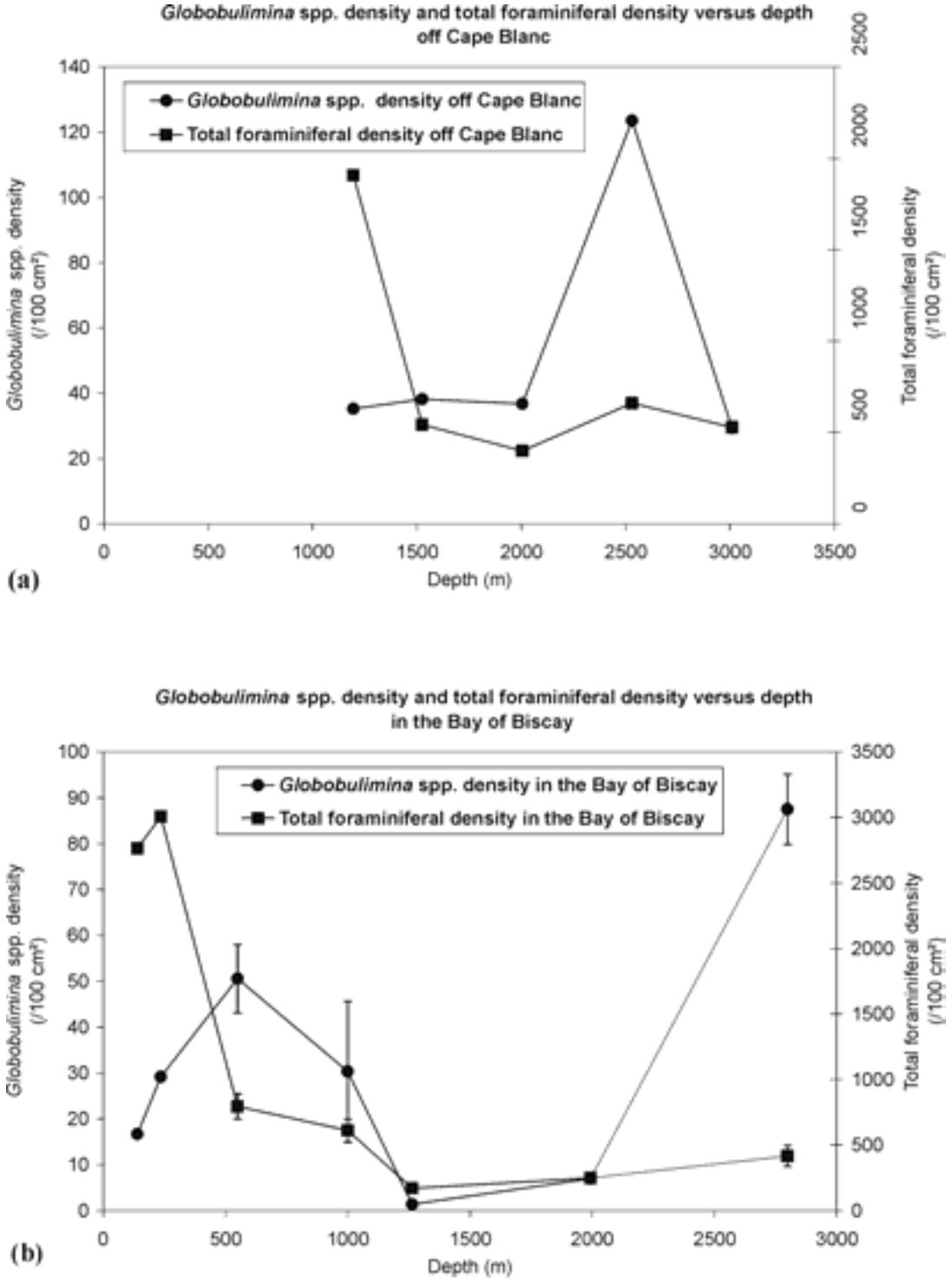


Fig. 3; 3a Density of live (stained) Globobulimina spp. (>150 µm) and total foraminiferal density along the bathymetric transect off Cape Blanc. 3b Density of live (stained) Globobulimina spp. (>150 µm) and total foraminiferal density along the bathymetric transect in the Bay of Biscay. Density is expressed as the number of individuals per 100 cm². Vertical bars represent standard errors calculated when duplicate cores are available.

In both our study areas, absolute and relative frequencies of *Globobulimina* spp. are positively correlated with each other but are totally uncorrelated to the density of the total foraminiferal fauna. Since the density of the total foraminiferal fauna is well correlated to the annual exported organic carbon flux and the organic carbon content of surficial sediment (Fig. 4), there is no significant relation between percentage (or density) of *Globobulimina* spp. and the exported organic matter flux from the surface waters, the organic carbon content of the surface sediment. There is no correlation either with the bottom water oxygenation (Fig. 5a-c).

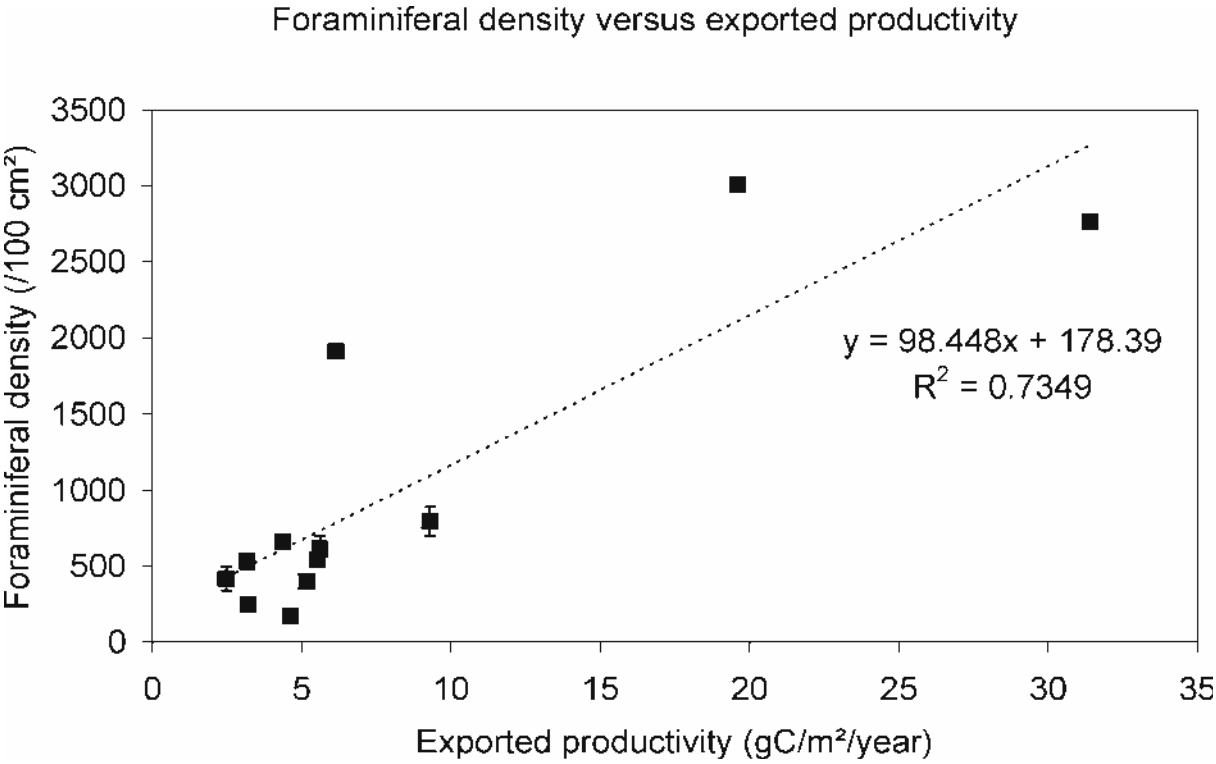
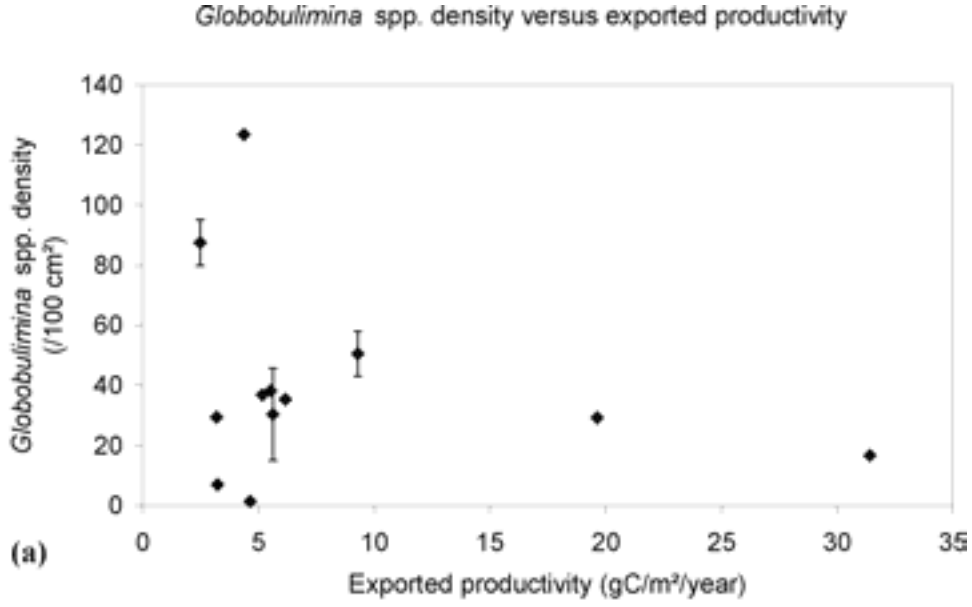
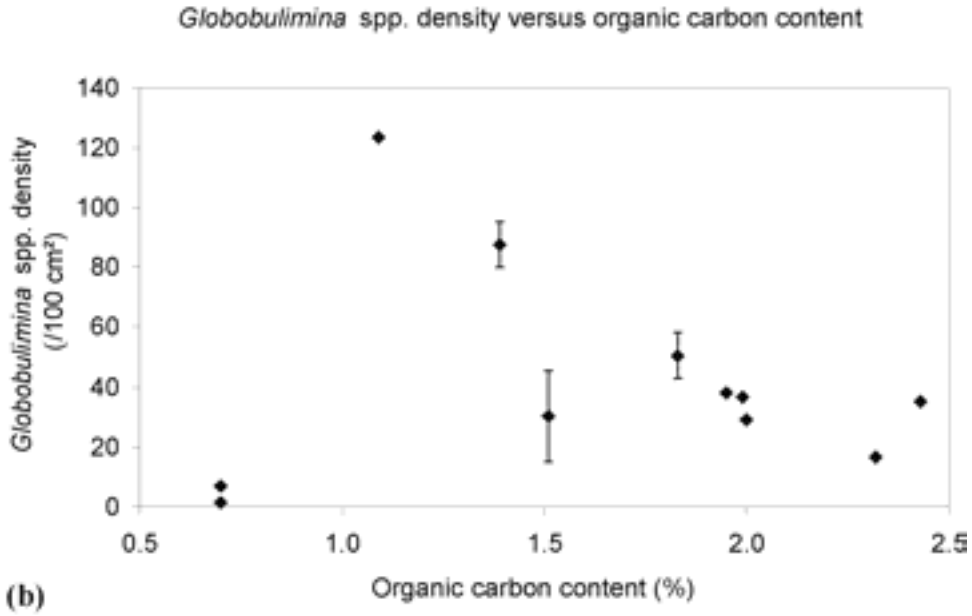
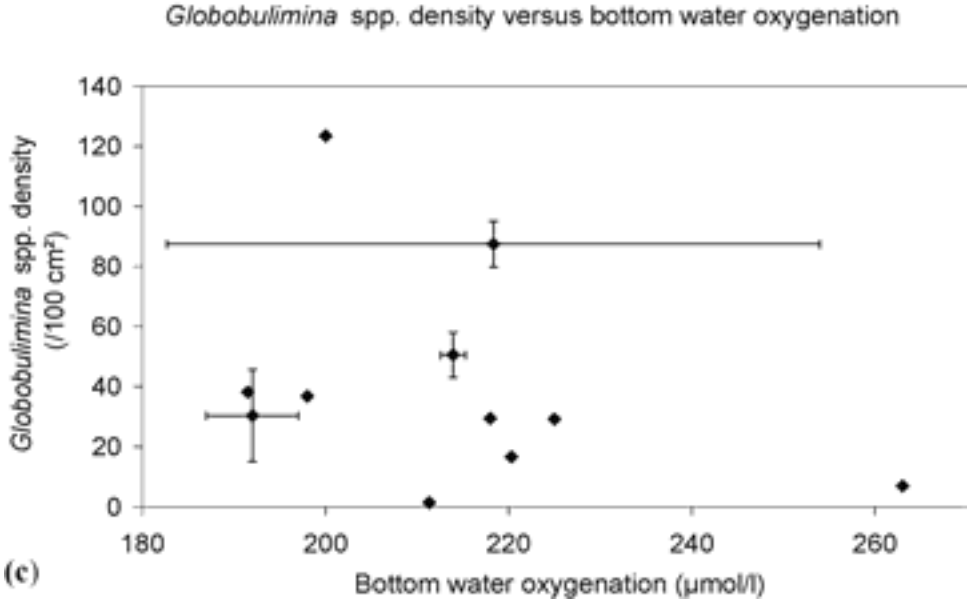


Fig. 4 Foraminiferal density normalised for 100 cm² versus exported organic carbon flux for both study areas. Dashed line is related to a simple linear regression. Vertical bars represent standard errors calculated when duplicate cores are available.

Fig. 5a-c; 5a Density of live (stained) Globobulimina spp. (>150 µm) in both our study areas versus exported organic carbon flux. 5b Density of live (stained) Globobulimina spp. (>150 µm) in both our study areas versus organic carbon content in surficial sediment. 5c Density of live (stained) Globobulimina spp. (>150 µm) in both our study areas versus bottom water oxygenation. Vertical and horizontal bars represent standard errors calculated when duplicate cores are available (see next page).


Globobulimina spp. density versus exported productivity
Globobulimina spp. density (/100 cm²)
Exported productivity (gC/m²/year)
(a)


Globobulimina spp. density versus organic carbon content
Globobulimina spp. density (/100 cm²)
Organic carbon content (%)
(b)


Globobulimina spp. density versus bottom water oxygenation
Globobulimina spp. density (/100 cm²)
Bottom water oxygenation (µmol/l)
(c)

Discussion

Since foraminiferal standing stocks decrease with depth, live benthic foraminiferal faunas (>150 µm) from the Bay of Biscay and from off Cape Blanc are obviously dependent on organic matter fluxes from the surface waters to the sea floor (Jorissen et al., 1998; Fontanier et al., 2002) (Table 1, Fig. 4).

This observation is in agreement with the commonly accepted paradigm that the exported organic carbon flux is a fundamental and major factor controlling foraminiferal density (e.g. Altenbach and Sarnthein, 1989; Fariduddin and Loubere, 1989). Nevertheless, our present observations show that the standing stocks (and percentages) of *Globobulimina* are not correlated to the vertically advected organic carbon exportation and the organic carbon content of surficial sediment in both our study areas (Fig. 5a-b). Also in the Mediterranean, *Globobulimina* is one of the few taxa for which the bathymetrical distribution appears not to be influenced by the downward organic flux (De Rijk et al., 2001). In the shallowest stations of our bathymetric transects, where the examined exported organic matter flux is maximum, the density of *Globobulimina* is very low. This is noticeably the case at our station D (140 m depth) in the Bay of Biscay. For this station, with a very shallow zero oxygen boundary (8 mm), Fontanier et al. (2002) suggest that *Globobulimina* is not able to compete for labile food particles with the very opportunistic taxa (*Nonion scaphum* and *Chilostomella oolina*) living in the very superficial sediment layers. High standing stocks of *Globobulimina*, on the contrary, are found in upper slope environments in rather mesotrophic conditions (stations A and B). At both these stations, *Globobulimina* occupies a deep infaunal microhabitat, where it is the only taxon able to take advantage of the peculiar conditions around and below the zero oxygen boundary (Fontanier et al., 2002). As suggested by Jorissen et al. (1998) and Fontanier et al. (2002), *Globobulimina* may feed either on bacterial consortia that concentrate around deep redox fronts or on slowly depolymerized resistant organic matter buried in the deeper sediment. Loubere (1994), Fariduddin and Loubere (1997) and Loubere and Fariduddin (1999b), who attempted to define major environmental factors controlling recent deep-sea foraminiferal faunas of superficial sediments from worldwide marine environments, grouped *Globobulimina* spp. in their high productivity assemblage (together with *Uvigerina peregrina* and *Melonis barleeanus*). They suggested that the species would prefer to live in sediments subject to relatively high exported organic matter fluxes from the surface waters. We find such a “high productivity” assemblage at our eutrophic station B (550 m depth) in the

Bay of Biscay, where *Uvigerina peregrina*, *Melonis barleeanus* and *Globobulimina* spp. are dominant taxa (Fontanier et al., 2002; 2003a).

In the Bay of Biscay, relatively high standing stocks (and percentages) of *Globobulimina* spp. are also recorded at station I (2800 m depth, see Fontanier et al., 2003c). It is positioned in the lower part of Cap Ferret Canyon where reworked organic matter concentrates as a result of suspension processes. The organic carbon content of the surficial sediment is close to 1.5% (Table 1). *Globobulimina* spp. is dominant in deep infaunal populations that live close to the zero oxygen boundary and other major redox fronts in anoxic sediments. As suggested by Fontanier et al. (2003c), we think that *Globobulimina* may benefit from the slow conversion of refractory organic matter in the deeper sediment by feeding on bacterial consortia that degrade those organic compounds, or by feeding on break-off products of bacterial activity, or by living in symbiosis with chemiosynthetic bacteria that live around redox fronts. Therefore, deep canyons that focus more or less labile organic matter, with well-oxygenated bottom waters, may be preferential biotopes for dense populations of *Globobulimina*.

In both our study areas, bottom waters are well oxygenated (with values ranging from 138 to 263 µmol/l). In this range of concentrations, bottom water oxygenation appears not to be a limiting ecological factor for the populations of *Globobulimina* (Fig. 5c). However, a relationship between *Globobulimina*, a strong organic matter flux and oxygen depletion of the bottom waters is suggested by several previous studies. Very high standing stocks of *Globobulimina* (1000-2000 individuals/100 cm²) have been recorded in live foraminiferal faunas from Californian Borderland Basins where the organic carbon content of the sediment is very high (>3%) and oxygen depletion in bottom and pore waters is marked (<20 µmol/l) (e.g. Phleger and Soutar, 1973; Douglas and Heitman, 1979; Mackensen and Douglas, 1989; Corliss and Silva, 1993; Silva et al., 1996) (Fig. 6). Therefore, dense populations of *Globobulimina* may reflect an enhanced accumulation of organic matter in severely oxygen depleted surface sediments. In both our study areas, where bottom water oxygenation is rather elevated (>138 µmol/l) and carbon content is moderate (0.7-2.4%), standing stocks of *Globobulimina* spp. are lower by a factor 10 than the densities recorded in these severely oxygen depleted environments (e.g. Silva et al., 1996). Rather surprisingly, also in some well-oxygenated upper and middle slope environments, high standing stocks and percentages of *Globobulimina* have been recorded (e.g. Corliss and Emerson, 1990; Corliss, 1991; Corliss and van Weering, 1993). For example, Corliss (1991) describes standing stocks of *Globobulimina* as high as those recorded in Californian basins (~2000 individuals/100 cm²)

by Silva et al. (1996) at a 200 m deep station in the Gulf of Maine (western north Atlantic Ocean) (Fig. 6).

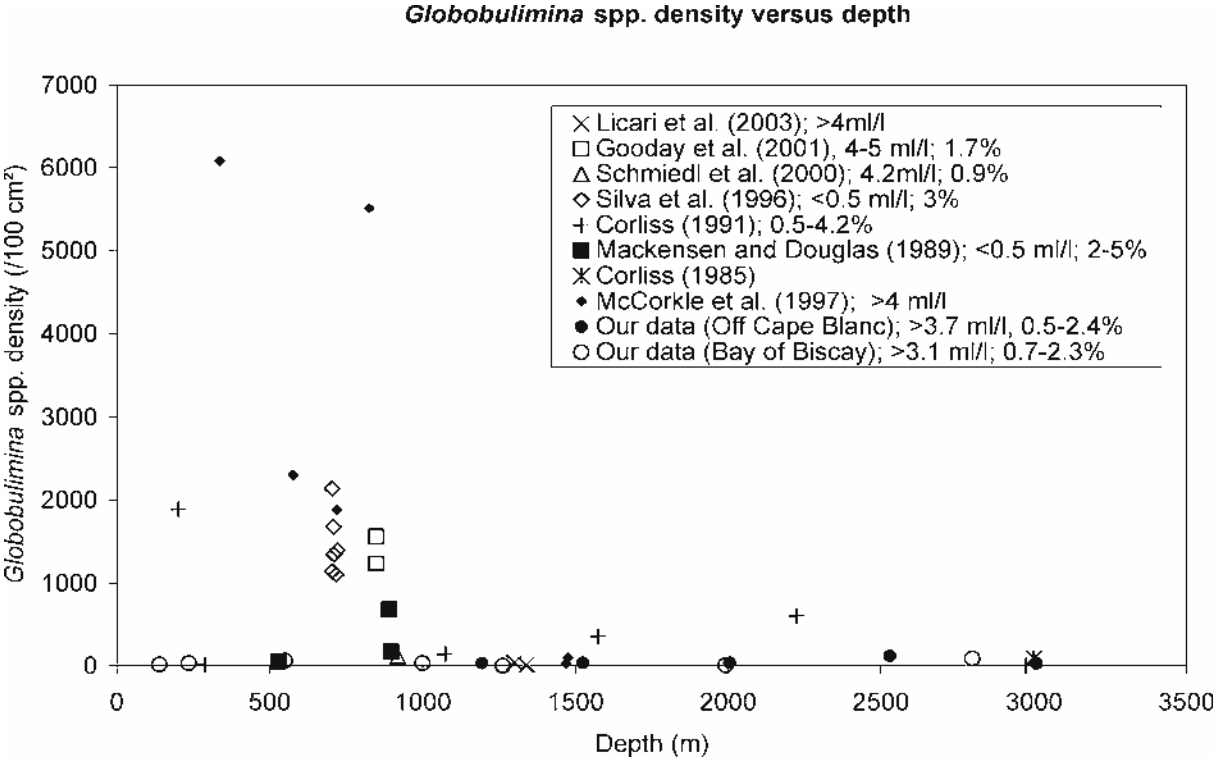


Fig. 6 Density of live (stained) Globobulimina spp. versus bathymetric depth in different study areas. Standing stocks of Globobulimina spp. are normalised for 100 cm². When available, bottom water oxygenation (ml/l) and organic content of surficial sediment (%) are presented.

From all these facts, it appears that *Globobulimina* is a very tolerant taxon that can spread in a wide range of environments. We suggest that bottom water oxygen depletion may indeed be a primary controlling parameter responsible for very high *Globobulimina* spp. densities, but is not exclusively so. Equally high densities may be found in rather well oxygenated settings such as those found at the shelf break and in upper slope environments or passive canyons as long as the organic matter flux from the surface waters and lateral sedimentary sources are high enough to induce enhanced bioturbation, high bacterial degradation and consequent food availability in the deep infaunal niches where *Globobulimina* lives. The investigation of the microhabitat of *Globobulimina* in relation to pore water oxygenation (not bottom water oxygenation) along bathymetric transects during seasonal studies could allow to better define the combination of environmental factors that limit the structure and dynamics of the populations of *Globobulimina.*

Microhabitat patterns

Our data sets

In order to determine the microhabitat of the genus *Globobulimina*, we calculated the Average Living Depth (ALD according to Jorissen et al., 1995) for *Globobulimina* spp., in all 10 cm long cores we collected in both our study areas. The ALD_{10} was not calculated for cores where less than 5 *Globobulimina* indivivuals were counted. A full description of the equation and the calculation method is in Fontanier et al. (2002; 2003a). Table 6 presents the ALD_{10} values of *Globobulimina* spp. and a microhabitat interpretation for *Globobulimina* in 26 cores sampled at our 7 stations in the Bay of Biscay and for the 5 cores collected off Cape Blanc.

Except in one core collected in January 1998 at station B (550 m depth) where *Globobulimina* appears as a shallow infaunal taxon, *Globobulimina* systematically occupies deep infaunal microhabitats. In the Bay of Biscay, the ALD_{10} ranges from 22 mm at station D to 66 mm at station I. Off Cape Blanc, the ALD_{10} ranges from 27 mm at station 11 to 59 mm at station 9. In figures 7a-b, vertical profiles of *Globobulimina* spp. are presented for our 12 stations. Density maxima of *Globobulimina* are recorded in suboxic and anoxic sediments close to the zero oxygen boundary. When we try to correlate the ALD_{10} with abiotic parameters such as bottom water oxygenation, the zero oxygen boundary and the exported organic carbon flux, we note that both the microhabitat of *Globobulimina* and the zero oxygen boundary are strongly correlated to the exported organic matter flux (Fig. 8). Furthermore, the ALD_{10} shows a fairly good correlation with the dissolved oxygen penetration depth (Fig. 8). However, for the observed range of values, bottom water oxygenation controls appears neither to control the penetration depth of dissolved oxygen, nor the microhabitat of *Globobulimina.* Finally, there is no clear relation between the density of *Globobulimina* spp. and its average living depth in the sediment.

Table 6 Live (stained) Globobulimina spp. and total live foraminiferal densities in the >150 µm fraction for all investigated samples for our both study areas. The ALD_{10}, of Globobulimina spp., the microhabitat of Globobulimina spp., bottom water oxygenation and zero oxygen boundary depth are also presented. Density values are normalised for 100 cm². Asterisks indicate duplicate samplings. DI = deep infaunal microhabitat; SI = shallow infaunal microhabitat (see next page).

Station (depth)	Sampling date	Live (stained) *Globobulimina* spp. density (/100 cm²) (>150 µm)	Live (stained) foraminiferal density (/100 cm²) (>150 µm)	ALD_{ID} (mm)	Microhabitat	Bottom water oxygenation (µmol/l)	Zero oxygen boundary (mm)
Off Cape Blanc							
11 (1195 m)	Mar-94	35	1907	27	DI	164	11
10 (1525 m)	Mar-94	38	543	52	DI	191.5	10
9 (2005 m)	Mar-94	37	400	59	DI	198	23
8 (2530 m)	Mar-94	124	660	37	DI	200	29
7 (3010 m)	Mar-94	29	528	48	DI	218	26
Bay of Biscay							
D (140 m)	Oct-97	17	2763	22	DI	220	8
C (235 m)	Oct-97	29	3008	27	DI	225	12
B (~550 m)	Oct-97	113	1874	24	DI	217	17
B (~550 m)	Oct-97*	15	667	-	-	217	17
B (~550 m)	Jan-98	26	1000	9	SI	216	24
B (~550 m)	Jan-98*	54	735	-	-	216	24
B (~550 m)	Jun-98	46	558	25	DI	212	19
B (~550 m)	Jul-98	25	390	23	DI	208	18
B (~550 m)	Oct-98	18	447	31	DI	205	21
B (~550 m)	Dec-98	76	854	41	DI	212	20
B (~550 m)	Jan-99	53	769	38	DI	220	26
B (~550 m)	Apr-99	43	340	29	DI	207	20
B (~550 m)	Apr-99*	99	646	27	DI	207	20
B (~550 m)	Jun-99	71	817	31	DI	215	21
B (~550 m)	Jun-99*	33	876	25	DI	215	21
B (~550 m)	Apr-00	57	1174	25	DI	221	23
B (~550 m)	Apr-00*	29	775	32	DI	221	23
A (~1000 m)	Oct-97	190	718	47	DI	196	18
A (~1000 m)	Jan-98	19	615	36	DI	201	31
A (~1000 m)	Jan-98*	4	476	-	-	201	31
A (~1000 m)	Jun-98	3	313	-	-	192	32
A (~1000 m)	Jul-98	4	246	-	-	189	30
A (~1000 m)	Oct-98	4	317	-	-	200	32
A (~1000 m)	Dec-98	28	424	50	DI	193	36
A (~1000 m)	Jan-99	15	571	47	DI	196	34
A (~1000 m)	Jun-99	18	707	40	DI	200	33
A (~1000 m)	Apr-00	1	726	-	-	199	29
A (~1000 m)	Apr-00*	14	1338	56	DI	199	29
A (~1000 m)	Apr-01	63	888	39	DI	138	8
F (1264 m)	Jan-98	1	169	-	-	211	64
H (1993 m)	Oct-98	7	249	61	DI	263	63
I (~2800 m)	Jan-99	81	336	47	DI	255	54
I (~2800 m)	Jun-99	103	574	51	DI	253	48
I (~2800 m)	Apr-00	79	338	66	DI	147	38
I (~2800 m)	Apr-00*	15	756	holothurian	holothurian	147	holothurian

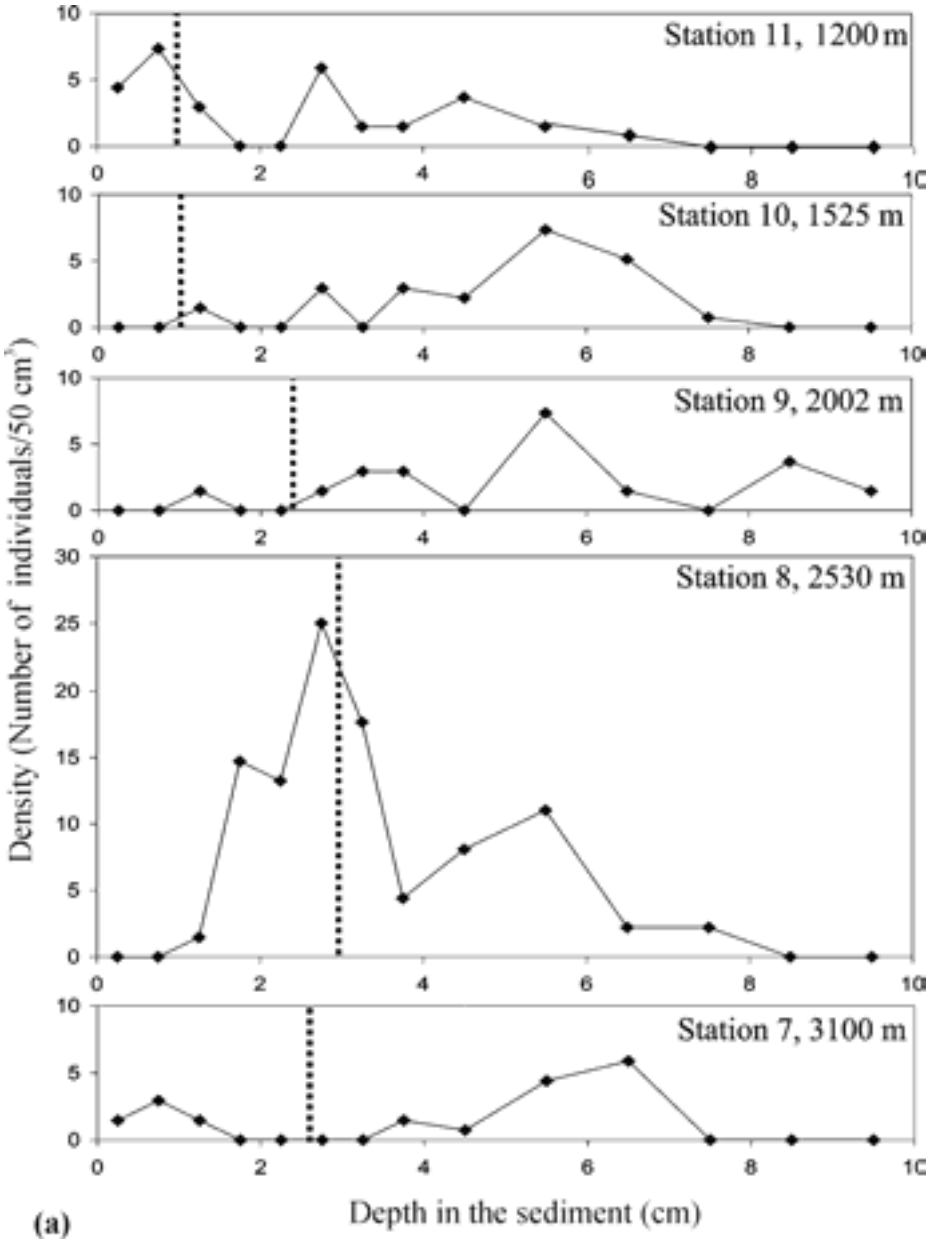
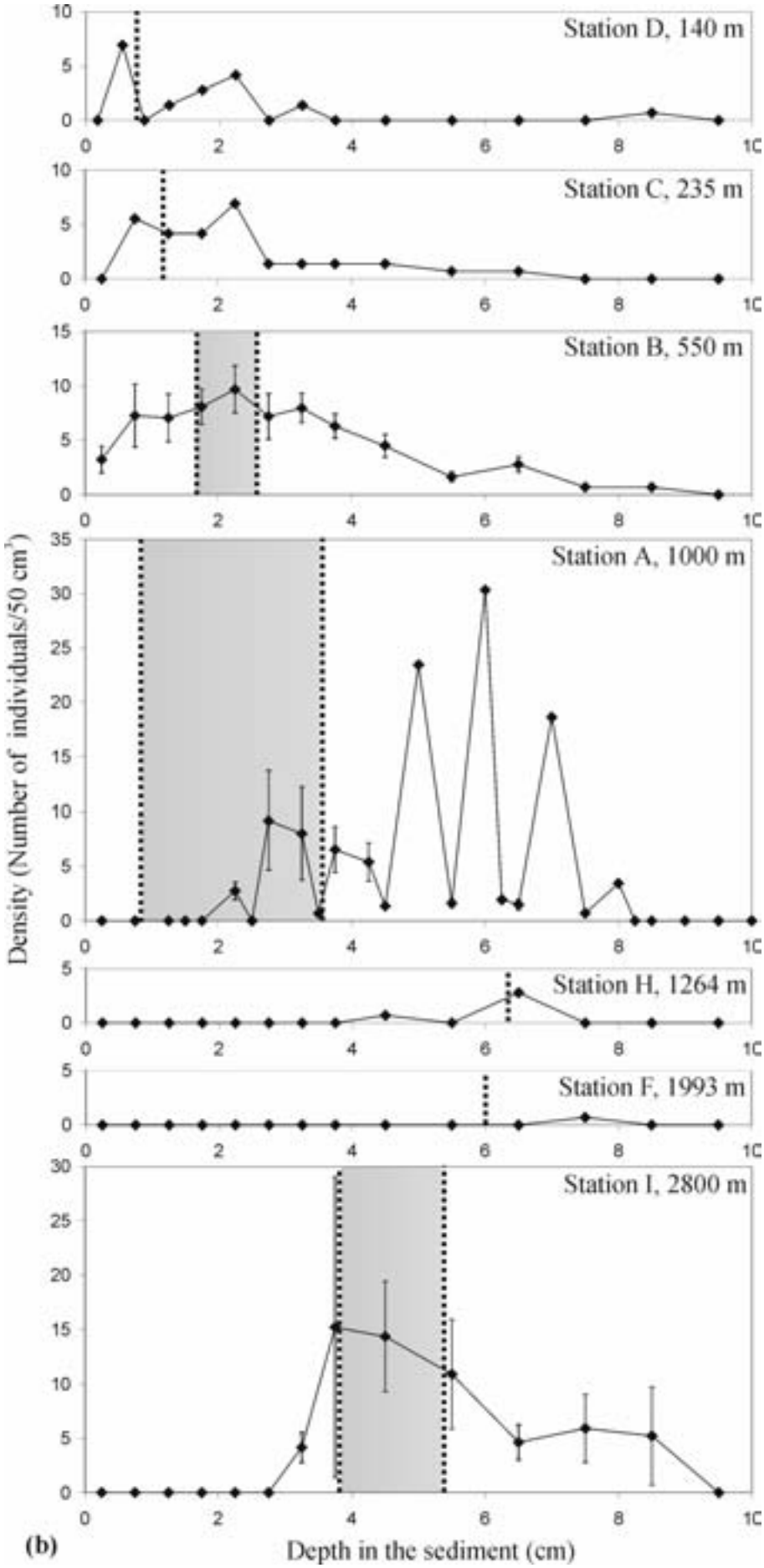


Fig. 7; 7a Vertical distribution of live (stained) Globobulimina spp. (>150 µm) for the 5 stations off Cape Blanc. Densities are standardised for a 50 cm^3 sediment volume. Standard errors are calculated when duplicate cores are available at the same station; 7b Vertical distribution of live (stained) Globobulimina spp. (>150 µm) for the 7 stations in the Bay of Biscay. Densities are also standardised for a 50 cm^3 sediment volume. Dotted lines represent zero oxygen boundaries. The two dotted lines indicating the zero oxygen boundary in figure 6b (with the shaded area) represent the minimum and maximum values observed during all samplings performed at stations, B, A and I.


Station D, 140 m
Station C, 235 m
Station B, 550 m
Station A, 1000 m
Station H, 1264 m
Station F, 1993 m
Station I, 2800 m
Density (Number of individuals/50 cm-3)
Depth in the sediment (cm)
(b)

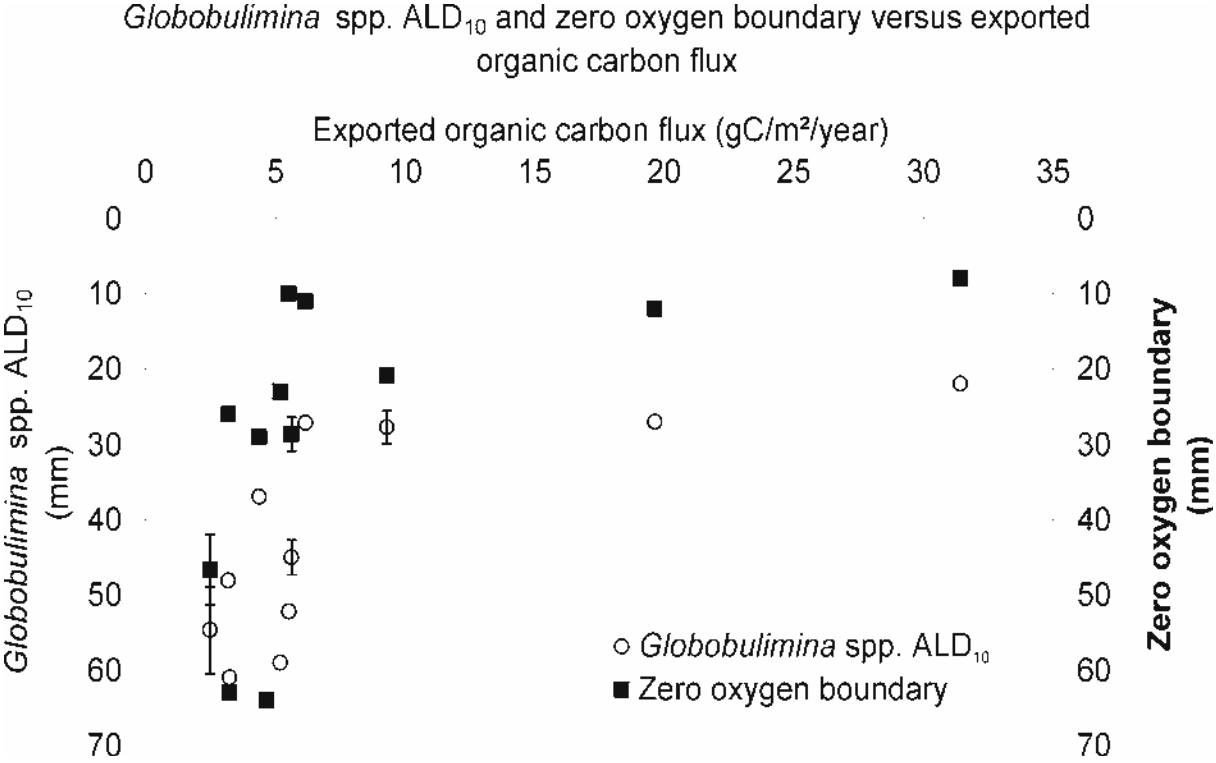


Fig. 8 ALD_{10} of Globobulimina spp. and zero oxygen boundary depth in function of exported organic carbon flux in the Bay of Biscay and off Cape Blanc. Vertical bars represent standard errors calculated when several duplicate cores are available.

Discussion

In view of our results from the Bay of Biscay and from off Cape Blanc, it appears that *Globobulimina* lives around and slightly below the zero oxygen boundary in a deep infaunal microhabitat. Since the oxidation of the exported organic matter flux in the superficial sediment (together with the porosity of the sediment) controls the zero oxygen boundary depth, we suggest that the microhabitat of *Globobulimina* in our well-oxygenated stations is determined by the exported productivity and the consequent mineralisation of organic compounds in the sediment. In the Bay of Biscay, such a pattern is illustrated in the regional adaptation of the TROX-model by Fontanier et al. (2002, their fig. 11). In upper slope environments, relatively high organic carbon exportation from the surface waters induces important organic carbon accumulation in the sediment and enhanced oxygen consumption in the topmost sediment. Sediment oxygen utilization in superficial sediments is reduced, on the contrary, in lower bathyal environments. As a direct result, the zero oxygen boundary is much shallower at upper slope than at lower slope stations, and the average living depth of

Globobulimina consequently varies with water depth. Other studies of bathymetric slope transects of well-oxygenated stations confirm that the microhabitat of *Globobulimina* shallows in upper slope and shelf environments (e.g. Corliss and Emerson, 1990; Corliss 1991; Bernhard, 1992).

Several assumptions have been made to explain the presence of deep infaunal foraminiferal assemblages in deep-sea environments (e.g. Shirayama, 1984; Gooday, 1986; Mackensen and Douglas, 1989; Corliss and Emerson, 1990; Bernhard, 1992; Den Dulk et al., 1998; Jorissen et al., 1998; Schmiedl et al., 2000; Fontanier et al., 2002). The causes of the existing vertical microhabitat zonation have been discussed by Gooday (1986). According to this author, three explanations account for the vertical zonation: biological competition, avoidance of predators, and/or a response to chemical and physical gradients. For Shirayama (1984) and Jorissen et al. (1995), the vertical distribution of benthic faunas in deeper sediment layers may be tributary to two major environmental factors that are (1) the exported organic matter flux to the sea floor and (2) the dissolved oxygenation at and below sediment-water interface (e.g. Shirayama, 1984; Jorissen et al., 1995; Jorissen et al., 1998; Gooday et al., 2001). In both our study areas, we think that the average living depth of *Globobulimina* is related to its metabolic requirements in terms of food and oxygen. Our data suggest that *Globobulimina* can be considered as a potential deep infaunal taxon that is able to live in anoxic conditions, or under very low dissolved oxygen concentrations, and feeds on bacterially converted organic matter, or bacterial biomass, concentrated around major redox fronts. The predation pressure on *Globobulimina* and the competition for space and food with other foraminiferal taxa will probably be considerably limited in the dysoxic and anoxic niches of the deeper sediments, which is an additional factor explaining the presence of consistent populations of *Globobulimina* in the apparently hostile deep infaunal niches.

Although *Globobulimina* is commonly documented as a deep infaunal taxon, which occupies the dysoxic and anoxic deeper layers of the sediment of well oxygenated stations (e.g. Corliss, 1985; Mackensen and Douglas, 1989; Corliss and Emerson, 1991; Corliss, 1991; Bernhard, 1992; Kitazato and Ohga, 1995; Silva et al., 1996; McCorkle et al., 1997; Jorissen et al., 1998; de Stigter et al., 1998; Kitazato et al., 2000; Schmiedl et al., 2000; Gooday et al., 2001; Kurbejweit et al., 2002; Licari et al., 2003), the genus can also occupy deep and shallow infaunal niches in oxygen depleted environments, with dysoxic to suboxic bottom waters (<2 ml/l) (e.g. Mackensen and Douglas, 1989; Bernhard, 1992; Silva et al., 1996; Nishi, 1992; Kitazato and Ohga, 1995; Silva et al., 1996; Jannink et al., 1998; Gooday et al., 2000). This is especially the case in the Californian Borderland Basins studied by Mackensen

and Douglas (1989) and Silva et al. (1996) where most stations are bathed by dysoxic bottom waters and present density maxima of *Globobulimina* close to sediment-water interface (<2 cm depth). In these environments, where bottom water oxygen depletion is caused either by elevated laterally and horizontally advected organic matter fluxes or by seasonally limited ventilation of bottom waters, *Globobulimina* lives in a shallow infaunal microhabitat around the zero oxygen boundary that is positioned close to sediment-water interface.

To summarise, it appears that *Globobulimina* tolerates low dissolved oxygen concentrations much better than almost all other taxa. It concentrates around and just below the zero oxygen boundary in the sediment, where it may profit from the availability of bacterially mediated/converted labile organic carbon, the absence of competitors and predators and a putative symbiosis with bacteria. As long as these ecological requirements are combined, *Globobulimina* can live in shallow as well as deep infaunal niches in environments with well oxygenated as well as severely dysoxic bottom waters.

Seasonal variability of *Globobulimina* faunas

Since the microhabitat of *Globobulimina* in the Bay of Biscay is strongly linked to the depth of the zero oxygen boundary, it seemed interesting to see whether this microhabitat varies with the potential seasonal changes of the depth of the oxygenated layer. Furthermore, since the density of *Globobulimina* should somehow be related with the quantity of organic matter available in its niche, we may wonder whether seasonal eutrophication of the topmost sediment after phytoplankton bloom events induces responses in the standing stocks of *Globobulimina*.

Our data sets

Fontanier et al. (2003a; 2003b) examined the seasonal changes of foraminiferal faunas in the Bay of Biscay at stations B and A (550 and 1000 m depth).

At 550 m depth, the microhabitat of adult *Globobulimina* spp. does not vary significantly throughout the 2.5 years period, and stays below and close to zero oxygen boundary, which does not exhibit any significant seasonal changes either (Fig. 9). In the larger size fraction (>150 µm), the density of *Globobulimina* is roughly constant throughout the 2.5 investigated years with density maxima recorded in October 1997, December 1998 and April 1999 (Table 6). In the smaller size fraction (63-150 µm fraction), where only the

first half cm of the sediment was studied, a single population of juvenile *Globobulimina* individuals has exceptionally been recorded in June 1998 (Fig. 10).

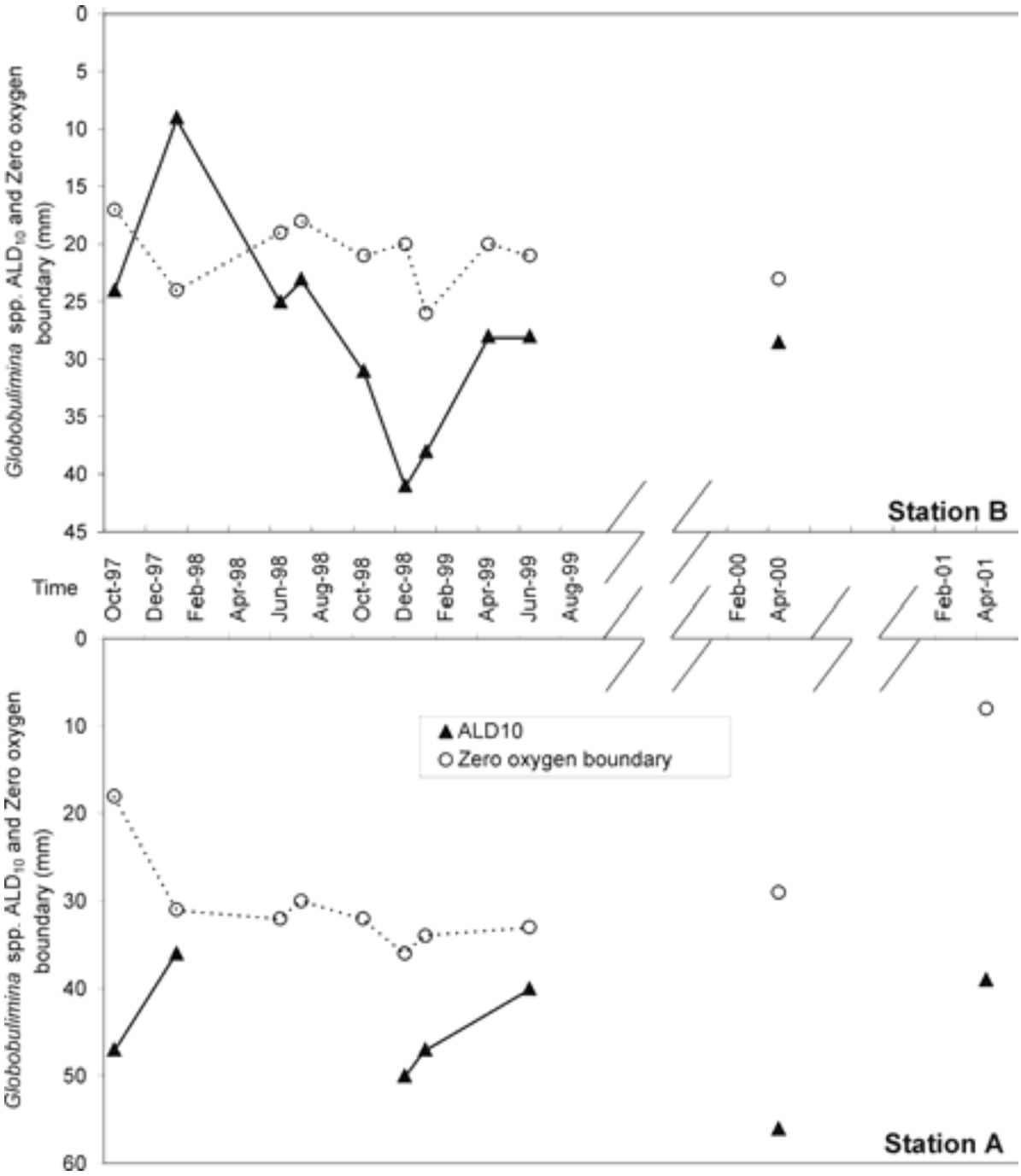


Fig. 9 Seasonal changes of the ALD_{10} of Globobulimina spp. and zero oxygen boundary depth at station B (~550 m depth) between October 1997 and April 2000 and at station A (~1000 m depth) between October 1997 and April 2001.

Also at 1000 m depth, the ALD_{10} of *Globobulimina* spp. is very constant (Fig. 9). At this station, the oxygen penetration depth shallowed drastically in October 1997 and April 2001, without a clear response in the vertical distribution of the adult population of *Globobulimina*. Densities of *Globobulimina* are generally low but depict significant increases in October 1997 and April 2001 (Table 3). There is no juvenile population recorded in the topmost 0,5 cm of the sediment throughout the 3.5 investigated years.

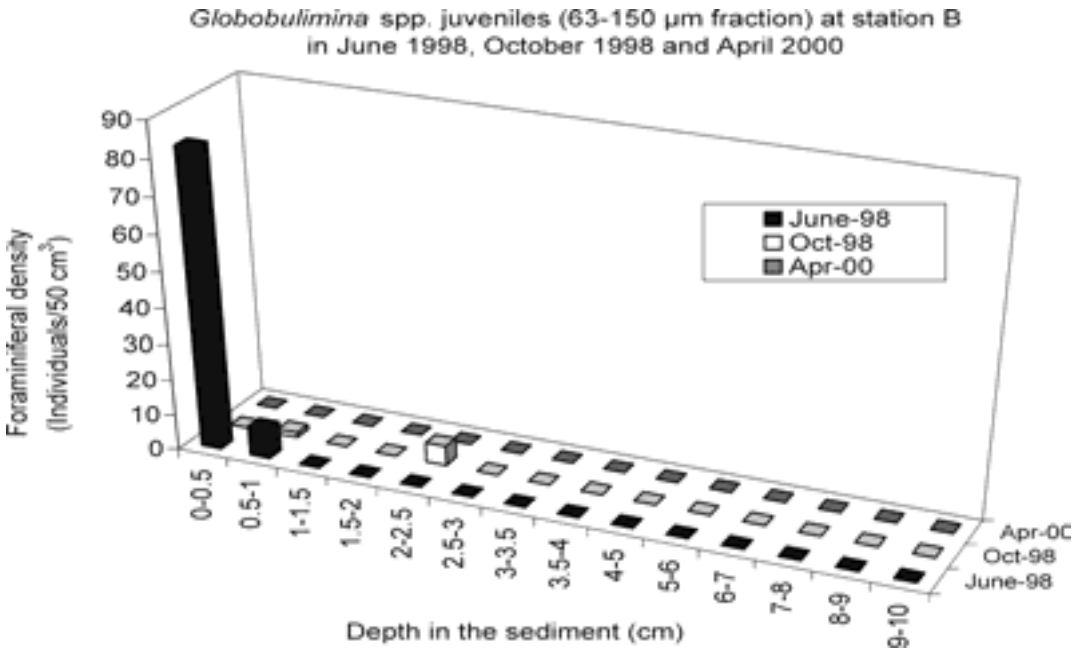


Fig. 10 Density profiles of live (stained) Globobulimina spp. in the 63-150 µm fraction for 3 cores collected in June 1998, October, 1998 and April 2000 at station B. Densities are standardised for a 50 cm^3 sediment volume.

Discussion

At station B in the Bay of Biscay, where zero oxygen boundary is almost invariable, *Globobulimina* stays in anoxic sediments around oxygen zero depth (Fontanier et al., 2003a). At station A, where two marked upward shifts of the zero oxygen boundary have been recorded in October 1997 and April 2001, probably in relation to phytodetritus deposits during the spring and autumn blooms (Fontanier et al., 2003b), the adult populations of *Globobulimina* (>150 µm) fail to show a migrational response. Most individuals remain in the deeper sediment more or less close to the zero oxygen boundary. Consequently, for both our

study areas, it is not evident that the observed seasonal changes of the depth of the zero oxygen boundary induce changes in the microhabitats of *Globobulimina*. In other areas, where bottom waters can be seasonally depleted in dissolved oxygen, such a relationship between the microhabitat of *Globobulimina* spp. and the depth of the zero oxygen boundary appears to be more straightforward (e.g. Kitazato and Ohga, 1995; Ohga and Kitazato, 1997; Kitazato et al., 2000). At our station B, the deep infaunal population of *Globobulimina* do not exhibit any drastic increase of the standing stocks during the spring and autumn bloom periods. This contrasts with many shallow infaunal, much more opportunistic taxa that can show spectacular density maxima in eutrophic periods (e.g. *Epistominella exigua*, *Uvigerina peregrina*, Fontanier et al., 2003a). The occurrence of shallow infaunal juveniles of *Globobulimina* in June 1998 suggests that *Globobulimina* may reproduce and initiate its juvenile development in the post-bloom period in the first cm of the sediment where bacterial biomass and phytodetrital remains may be available as food sources, and where several weeks after the bloom event, competition may be limited (Fontanier et al., 2003a). In October 1998, a very low density juvenile population is recorded at the same depth in the sediment (Fig. 10), suggesting that *Globobulimina* may present very short reproductive events after bloom events. At our station A, we do not observe any late reproductive events in post-bloom periods. The moderate increase of density of adult *Globobulimina* spp. in October 1997 and April 2001 may be due to enhanced reproduction in the deep sediment, which would be triggered by a rapid incorporation by bioturbation of freshly deposited labile organic compounds in suboxic and anoxic sediments following bloom periods (Fontanier et al., 2003b). We also think that the shallow bioturbation zones (less than 2 cm; Fontanier et al., 2003a; 2003b) in both stations is a limiting factor for the dynamics of *Globobulimina* since it limits severely the availability of freshly deposited and labile phytodetritus in the deeper infaunal niches where *Globobulimina* preferentially lives.

The population dynamics of *Globobulimina* appear to be totally different in environments where bottom water oxygenation is permanently very low. Silva et al. (1996), using complete data from Corliss and Silva (1993), give important information about the seasonal dynamics of *Globobulimina* in oxygen depleted environments from Californian Borderland Basins. *Globobulimina pacifica* always occupies deep infaunal microhabitats without showing any obvious migration towards shallower infaunal niches. It exhibits its highest absolute frequency in the >150 µm size fraction in July, two to three months after a maximum organic carbon flux related to an upwelling event. Silva et al. (1996) suggest that in this way, *Globobulimina pacifica* may respond to phytodetritus deposited in April-May.

Since no juvenile individuals are observed in the 63-150 µm fraction in May-April and July samplings, Silva et al. (1996) conclude that an adult size must be reached very quickly. Kitazato and Ohga (1995) study the dynamics of live foraminiferal faunas in Sagami Bay at a 1450 m deep oxygen depleted station, where *Globobulimina* (mainly *G. affinis*) is a common deep infaunal taxon. Rather surprisingly, these authors show density increases in November through February, definitely before the eutrophic period (spring bloom). In Sagami Bay, the shallowing of the oxygen zero boundary in relation to phytodetritus deposits is effective from late spring (May) to late autumn (November). As a result, benthic foraminifera migrate vertically within the sediment, concentrating into the shallower part of the sediment in spring. In these shallower niches, they may take advantage of the newly deposited organic matter and avoid oxygen stress. In a more recent study, Kitazato et al. (2000) show that deep infaunal populations of *Globobulimina affinis* from the same bathyal environment of Sagami Bay (Japan, 1430 m depth, station SB) show less pronounced seasonal fluctuations in population size than very opportunistic taxa such as *Textularia kattegensis*. Nevertheless, *Globobulimina* appears to exhibit some reproductivie and/or growth response to phytodetrital deposits following the spring bloom periods, when the zero oxygen boundary is close to the sediment-water interface and when a fluffy layer is recorded on the sea floor. Reproduction events may explain those periodic absolute frequency increases (Ohga and Kitazato, 1997). Newly born juveniles specimens indeed show marked density increases in the fluffy layer and in deep niches (2-5 cm deep interval) some weeks after the beginning of spring bloom (Kitazato et al., 2000). According to those authors, the population of *G. affinis* may follow the upward shallowing of zero oxygen boundary in phytodetritus-enriched sediment where it may reproduce. As proposed by Sen Gupta and Machain-Castillo (1993), *Globobulimina* could show remarkable population blooms when a drastic oxygen depletion of surface sediments is coupled with a significant increase in the substrate organic matter.

It seems that in the Bay of Biscay, *Globobulimina* behaves as a stable and highly specialised taxon that occupies rather stable niches around the zero oxygen boundary. It does not show an opportunistic behaviour such as some shallow infaunal taxa (e.g. *Epistominella exigua*), which can rapidly reproduce in the surface sediment after bloom events. As suggested by Ohga and Kitazato (1997), we think that *Globobulimina* has a rather long life cycle (>1 year). When labile organic matter is available in their deep infaunal microhabitat, *Globobulimina* seems able to slightly accelerate its growth and reproduction rate (station A). At station B, *Globobulimina* juveniles may migrate upward in surface sediment after bloom events in purpose to benefit from organic matter remains or bacterial biomass. In shallow

infaunal niches, *Globobulimina* juveniles would find higher quality food sources, which are normally not available in the deeper sediment layers, but which could be essential for the earlier growth stages.

Isotopic composition of *Globobulimina* tests

In our study area

Isotopic measurements were performed on *Globobulimina* individuals collected at stations D, B, A, F and H. They were compared with bottom water isotopic signatures and with the isotopic signature of shallow infaunal *Uvigerina peregrina*.

In all stations, *Globobulimina* presents $\delta^{13}C$ lower than the $\delta^{13}C$ of *Uvigerina peregrina*. Its $\delta^{13}C$ signature ranges from –1.16 to –2.28‰ (Table 2). Along the bathymetric transect, its signature is not correlated with bottom water $\delta^{13}C_{DIC}$. $\Delta\delta^{13}C$ between *Globobulimina* spp. and *U. peregrina* is constant from 150 to 1000 m depth but increases at still greater depth (Fig. 11a). At station B, where a seasonal study was performed, $\delta^{13}C$ is almost invariable throughout the 2.5 investigated years (Table 2, Fig. 12).

Along the same bathymetrical transect, the $\delta^{18}O$ of *Globobulimina* varies from 1.83 to 3.43‰ whereas $\delta^{18}O_{e.c.}$ increases by 1.8‰ and temperature decreases by about 8°C. From 140 to 1993 m, $\Delta\delta_{18}O$ between *Globobulimina* spp. and *U. peregrina* is very constant with a significant positive correlation coefficient ($r^2 = 0.99$) (Fig. 11b). At station B, $\delta^{18}O$ values are almost constant for both taxa throughout the 2.5 investigated years (Table 2, Fig. 12).

Discussion

Data about $\delta^{18}O$ and $\delta^{13}C$ isotopic signatures of live benthic foraminiferal tests have been significantly increased during the two last decades, especially due to several multispecies studies, in which the relation between the isotopic composition of the various species and the chemical properties of bottom and interstitial waters are studied (e.g. Woodruff et al., 1980; Bélanger et al., 1981; Grossman, 1984a,b; Grossman, 1987; Mackensen et al., 1993; McCorkle et al., 1990, 1994; Rathburn et al., 1996; McCorkle et al., 1997; Mackensen et al., 2000).

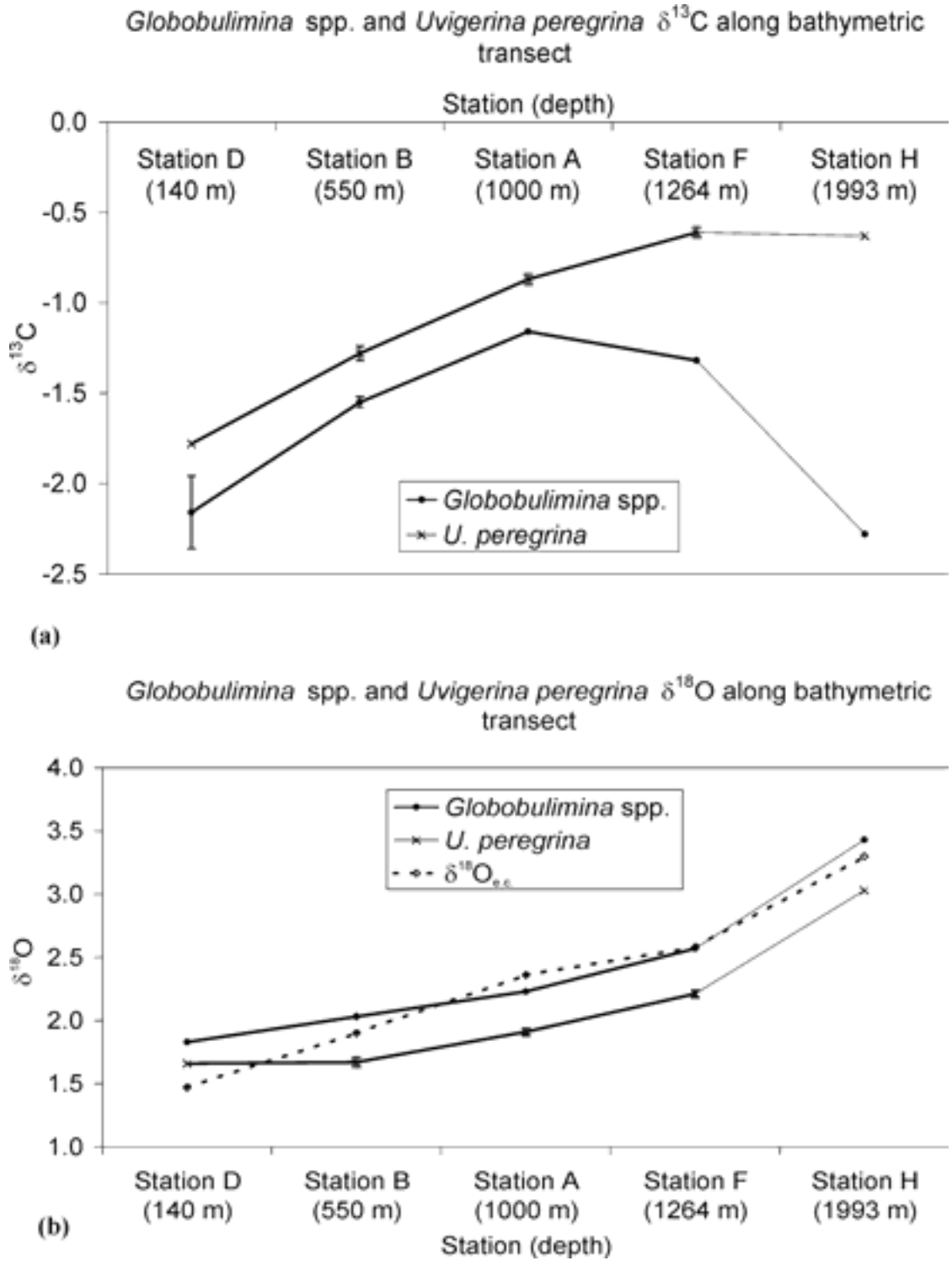


Fig. 11; 11a $\delta^{13}C$ of Globobulimina spp. and Uvigerina peregrina between 140 and 1993 m depth in the Bay of Biscay. 11b $\delta^{18}O$ of Globobulimina spp. and Uvigerina peregrina between 140 and 1993 m depth in the Bay of Biscay. The dotted line represents bottom water $\delta^{18}Oe.c$. Vertical bars represent standard errors calculated when several isotopic measurements are available.

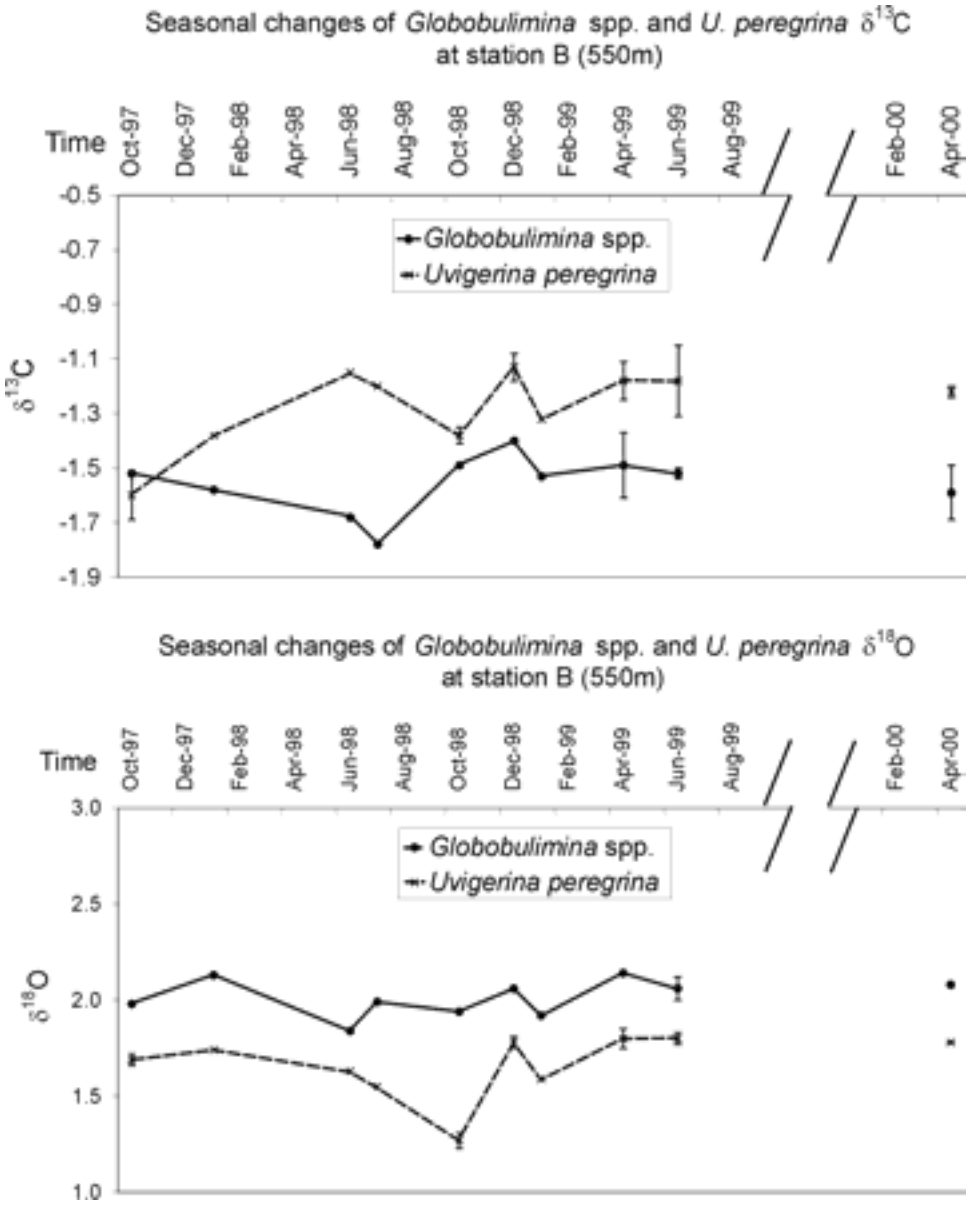


Fig. 12 Seasonal changes of $\delta^{13}C$ and $\delta^{18}O$ of Globobulimina spp. and Uvigerina peregrina at station B between October 1997 and April 2000 (Bay of Biscay). Vertical bars represent standard errors calculated when several isotopic measurements are available.

Our results suggest that *Globobulimina* biomineralises its test with a constant offset of about 0.15‰ with respect to calcite formed in equilibrium with bottom water $\delta^{18}O$. Even if the magnitude of this shift is questionable in view of the uncertainty of the calculated $\delta^{18}O_{bw}$, the $\delta^{18}O$ of *Globobulimina* spp. (as well as of *U. peregrina*) is well correlated to bottom waters $\delta^{18}O_{e.c.}$ ($r^2 = 0.93$). As demonstrated by Grossman (1984a, 1984b) and McCorkle et al. (1990;

1997), *Globobulimina* would have a $\delta^{18}O$ isotopic signature close to bottom water signature (= $\delta^{18}O_{e.c.}$). The *Globobulimina* isotopic enrichment along our bathymetric transect reflects a temperature decrease of about 8°C with a mean ratio of about 0.2‰ of enrichment per 1°C of decrease. Because bottom waters $\delta^{18}O$ at station B (550 m) is presumably invariable throughout the year, it is not surprising to find a rather constant isotopic signature for both presented taxa.

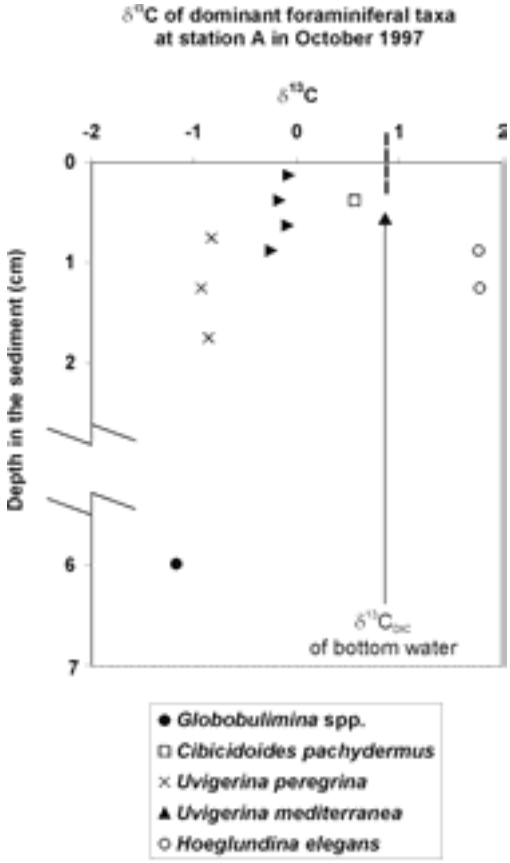


Fig. 13 $\delta^{13}C$ isotopic signature for dominant foraminiferal taxa in a 10 cm long core collected at station A (~1000 m deep) in October 1997 (Bay of Biscay).

In the Bay of Biscay, the $\delta^{13}C$ signature of *Globobulimina* spp. seems to be strongly controlled by microhabitat effects. Its light $\delta^{13}C$ signature reflects the deep infaunal microhabitat where it preferentially lives. The progressive organic matter remineralization in deeper sediments induces an increasing ^{12}C enrichment of the pore water with depth, and a related low $\delta^{13}C_{DIC}$ signature of deep infaunal taxa. Microhabitat effects on the $\delta^{13}C$ signatures of foraminiferal taxa have been documented in various studies (e.g. McCorkle et

al., 1990, 1994; Rathburn et al., 1996; McCorkle et al., 1997; Mackensen et al., 2000). In our study area, the impact of microhabitat effects is very clear when we compare the $\delta^{13}C$ of *Globobulimina* spp. with the isotopic signature of other shallow infaunal dwellers. For example, figure 13 shows the $\delta^{13}C$ of dominant taxa picked in a core collected at station A in October 1997. The differences (due to the microhabitat effect) between very shallow infaunal calcitic taxa (*Cibicidoides pachydermus*, *Uvigerina mediterranea*) and deep infaunal taxon (*Globobulimina* spp.) are obvious. At station B, the $\delta^{13}C$ of *Globobulimina* spp. (and *U. peregrina*) does not vary seasonally. This suggests that seasonal phytodetritus exportation to the sea floor affects only the sediment surface niches, but does not induce drastic isotopic changes of pore water $\delta^{13}C$ within shallow or deep infaunal niches. Most of the phytodetritus will be rapidly degraded at the sediment-water interface where only very opportunistic taxa that are actually colonising the phytodetritus (e.g. *Epistominella exigua*) and perhaps newly born juveniles (e.g. *Uvigerina peregrina*) may record the ephemeral ^{12}C enrichment of the bottom waters in the $\delta^{13}C$ of their test.

Figure 14 depicts the vertical distribution of deep infaunal *Globobulimina* spp. and shallow infaunal *Uvigerina peregrina* in cores collected along our bathymetric transect. The average $\delta^{13}C$ signature of both taxa and the $\Delta\delta^{13}C$ between *Uvigerina peregrina* and *Globobulimina* spp. are also presented for each station. Both foraminiferal taxa are supposed to calcify their test in close equilibrium with pore water $\delta^{13}C$ of the sediment interval in which they preferentially live (assuming a dominant microhabitat effect). Along the bathymetric transect, the impact of the decreasing organic matter flux with depth is well recorded in the $\delta^{13}C$ of shallow infaunal *U. peregrina,* which shows the lowest value at station D and the heaviest one at station H (Fig. 14). The shallower the station is, the more intense the ^{12}C enrichment of the pore water of the superficial sediment will be. As shown by McCorkle et al. (1997), as a direct consequence, there is a strong negative correlation between the $\Delta\delta^{13}C$ bottom water versus *U. peregrina* and the exported organic carbon flux. The decrease of organic matter remineralization in the oxic superficial sediments with water depth is probably accompanied by a relative increase (with respect to the oxic degradation at the sediment surface) of the anaerobic degradation of more refractory organic compounds deeper in the sediment. As a consequence, in these more oligotrophic areas, the $\delta^{13}C$ profile will be much less steep in the uppermost sediment. Since a major part of the scarce organic carbon is degraded in dysoxic and anoxic sediment layers, most ^{12}C will be released deeper in the sediment, where we will find a gradual $\delta^{13}C$ pore water shift over a relatively large depth

interval. Such a scenario can explain why the $\Delta\delta^{13}C$ between shallow infaunal *U. peregrina* and deep infaunal *Globobulimina* spp. is minimal in eutrophic areas, but shows an important increase towards oligotrophic areas. If true, this could mean that the $\Delta\delta^{13}C$ can inform us about the relative importance of the two pathways, aerobic and anaerobic, of organic matter mineralisation.

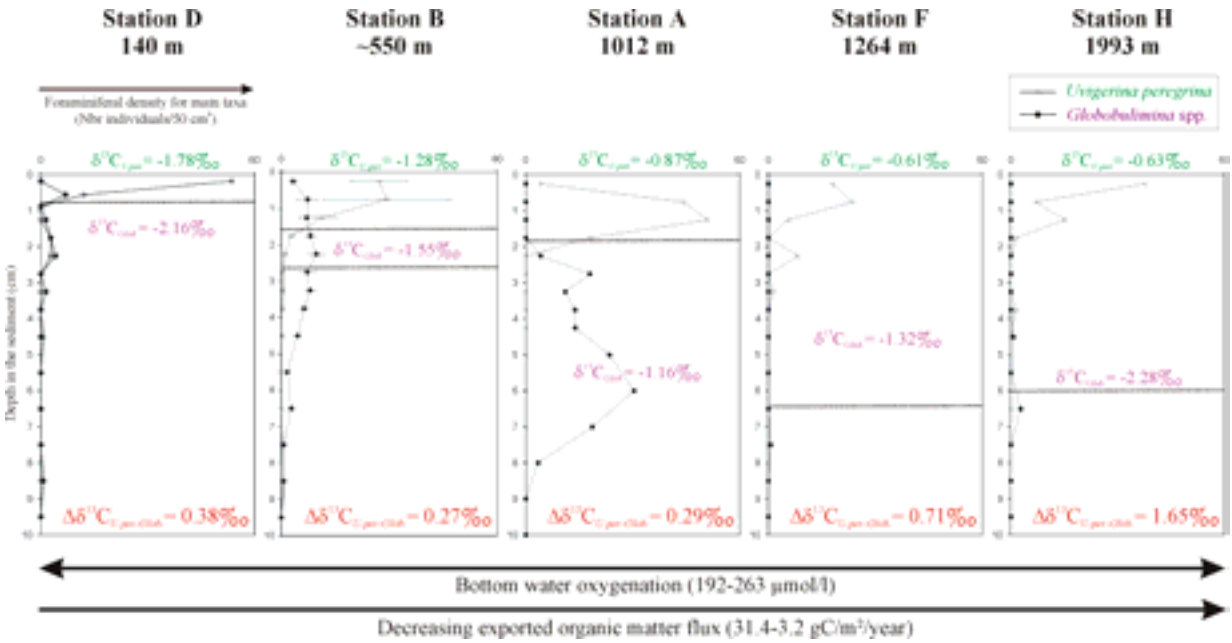


Fig. 14 Synthetic scheme showing the carbon isotopic signatures of Globobulimina spp. and Uvigerina peregrina along a bathymetric transect in the Bay of Biscay. Both foraminiferal taxa are supposed to record pore water $\delta^{13}C_{DIC}$ of the sediment interval where they preferentially live (microhabitat effect), see text for further explanation. The vertical density profiles of Globobulimina spp. and Uvigerina peregrina are added. Foraminiferal densities are expressed as number of individuals per 50 cm³. The $\delta^{13}C$ of Uvigerina peregrina and Globobulimina spp. and the $\Delta\delta^{13}C$ between both taxa are presented for the 5 stations.

Metabolic strategies of *Globobulimina*: Experimental studies and ultrastructural observations

Just like all living organisms, benthic foraminifera need energy to grow, reproduce and bio-mineralise. Energy is indispensable to perform metabolic activities (catabolism and anabolism). For most heterotrophic and aerobic organisms, intracellular oxidative reactions between electron acceptors (oxidants) and organic substrates (reducers) supply energy. These

energy supplying redox reactions are more commonly known as “respiration”. In its most basal form, the oxidant is free oxygen, the reducer is the organic matter and energy consists mainly of ATP molecules. Obligate aerobic organisms need oxygen as electron acceptor in purpose to degrade organic matter and to obtain energy. Facultative anaerobic organisms are able to use alternative pathways when confronted to temporary anoxic conditions. Both recent and fossil data show that even foraminiferal typical of oxygen-depleted environments can not survive prolonged anoxia (Bernhard and Reimers, 1991). The fact that live *Globobulimina* specimens are consistently found in oxygen depleted biotopes, evokes numerous questions. How does this taxon manage to survive in such apparently adverse conditions? In the deep infaunal biotope where *Globobulimina* is commonly found, dissolved oxygen is rare or absent and organic matter presumably consists of resistant and refractory biomolecules. If the *Globobulimina* individuals are active, how can they gain energy and sustain their metabolic activities? If they are organoheterotrophic, what electron acceptor and organic substrate do they use? In other terms, do they have access to free oxygen or do they exploit another metabolic pathways? And what precise food source do they require? Experimental studies about deep-sea foraminifera are still scarce, but the first results of these studies give some interesting pieces of information about the dynamics and ecological tolerances of foraminiferal faunas (e.g. Heinz et al., 2001; 2002; Gross, 2000; Geslin et al., 2002; Ernst and Van der Zwaan, 2003). Unfortunately, in studies based on superficial sediments, *Globobulimina* is often very rare or even absent (e.g. Alve and Bernhard, 1995). Only very few relatively large-scale ecological mesocosm experiments have been performed, and only limited data are available for *Globobulimina* (e.g. Ernst and Van der Zwaan, 2003).

Oxidative/non-oxidative pathways

In shallow or deep oxygen-depleted microhabitats, heterotrophic organisms may adopt different strategies to obtain the electron acceptors necessary to oxidise organic resources. In both our study areas, several metabolic pathways can be envisaged for *Globobulimina.* However, these theoretically feasible pathways remain strictly speculative as long as ultrastructural observations have not yet been performed, and experimental observations for faunas from the Bay of Biscay are still very scarce.

1. Obligate Aerobic metabolism

Leutenegger and Hansen (1979) noted that *Globobulimina pacifica* collected from low-oxygen (<0.3 ml/l) environments (750-898 m depth in San Pedro Basin) has a lower density of mitochondria in comparison with other taxa from well oxygenated environments. The mitochondria are concentrated under the pore openings, whereas they are more evenly distributed in taxa living in well-oxygenated environments. The concentration of mitochondria close to pore entrance suggests an optimisation of respiration processes through the pores under low-oxygen conditions. The absence of an osmiophilic organic lining at the pore entrance of *G. pacifica* would favour a higher rate of molecular diffusion through the pores. Moreover, *Globobulimina* has pores evenly distributed over most of the test surface, which should be desirable for enhancing gas exchange in a low-oxygen environment (Corliss, 1985). Such ultrastructural evidence suggests that foraminifera from low-oxygen microhabitats could behave as obligate aerobic organisms that optimise gas exchange between their protoplasm and the pore waters. In the protoplasm of other foraminiferal taxa collected in low oxygen environments, a high concentration of mitochondria has been observed in the apertural cytoplasm, which is supposed to form the deployment of the pseudopodial network (Bernhard and Alve, 1996). Since pseudopodia may extend to at least ten times the test diameter of a foraminifer (Travis and Bowser, 1991), foraminifera from anoxic deep sediments like *Globobulimina* may take oxygen from shallower and more oxygenated sediment levels and maintain energetic oxidative phosphorylation (Bernhard, 1992; Bernhard and Sen Gupta, 1999, Gooday et al., 2001). In this manner, deep infaunal *Globobulimina* individuals from both our study areas, living close (less than 1 cm) to the zero oxygen boundary, could collect oxygen in the overlying oxic or dysoxic sediment layer. However, such a life strategy can not be envisaged for very deep infaunal taxa that are found several centimetres below the zero oxygen boundary (station I) (Fig. 7b).

2. Microaerophilic metabolism

Microaerophilic metabolism is generally described for bacteria, which have an optimal metabolic activity under very low oxygen concentrations (3-5 µmol/l). Microaerophilic bacteria use oxygen as a final electron acceptor and behave like aerotactic organisms tracking oxygen concentration gradients (Singleton, 1999). As demonstrated by Ernst and Van der Zwaan (2003) who worked on foraminiferal cultures based on material collected at our station

B from the Bay of Biscay, *Globobulimina* individuals are able to migrate towards infaunal microhabitats around the zero oxygen boundary, after initial mixing and homogenisation of the samples. When mesocosms are subjected to anoxic conditons during three weeks (Ernst and Van der Zwaan, 2003), a slight shallowing of the vertical distribution of *Globobulimina* is observed, and some specimens are found in the superficial first cm of the sediment, a depth interval where they are rarely found in the oxygenated control situations or in in situ cores (Fontanier et al., 2003a). An experiment with material from our Bay of Biscay station A (1000m) was conducted in order to analyse the vertical microhabitat distribution of individual taxa in sediments with normal and reversed oxygen profiles, without supplying food (Geslin et al., 2002). Aquaria with a normal oxygen profile (i.e., well-oxygenated surface layer and anoxia at the bottom) contain mainly living *Globobulimina* specimens in the deeper parts of the sediment (dysoxic to anoxic zones). In the aquaria with a reversed oxygen profile (i.e., anoxia in the surface layer and well-oxygenated sediment at the bottom) living *Globobulimina* specimens are exclusively found in the anoxic superficial sediments. These observations prove that *Globobulimina* is able to migrate upward or downward in the sediment towards its favored habitats, around and slightly below the zero oxygen boundary. Both in in situ and laboratory samplings, where the microhabitat of *Globobulimina* seems to be close to the zero oxygen boundary (Fig. 8), *Globobulimina* individuals may behave as a microaerophilic foraminiferal taxon using very low dissolved oxygen contents (<5 µmol/l) of the pore waters to perform optimal metabolic activity.

3. Facultative anaerobic metabolism

Some foraminifera can survive under episodic anoxia and even in sulphide rich pore waters (e.g. Bernhard and Reimers, 1991; Moodley et Hess, 1992; Bernhard, 1993; Sen Gupta and Machain-Castillo, 1993; Alve, 1994). An unpublished experimental study with material collected at our station A in the Bay of Biscay shows that *Globobulimina* individuals are able to survive simulated anoxic conditions for at least 10 days, but can not survive prolonged period (>5 months). Therefore, *Globobulimina* may exploit alternative anaerobic metabolic pathways to survive short periods of total oxygen depletion in its microhabitat.

According to Bernhard et Reimers (1991), foraminifera sampled in deep anoxic sediments from oxygen depleted environments in the Santa Barbara basin are not able to use pore water or bottom water dissolved oxygen for respiration since their pseudopodial web can not reach aerated sediments. They may use an alternative oxidative pathway with an

anaerobic respiration without oxygen, but with another electron acceptor. Nitrate is commonly used by facultative anaerobic ciliates (Finley et al., 1983; Finlay, 1985). The presence of abundant mitochondria in ciliates capable of nitrate respiration has been suggested as a compensation for the decreased efficiency of nitrate respiration compared to aerobic respiration (Finlay et al., 1983). Thus, as far as pore water nitrates are not totally used by nitrate-reducing bacteria, the mitochondria in foraminiferal cells could play a fundamental role in nitrate respiration processes in anoxic sediments. *Globobulimina* may opt for such an anaerobic nitrate respiration, which could permit this taxon to inhabit a very narrow sediment layer where oxygen is absent and nitrate is still present. At our stations, this zone corresponds with the top of anoxic sediment, several mm below the zero oxygen boundary (Jorissen et al., 1998; Fontanier et al., 2002; 2003a; 2003c). If such a nitrate reducing strategy exists, a remaining question is why *Globobulimina* does not thrive in the basal part of the oxic sediment layer where nitrate is present in high concentrations. Would high dissolved oxygen concentrations be lethal, toxic, or adverse for *Globobulimina*? This looks quite improbable, since *Globobulimina* juveniles are sometimes found in oxic shallow infaunal niches. A possible explanation would be the fact that *Globobulimina* can not bear substantial predation or competition for food and space with the oxyphylic taxa in the more superficial sediment (Fontanier et al., 2002).

Fermentative glycolysis is another anaerobic pathway that has been localized in the peroxisomes of certain protozoans (van den Bosch et al., 1992). It consists of the transformation of glucose to pyruvate and lactate and provides ATP. As suggested by Bernhard (1993; 1996), fermentation would be sufficient to supply energy to active or "dormant" facultative anaerobic organisms. Anaerobic glycolysis does not require oxygen as exogeneous electron acceptor; it does not require any exogeneous electron acceptor at all. The abundance of peroxisomes in foraminifera from anoxic and dysoxic environments could suggest the importance of this pathway in their metabolism (Nyholm and Nyholm, 1975; Bernhard and Reimers, 1991; Bernhard and Alve, 1996; Bernhard, 1996; Bernhard et al., 2001). Glycogen is the primary storage substrate used in anaerobic metabolism (Hochachka and Somero, 1984). Glycogen synthesis is often associated with smooth endoplasmic reticles and peroxisomes (Nyholm and Nyholm, 1975). According to Bernhard and Reimers (1991), facultative anaerobic foraminifera (*Nonionella stella*) could use glycogen when anoxic conditions prevail, until dissolved O_2 returns. If true, benthic foraminifera may switch from fermentation to mitochondrial respiration in function of the environmental conditions. Numerous peroxisomes were observed in *Globobulimina* individuals collected in a 906 m

deep cold seep site (Bernhard et al., 2001). It suggests that fermentative glycolysis may be used by deep infaunal *Globobulimina* as a strategy to resist to temporary anoxia.

Potential sources of organic carbon

1. Labile organic matter

1a. Phytodetritus

Phytodetritus is surely the best-described source of organic carbon for deep-sea benthic foraminifera. Phytodetritus is well known to constitute ephemeral and labile organic compounds directly usable by most opportunistic shallow infaunal or epifaunal foraminifera (e.g. Gooday, 1988, Kitazato et al., 2000). Phytodetritus deposits result from seasonal vertical or lateral rapid advection of phytoplankton aggregates falling from surface or sub-surface waters to the sea floor. Goldstein and Corliss (1994), who worked on food selectivity of some foraminiferal species, noted that *Globobulimina pacifica* does not obviously ingest phytodetritus such as diatoms but would prefer to phagocytize complete sediments parcels. At our stations, it is improbable that labile organic compounds such as phytodetritus can be introduced into the deep oxygen depleted microhabitats where *Globobulimina* adults generally thrive. According ^{210}Pb and ^{234}Th data (Chaillou et al., 2002), the superficial bioturbation zones at stations B, A and I are less than 2 cm deep. This suggests that the burial of freshly deposited organic matter is limited to shallow infaunal niches. Ernst and Van der Zwaan (2003) simulated in a series of mesocosms the effects of the arrival of an organic matter pulse at the seafloor. This was achieved by the addition of a mix of heat-killed algae and diatoms, offered directly at the surface of the sediment collected at our station B in the Bay of Biscay. The mesocosms were harvested after three weeks, and no siginificant change in the average living depth of *Globobulimina* was observed in comparison to the unfed replicates, although some adult specimens were found at shallower depth in comparison with the control situations. The size-fraction smaller than 63 μm did not contain *Globobulimina* individuals at all. These results seem to confirm that *Globobulimina* does not migrate upward in the sediment in order to utilize fresh organic matter. They also suggest that *Globobulimina* is dependent on more altered food sources, although the experimental period was perhaps too short and a response to labile organic mater input would only be seen after a longer period of time. However, it can also be envisaged that enhanced bioturbation during eutrophic periods

may cause a more efficient burial of labile compounds to deep infaunal microhabitats where *Globobulimina* adults commonly live. This is suggested by in situ feeding experiments in Sagami Bay where deep infauna *Globobulimina* can ingest freshly deposited algal material in less than two days (Kitazato et al., 2003).

1b. Bacterial food

According to Bernhard (1993; 1992), deep infaunal taxa living in anoxic sediment may benefit from the lack of predation and the abundant bacterial biomass as a food source. Bacteria without carboxysome were observed in digestive vacuoles of *Globocassidulina* cf. *G. biora* individuals collected in situ in anoxic sediments at 12.2 m water depth in Winter Quarter's Bay, McMurdo Sound (Bernhard, 1993). According to Goldstein and Corliss (1994), *Globobulimina* is a deposit-feeder that can ingest relatively large amounts of organic detritus found in the sediment. As a potential deep infaunal taxon, it would feed on bacterial biomass associated with aged organic detritus and would be less affected by fluxes of fresh phytodetritus. Jorissen et al. (1995; 1998) suggest that *Globobulimina* may prey on heterotrophic bacterial consortia involved in fundamental redox reactions or could feed on their break-up products. It may be the case at our stations where *Globobulimina* lives close to zero oxygen boundary where heterotrophic and chemotrophic bacterial consortia are concentrated. Denitrifying and metal-reducing bacteria as well as nitrifying and metal-oxidizing microbiota may serve as a primordial and rather constant food source for *Globobulimina* individuals.

2. Altered organic matter

According to many authors (e.g. Kitazato and Ohga, 1992; Kitazato and Ohga, 1995; Kitazato et al., 2000; Schmiedl et al., 2000; Kurbjeweit et al., 2000; Gooday et al., 2001), deep infaunal foraminifera, (e.g. *Globobulimina affinis*) presumably prefer to feed on older organic detritus buried in the deeper parts of the sediment. For example, Kitatzato and Ohga (1995) showed in culture experiments that *Globobulimina* individuals are slow in the assimilation of organic matter and prefer dried algae (*Chlorella*) to heat-killed algae. They would prefer altered organic matter instead of fresh organic detritus. However, in view of more recent observations showing a response to fresh organic matter (Kitazato et al., 2003), such a preference for low quality food seems improbable. We think that in most natural

ecosystems *Globobulimina* is precluded from more labile food particles by its lower competitive ability with in comparison to more competitive superficially living taxa.

3. Symbiosis

Chemolithotrophic bacteria use energetic sources like methane, hydrogene, ammonia or reduced iron in the deep sediment. They do not require organic substrates but fix inorganic carbon from pore waters and take advantage of energy by catalysing oxidation reactions (Singleton, 1999; Jørgensen, 2000). Bernhard and Reimers (1991) were the first to propose a symbiotic role for bacteria observed in deep-sea foraminifera from oxygen-depleted environment (*Nonionella stella*). One *Globocassidulina* cf. *G. biora* individual collected in situ in anoxic sediments from 12.2 m water depth from Winter Quarter's Bay, McMurdo Sound, presents in its organic lining a high density of bacteria (Bernhard, 1993). Those bacteria have carboxysome-like inclusions and could be endosymbiotic myxotrophic chemolithotrophic *Thiobacillus*-like bacteria that would be able to use carboxysomes to fix inorganic carbon and provide organic compounds and energy to their host. It would be a mutualistic association, since these "endo-symbiotic" bacteria could benefit from a stable microenvironment in the foraminiferal test. *Buliminella tenuata* has numerous intact and dividing rod-shaped bacteria within its cytoplasm, which could equally be endo-symbiotic bacteria (Bernhard, 1996, Bernhard et al., 2000). More recently, Bernhard (2003) has shown multiple symbiosis in *Virgulinella fragilis*, benthic foraminifera of oxygen-depleted and sulfide enriched bathyal environments from Cariaco Basin (Venezuela). This taxon host intact chloroplasts but also rod-shaped sulfide oxidizing bacterial symbionts that may use a part of the available oxygen and detoxify the foraminiferal microbiotope from sulfidic components. The other part of the oxygen is probably sequestered in mitochondria for oxidative phosphorylation. As suggested by studies about symbiotic associations between chemolithotrophic bacteria and macrofaunal benthic organisms, the translocation of organic compounds synthetised by bacterial guests from bacteria to the inner tissues of the host may be a fundamental process to provide organic carbon to heterotrophic organisms. Bacterial symbionts may also detoxify the microbiotope inhabited by their foraminiferal host.

In our study areas, *Globobulimina* may present endosymbiotic chemolithotrophic bacteria that could grow in redox gradients situated in hypoxic and anoxic sediments. Fontanier et al. (2003c) suggest that dense populations of deep infaunal *Globobulimina* at canyon station "I" could host iron-oxidative bacteria that are putatively associated with the

precipitation of iron oxihydroxide in the anoxic sediments. *Globobulimina* could gain carbon by translocation processes from bacterial guests to its own protoplasm. Bacterial synthesis could be a carbon source disconnected from seasonal and annual exported organic matter flux from surface waters.

No metabolic pathway

In the adverse conditions of deep anoxic or suboxic infaunal niches, deep infaunal *Globobulimina* spp may become dormant; they would stop their development and strongly reduce their metabolic activity. Dormancy, which is defined as a seasonally recurring period in the life of an organism during which growth, development, reproduction and biomineralization are suppressed, and/or the ability to encyst may be alternative physiological adaptations allowing the survival of foraminifera during episodic anoxia and reducing conditions (Bernhard and Reimers, 1991; Bernhard, 1993). Bernhard (1992) and Bernhard and Alve (1996) showed that specimens living in oxygen-depleted or anoxic sediment had lower ATP concentrations, which could be indicative of a lower metabolism and dormant behaviour. Hannah and Rogerson (1997) explained that foraminifera buried in an anoxic layer become dormant and suggested that such specimens would require a passive transport (via bioturbation) to return to aerated conditions.

However, lower metabolism is not systematically recorded in species from oxygen-depleted environments. Some individuals present relatively high ATP concentration even after prolonged experimental exposition to anoxia (Moodley and Hess, 1992; Bernhard, 1993). Gooday et al. (2001) showed *Globobulimina* individuals in cysts in shallow and putatively oxic sediment whereas most of non-cysted *Globobulimina* spread in the deeper part of the sediment. The development of cysts could serve to create a chemical microhabitat similar to that occurring deeper in the sediment column.

No ATP analysis were performed on *Globobulimina* individuals from our study area and no encystment was observed for our deep infaunal *Globobulimina* individuals. Thus, in our case it does not appear feasible that *Globobulimina* individuals reduce ATP production and become dormant, quiescent or shift to a diapause stage in the oxygen depleted microhabitats where they are commonly observed. A study of the pseudopodial activity and motility of *Globobulimina* spp. was attempted with specimens from our station B (Bay of Biscay). Some 30 individuals were selected that looked very vital (apertural cyst and presence of coloured cytoplasm). None of these specimens showed pseudopodial activity on the glass

surface of petridishes. *Globobulimina* spp. from our station A (Bay of Biscay) were observed and studied in detail to distinguish between living and dead specimens. Specimens that appeared to be living (i.e., transparent test, violet to black cytoplasm, small sediment cyst around the aperture) were placed on a very thin layer of sediment. After some days, a number of trails on the sediment were observed, resulting from moving *Globobulimina* individuals. *Globobulimina* seems to display a very low motile activity, but which could be sufficient to migrate towards favourable habitats when necessary. Finally, systematic occurrence of mature *Globobulimina* spp. (>150 μm) in the suboxic and anoxic sediment of our stations from the Bay of Biscay would suggest that *Globobulimina* accomplishes the final period of its growth and the related biomineralisation in the deep sediment close to zero-oxygen boundary. No live *Globobulimina* adults were ever recorded in shallow infaunal niches. Also the $\delta^{13}C$ signatures of *Globobulimina* tests suggest a strong microhabitat effect related to biocalcification processes in deeper sediments. Calcification requires metabolic energy, which excludes any permanent dormancy stage in the deep dysoxic, suboxic and anoxic sediment.

Synthesis and paleoceanographic implications

In both our study areas as well as in other places of the world ocean, the genus *Globobulimina* appears like an eurybathial taxon, which occurs from shelf to abyssal environments. Although *Globobulimina* spp. thrive in upper slope and shelf environments where the exported organic matter flux is high and related bottom water oxygen depletion may be prominent (e.g. Mackensen and Douglas, 1989; Silva et al., 1996; Gooday et al., 2000), high densities of *Globobulimina* are also recorded in well-oxygenated environments (e.g. Corliss and Emerson, 1990, Corliss, 1990, McCorkle et al., 1997; Gooday et al., 2001) (Table 5; Fig. 6). Moreover, *Globobulimina* can dominate live foraminiferal faunas from well-oxygenated and organic enriched canyon environments (e.g. Jorissen et al., 1994; Schmiedl et al., 2000). This is the case in the Bay of Biscay where *Globobulimina* dominates live foraminiferal faunas from a well-oxygenated 3000 m deep station from the Cap Ferret Canyon, which actually acts as a depocenter for reworked organic compounds. Therefore, although our literature review suggests that water oxygen depletion can be an important controlling parameter that may cause very high densities of *Globobulimina* spp., elevated exported organic matter fluxes from the surface waters and from lateral sources are also necessary and may be sufficient to entertain important standing stocks of *Globobulimina.*

This means that the genus *Globobulimina* appears also as typical of rather "high productivity" foraminiferal assemblages (with *U. peregrina* and *M. barleeanus*) from mesotrophic upper slope environments (Fontanier et al., 2002; 2003a).

As shown in both our study areas, *Globobulimina* tolerates dysoxic and anoxic conditions prevailing in deep infaunal microhabitats in well-oxygenated environments (e.g. Corliss, 1991; Jorissen et al., 1998, Fontanier et al., 2002). It is also adapted to thrive in superficial sediments that are seasonally or permanently oxygen depleted (e.g. Mackensen and Douglas, 1989; Silva et al., 1996; Gooday et al., 2000). As suggested by Gooday (1986), by experimental observations (Geslin et al., 2002; Ernst and Van der Zwaan, 2003) and by our data from the Bay of Biscay and from off Cape Blanc, the microhabitat of *Globobulimina* is strongly related to geochemical gradients within the sediment, and more especially to the zero oxygen boundary. In such a microenvironment, competition for food and space and predation are presumably limited, which favours the presence and dominance of the highly specialized *Globobulimina*. *Globobulimina* may be aerobic microaerophilic or facultative anaerobic and probably uses small amounts of free oxygen or other oxy-anions (nitrate + nitrite) as electron acceptors to perform its metabolic activities (calcification and growth). It may feed on various sources of organic carbon. This may be either altered organic matter slowly conversed by bacterial activity, bacterial biomass, or freshly deposited phytodetritus. We suggest that *Globobulimina* exhibits high standing stocks and relative frequencies in environments where its microhabitat (around and below the zero oxygen boundary) corresponds to sediment layers that are preferentially enriched in more or less degraded organic matter compounds. This is the case in shallow sediments from the oxygen minimum zone, in canyon environments where important quantity of reworked organic matter concentrates as well as in well oxygenated upper slope and shelf environments where a high exported organic matter flux and enhanced bioturbation induce a rather efficient burial of organic components into dysoxic and anoxic sediments. As detritus feeders and/or bacteriovores, and thanks to the presence of bacterial biomass and/or more or less altered phytodetritus in its microhabitat, *Globobulimina* individuals would find the fundamental food sources it needs to perform its metabolic activities (e.g. growth and reproduction). Biotic parameters such as increased competition and predation pressure by meiofaunal and macrofaunal organisms in superficial sediments would severely limit the success of *Globobulimina* in superficial niches, even if the previously conditions are effective (zero oxygen boundary in organic matter enriched sediment). When also bottom waters are oxygen depleted, however, *Globobulimina* may live close to the sediment-water interface as a response to the disappearance of all less resistant taxa. Such a

low oxygenation at the sediment-water interface will specifically exclude oxyphilic opportunistic taxa, which commonly thrive when labile organic compound are available in shallower niches.

In terms of population dynamics, *Globobulimina* does not present the opportunistic behaviour of shallow infaunal taxa such as *Epistominella exigua,* which can invade phytodetritus floccules during bloom events. *Globobulimina* has a rather long life cycle (>1 year) and can probably feed on various organic substrates it collects around the zero oxygen boundary. However, when labile organic matter becomes available in their deep infaunal microhabitat, *Globobulimina* may accelerate its growth and/or reproduce. At our station B, *Globobulimina* juveniles may migrate upward to surfacial sediment layers after bloom events in purpose to benefit from organic matter remains or bacterial biomass. In shallow infaunal niches, *Globobulimina* spp. juveniles would find high quality food, which normally is not available in a deep infaunal microhabitat and which could be fundamental for their early life stages.

For paleo-oceanographic reconstitutions, it is commonly accepted that *Globobulimina* is a good marker of oxygen-depleted environments in a high productivity context (e.g. Mullineaux and Lohmann, 1981; Ross and Kennett, 1984; Bass et al., 1998). In view of the available data on living faunas, this interpretation appears like an oversimplification. We consider *Globobulimina* as a good marker of organic matter enriched sedimentary paleo-environments, such as high productivity open slope environments and canyon environments subject to focusing of refractory organic matter. Since *Globobulimina* may also dominate live foraminiferal faunas and fossil assemblages from well-oxygenated environments, the genus can not be exclusively considered as a good proxy of oxygen-depleted paleo-environments. As suggested by our isotopic measurements in the Bay of Biscay, the use of $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. could be a relevant proxy to reconstruct the relative interest of the main pathways (aerobic and anaerobic) of organic matter degradation in surface sediments. Because *Globobulimina* biomineralises its test with a constant and small offset related to calcite in equilibrium with $\delta^{18}O_{e.c.}$, it can be useful as an additional species allowing the refinement of $\delta^{18}O$ isotopic frameworks used in paleoceanographic studies.

Further ecological and ultrastructural studies are necessary to define clearly the trophic and symbiotic relationships between our two *Globobulimina* species and bacteria involved in redox reactions. Furthermore, complementary calibrations between the characteristics of

Globobulimina faunas and abiotic environmental parameters are necessary to better define the potential use of *Globobulimina* in paleoceanographic studies.

Acknowledgements

We would like to thank the French national program PROOF (INSU-CNRS) for sponsoring the OXYBENT program in the Bay of Biscay. We have special and kind thoughts for the crews and the captains of the Côte de la Manche, our scientific ship during all campaigns in the Bay of Biscay. All participants of the Sedorqua I cruise are thanked for their help with sampling off Cape Blanc. We thank Günter Meyer and Katrin Blancke for their precious technical help to perform isotopic measurements in Bremerhaven (AWI).

CHAPITRE 6

Isotopes stables de l'oxygène et du carbone ($\delta^{18}O$, $\delta^{13}C$) des faunes vivantes de foraminifères benthiques dans le Golfe de Gascogne.

Stable oxygen and carbon isotopes ($\delta^{18}O$, $\delta^{13}C$) of live benthic foraminiferal faunas in the Bay of Biscay

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Résumé

Des mesures isotopiques de $\delta^{18}O$ et de $\delta^{13}C$ ont été réalisées sur six espèces de foraminifères benthiques (>150 μm) collectées le long d'un transect bathymétrique dans le Golfe de Gascogne. A nos cinq stations situées en bordure de plate-forme ou sur la pente, *Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea* occupent préférentiellement des niches endopéliques peu profondes. *Melonis barleeanus* occupe un microhabitat endopélique intermédiaire et *Globobulimina* spp. vit dans une niche endopélique profonde proche de la « limite oxygène zéro ». Tandis qu'*U. mediterranea* forme son test en équilibre avec le $\delta^{18}O$ des eaux de fond, les autres espèces de foraminifères biominéralisent leur test avec un décalage constant par rapport à la calcite formée à l'équilibre avec le $\delta^{18}O$ des eaux de fond, suivant un fractionnement dépendant de la température. Nous proposons des facteurs correctifs pour chacune des espèces étudiées, facteurs qui seront utiles pour construire, dans le cadre des études paléo-océanographiques, les courbes stratigraphiques isotopiques $\delta^{18}O$ basés sur les espèces. Les signatures $\delta^{13}C$ des espèces de foraminifères ne sont pas corrélées avec le $\delta^{13}C_{DIC}$ des eaux de fond, mais semblent principalement contrôlées par des effets de microhabitat. En outre, l'augmentation le long de la pente du $\delta^{13}C$ des espèces endopéliques superficielles reflète la diminution du flux exporté de carbone organique le long de notre transect bathymétrique, ainsi que les processus plus ou moins intenses de la diagenèse précoce dans le sédiment superficiel que ces espèces occupent. C'est particulièrement le cas d'*Uvigerina peregrina*. Les signatures $\delta^{13}C$ de *Globobulimina* spp. sont beaucoup moins dépendantes du flux exporté de matière organique. Nous suggérons que le $\Delta\delta^{13}C$ entre *U. peregrina* et *Globobulimina* spp. peut donner des éclaircissements sur les processus variés de la dégradation passée des détritus organiques dans le sédiment. D'une façon surprenante, à la station B (550 mètres de profondeur) où nous avons réalisé une étude saisonnière et inter-annuelle des faunes de foraminifères et où une eutrophisation périodique des niches superficielles a été démontrée, il n'y a pas de changements saisonniers notables du $\delta^{13}C$ des espèces de foraminifères endopéliques peu profonds, intermédiaires ou profonds. Nous proposons que le $\delta^{13}C$ des foraminifères appartenant à la fraction >150 μm résulte de processus de calcification plutôt longs (plusieurs semaines ou mois), ce qui limite l'impact d'un enrichissement éphémère en ^{12}C des niches endopéliques peu profondes lors de périodes eutrophes sur la chimie isotopique des individus adultes. Seuls les espèces fortement opportunistes, qui se reproduisent ou vivent

exclusivement lors des périodes de blooms, devraient montrer des signatures $\delta^{13}C$ particulièrement basses, indicatives de ces courtes périodes productives.

Mots-clés : Isotopes stables du carbone et de l'oxygène ; Foraminifères benthiques ; Microhabitat ; Saisonnalité ; Flux exporté de matière organique.

Abstract

Oxygen and carbon isotopic measurements were performed on six benthic foraminiferal taxa (>150 µm size fraction) collected along a bathymetric transect in the Bay of Biscay. At our 5 shelf and open slope stations, *Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea* preferentially occupy shallow infaunal niches. *Melonis barleeanus* occupies an intermediate infaunal microhabitat and *Globobulimina* spp. lives in a deep infaunal niche close to the zero oxygen boundary. Whereas *U. mediterranea* forms its test in equilibrium with bottom water $\delta^{18}O$, all other foraminiferal taxa biomineralise their tests with a constant offset to calcite formed in equilibrium with bottom water $\delta^{18}O$, following a temperature dependent fractionation. We propose correcting factors for the various taxa, which may be useful to build multispecies-based oxygen isotope stratigraphic records for paleoceanographic studies. The $\delta^{13}C$ signatures of foraminiferal taxa are not correlated to bottom water $\delta^{13}C_{DIC}$ and appear to be mainly controlled by microhabitat effects. The downslope increase of $\delta^{13}C$ values of shallow infaunal taxa reflects the decrease of exported organic carbon flux along our bathymetric transect and the more or less intense early diagenetic processes in the surficial sediment. This is especially the case for *U. peregrina*. The $\delta^{13}C$ signatures of deep infaunal *Globobulimina* spp. are much less dependent on the exported organic matter flux. We suggest that the $\Delta\delta^{13}C$ between *U. peregrina* and *Globobulimina* spp. can shed light on the various pathways of past degradation of organic detritus in the sediment. Surprisingly, at our 550 m deep station (station B) where we performed an inter-annual and seasonal survey of foraminiferal faunas, and where periodic eutrophication of surficial niches was demonstrated, there are no marked seasonal changes of the $\delta^{13}C$ of shallow, intermediate and deep infaunal foraminiferal taxa. We propose that $\delta^{13}C$ of all foraminiferal individuals belonging to the >150 µm fraction results from rather long-term calcification processes (several weeks or months), which limit the impact of ephemeral ^{12}C enrichment of shallow infaunal niches during eutrophic periods on the isotope chemistry

of adult individuals. Only highly opportunistic like taxa reproducing or exclusively living during bloom periods should exhibit a particularly low $\delta^{13}C$, indicative of these short productive periods.

Key words: Stable oxygen and carbon isotopes; Benthic foraminifera; Microhabitat; Seasonality; Exported organic matter flux.

Introduction

Knowledge about the stable isotope chemistry of benthic foraminiferal tests has been strongly improved by the last three decades of studies on live and dead foraminiferal faunas and their isotopic compositions (e.g. Shackleton and Opdyke, 1973; Shackleton, 1977; Woodruff et al., 1980; Grossman, 1984a, 1984b, Grossman, 1987; McCorkle et al., 1990; Mackensen et al., 1993; McCorkle et Keigwin, 1994; Rathburn et al., 1996; McCorkle et al., 1997; Rathburn et al., 2000; Mackensen et al., 2000). Paleoceanographic applications of stable oxygen and carbon isotopes in benthic foraminiferal carbonate tests are considerable. $\delta^{18}O$ isotopic signatures of many benthic foraminifera are considered to be in equilibrium with bottom water $\delta^{18}O$, or to have a constant offset (e.g. Shackleton and Opdyke, 1973; Shackleton, 1977). Therefore, by recording the $\delta^{18}O$ changes in ocean water masses, benthic foraminiferal oxygen isotopes provide a fundamental tool to reconstruct fluctuations in global ice volume during the Quaternary and to construct reliable time scales (Shackleton and Opdyke, 1973, Imbrie et al., 1992, see also review by Rohling et Cook, 1999).

Although carbon isotopes in foraminiferal carbonate shells are generally applied as proxies of paleoproductivity and water mass movements (e.g. Shackleton, 1977; Mackensen et al., 1993; McCorkle et al., 1997; Mackensen et al., 2000), the use of $\delta^{13}C$ isotopic signatures of benthic foraminifera for paleoceanographic studies is still debated. Carbon fractionation between bottom (and pore) waters and foraminiferal calcium carbonate is widely discussed since it has been shown that many benthic foraminiferal taxa do not calcify their test in equilibrium with bottom water. Several papers (e.g. Woodruff et al., 1980; Belanger et al., 1981; Grossman, 1984a,b, 1987; McCorkle et al., 1985; Zahn et al., 1986; McCorkle et al., 1990; Wefer and Berger, 1991; Loubere et al., 1995 McCorkle et al., 1997) show that the carbon isotope signature of infaunal benthic foraminifera is strongly influenced by ambient pore water $\delta^{13}C$. The profile of ambient pore water $\delta^{13}C$ shows a rapid isotopic depletion with

depth in the sediment, caused by the decomposition of sedimentary organic matter (Grossman, 1984a,b; McCorkle et al., 1985; Grossman, 1987). According to this so-called "microhabitat effect", foraminiferal taxa calcify preferentially in equilibrium with pore waters from the sediment interval in which they preferentially live. Only purely epifaunal taxa form their test in equilibrium with bottom water and thus provide a measure for the past isotopic composition of the bottom waters (e.g. Woodruff et al., 1980; Graham et al., 1981; Zahn et al., 1986; Grossman, 1987; Wefer and Berger, 1991). All available evidence shows that the interpretation of carbon isotopes in benthic foraminiferal tests in relation with the chemical properties of bottom and interstitial waters requires an exhaustive knowledge of the ecology of the investigated taxa (microhabitat, population dynamics, food preferences) (McCorkle et al., 1990; Mackensen et al., 1993; McCorkle and Keigwin, 1994; Rathburn et al., 1996; McCorkle et al., 1997; Mackensen et al., 2000; Rathburn et al., 2000). As suggested by Mackensen et al. (1993) and Corliss et al. (2001), the intermittency of the phytodetritus supply to the sediment-water interface has significant echoes in the $\delta^{13}C$ of benthic foraminifera living in superficial niches. Mackensen et al. (1993) proposed that the $\delta^{13}C$ of *Fontbotia wuellerstorfi* (= *Cibicides wuellerstorfi*), which is generally described as a epifaunal taxon, could respond to the seasonal input of organic matter at the sediment-water interface by a colonization of the phytodetritus deposits. It could form it test within this particular substrate with a very lighter $\delta^{13}C$ signature. Therefore, the $\delta^{13}C$ of *C. wuellerstorfi* could perhaps not really reflect bottom water $\delta^{13}C$. Such a putative linkage between the $\delta^{13}C$ of supposedly epifaunal taxon and intermittent organic carbon supplies has been termed the "Mackensen effect".

In this study, we concentrate on oxygen and carbon isotopes in tests of live benthic foraminifera collected in the Bay of Biscay. In a number of recent papers, we described ecological patterns of live foraminiferal faunas in this area. Fontanier et al. (2002) show that the density and composition of foraminiferal faunas along a bathymetric transect from shelf to mesobathyal environments are mainly controlled by the mean annual exported organic matter flux from the surface waters to the sea floor. Dissolved oxygen concentration and redox levels at and below the sediment water interface play a secondary role. These factors control the microhabitat of some intermediate and deep infaunal taxa (e.g. *Melonis barleeanus*, *Globobulimina affinis*). Furthermore, Fontanier et al. (2003a, 2003b) showed that phytodetritus deposits related to spring and autumn surface waters blooms induce seasonal changes of the composition and density of foraminiferal fauna at stations B (~550 m depth)

and A (~1000 m depth). Opportunistic foraminiferal taxa occupying shallow infaunal microhabitats exhibit marked density increases in eutrophic periods. This concerns especially *Epistominella exigua, Reophax guttiferus, Uvigerina peregrina, Uvigerina mediterranea* at station B and *Nuttallides pusillus*, *Uvigerina peregrina, Uvigerina mediterranea* at station A. Deeper in the sediment, intermediate and deep infaunal foraminiferal taxa (such as *Melonis barleeanus*, *Globobulimina* spp.) show minor seasonal changes, which can be explained by the much larger stability of their deep infaunal microhabitat. In the present paper, we will concentrate on the isotopic signatures of 6 benthic foraminiferal taxa (*Cibicidoides pachydermus*, *Hoeglundina elegans*, *Uvigerina mediterranea*, *Uvigerina peregrina*, *Melonis barleeanus*, *Globobulimina* spp.), along the bathymetric transect described by Fontanier et al. (2002) and we will compare their isotopic signatures with the the physico-chemical properties ($\delta^{18}C$, $\delta^{13}C$, temperature, exported organic matter flux and pore and bottom water oxygenation) of bottom and pore waters in the Bay of Biscay (Fig. 1; Table 1). The exported organic matter flux from the surface waters to the sea floor shows a significant gradient from high values in shallow environments (Station D, 140 m deep) to very low values in the deepest part of the basin (Station H, 1964 m deep) (Fontanier et al., 2002). The organic supply is supposed to play a major role on the $\delta^{13}C$ isotopic signature of Dissolved Inorganic Carbon of bottom and interstitial waters, and should provoke consistent downslope changes of the $\delta^{13}C$ isotopic signature of our taxa. We expect also to observe a significant increase of the $\delta^{18}O$ of our foraminiferal taxa with depth as a direct result of a temperature decrease. Next, thanks to 10 successive seasonal samplings at station B (550 m depth) between October 1997 and April 2000 (Fontanier et al., 2003a), we propose to appreciate carbon and oxygen isotope changes in benthic foraminiferal tests related to seasonal supplies of food at the sediment-water interface. Our seasonal investigation should give new insights into the isotopic signals of live benthic foraminiferal communities from deep-sea environments in relation to phytodetritus deposits.

Study area, material and methods

Hydrological settings

The water masses that fill the semi-enclosed basin of the Bay of Biscay are derived from a branch of the north Atlantic drift. The current velocity of the various water masses is

less than 10 cm s^{-1} (Tréguer et al., 1979). The surface waters that enter from the north, along the Irish shelf-break, leave the area near Cape Finisterre after only two years of slow transit. The surface water patterns are strongly tributary to the seasonal variations of the thermocline and mixed layer (Tréguer et al., 1979; Lampert, 2001), and of the riverine discharge (Lampert, 2001). Surface currents (velocity and directions) are widely influenced by local wind regimes (Boucher, 1985). The five open-slope stations of our study area are positioned between 140 m depth and 1993 m depth (Table 1).

Station	Depth (m)	Latitude	longitude	Sampling Date	Cruises	Cores	Temperature (°C)	Salinity (PSU)
D	140	43°41'93N	1°34'10W	Oct-97	1	1	12.5	35.50
B	~550	43°49'98N	2°23'04W	Oct-97 -- Apr-00	10	15*	11.0	35.60
A	1012	44°09'78N	2°20'27W	Oct-97	1	1	9.5	35.75
F	1264	44°17'10N	2°44'95W	Jan-98	1	1	8.0	35.50
H	1993	44°17'10N	2°44'95W	Oct-98	1	1	4.0	35.00

Station	Bottom water oxygenation (µmol/l)	Zero oxygen boundary (mm)	Jz (gC/m²/year)	Bottom water $\delta^{13}C_{DIC}$ (PDB)	Bottom water $\delta^{18}O$ (SMOW)	Bottom water $\delta^{18}Oe.c.$ (PDB)
D	220	8	31.4	1.20	0.66	1.47
B	205-221	17-26	9.3	1.08 +/- 0.01	0.72	1.90
A	196	18	5.6	0.89	0.81	2.36
F	211	63	4.6	0.93	0.66	2.58
H	263	60	3.2	1.09	0.35	3.30

Table 1 Main characteristics of the five stations in our study area. Temperature and salinity data come from Ogawa and Tauzin (1973), Durrieu de Madron et al. (1999) and CTD measurements performed during PROTAGO program (February 2003). Bottom water dissolved oxygen concentration was calculated 5 mm above sediment-water interface (Fontanier et al., 2002). Jz represents exported organic carbon flux calculated using a mean annual primary production value of 150 gC/m²/year and according to formula proposed by Berger et Wefer (1990) and improved by Herguera (1992). Bottom water $\delta^{18}O$ (=$\delta^{18}O_w$), Dissolved inorganic carbon $\delta^{13}C$ in bottom water (=$\delta^{13}C_{DIC}$) and $\delta^{18}O$ of calcite in equilibrium with bottom water (=$\delta^{18}O_{e.c.}$) are also presented (see material and methods section for details of calculation). The asterisk indicates that 5 duplicate cores that are available at station B (Fontanier et al., 2003a).

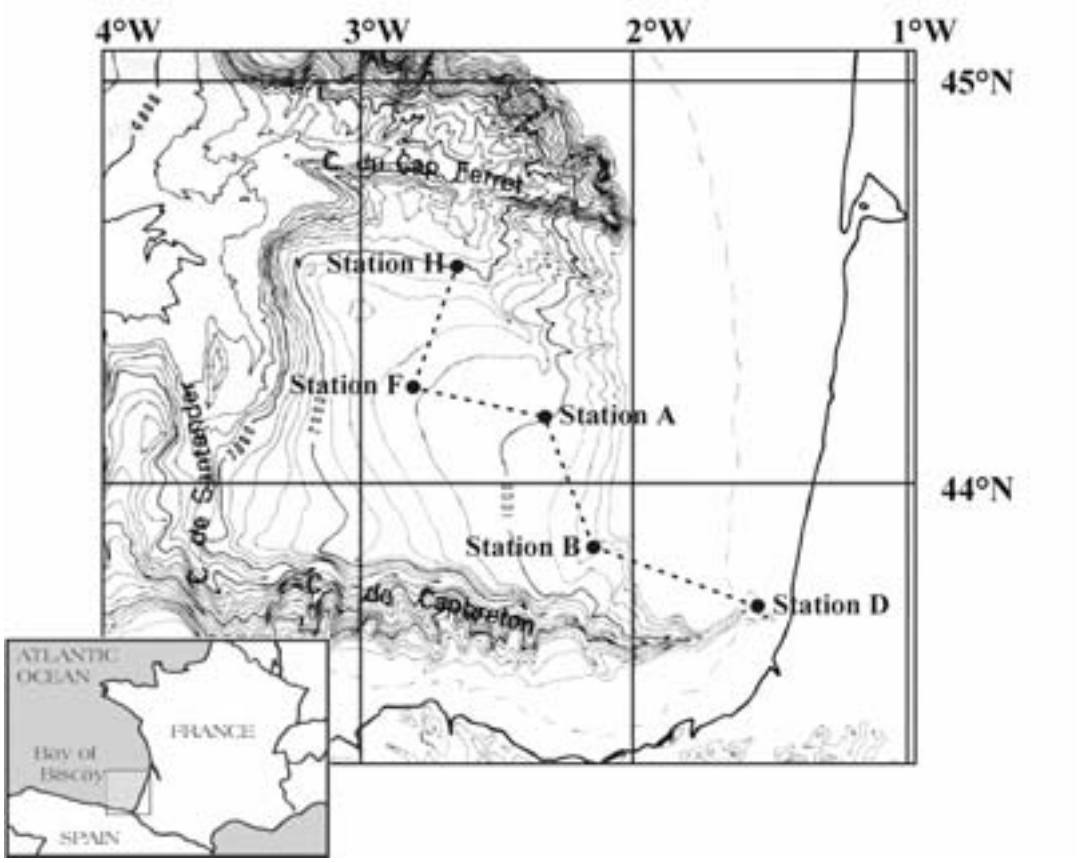


Fig. 1 Study area, bathymetry and geographical position of our 5 stations.

Station D (140 m depth) is situated at the boundary between surface waters (≤150 m depth) and the North Atlantic Central Water (Ogawa and Tauzin, 1973). According to CTD data performed in February 2003, temperature at 140 m depth is 12.5° C and salinity is close to 35.50 PSU. According to Fontanier et al. (2002), bottom water dissolved oxygen concentration measured in October 1997 is 220 µmol/l. Station B (550 m depth) settles in the Northern Atlantic Central Waters (NACW). As presented by Fontanier et al. (2002; 2003a), bottom water has a salinity of 35.60 PSU and a temperature of about 11.0° C. Bottom water dissolved oxygen concentration ranges from 205 to 221 µmol/l for the ten samplings performed between September 1997 and April 2000 (Fontanier et al., 2003a). Station A (1012 m deep) is in the Mediterranean Waters (MW) that spread between 800 and 1200 m depth in our study area (Ogawa and Tauzin, 1973). The Mediterranean Waters are generally characterized by a high salinity (between 35.80 and 35.85 PSU, Le Floch, 1968) and a minimum bottom water oxygenation value (3.8 ml/l, Le Floch, 1968). At station A, temperature is about 9.5° C and salinity is about 35.75 PSU (Durrieu de Madron et al., 1999). In October 1997, bottom water dissolved oxygen concentration was 196 µmol/l (Fontanier et al., 2002). Station F (1264 m deep) is positioned in transitional waters resulting from the

mixing between the MW and the upper layers Northern Atlantic Deep Waters (Ogawa and Tauzin, 1973). Data collected in the Cap-Ferret Canyon (close to our study area, Figure 1) suggest that the temperature at station F is about 8° C and salinity would be close to 35.50 PSU (Durrieu de Madron et al., 1999). The oxygen concentration measured in January 1998 is 211 µmol/l (Fontanier et al., 2002). Station H (1993 m deep) settles in the Northern Atlantic Deep Waters (NADW) (senso lato). NADW originate from the Labrador Sea and Norwegian Sea and have been described off Brittany, north of our study area (Vangrieshem, 1985). Although station H is geographically rather close to the Cap Ferret Canyon, it is an open slope environment with muddy sediments. Water temperature is about 4° C and salinity is close to 35.00 PSU. Bottom water oxygenation is 263 µmol/l in October 1998 (Fontanier et al., 2002).

Primary production

Primary production in the surface waters from the Bay of Biscay is dominated by an intense spring bloom (Tréguer et al, 1979, Laborde et al., 1999, Lampert, 2001). It starts at the end of boreal winter (March) and lasts for about two months until May (Laborde et al., 1999, Fontanier et al., 2003a). Diatoms are the dominant phytoplankton components of spring blooms (*Chaetoceros* spp. and *Nitzschia* spp.) (Tréguer et al., 1979). In summer, coccolithophorid blooms are associated to active up-welling cells at the French shelf-break (Fernandez et al., 1993; Antoine et al., 1996; Froidefond et al., 1996; Beaufort and Heussner, 1999). In autumn, a short fall bloom may occur, that is generally characterized by subsurface primary production maxima consisting of dinoflagellates (*Gonyaulax* spp.) and small amounts of diatoms (Tréguer et al., 1979; Sellmer et al., 1998).

Only very few quantitative data are available about the primary production in our study area. Tréguer et al. (1979) evaluate a production between 0.4 and 1.9 g C/m^2/day for the spring bloom of 1973 in the Bay of Biscay. Primary production measurements during the autumn of 1972 indicate a bloom with values of 0.3 - 0.4 g C/m^2/day (Le Corre and Tréguer, 1976). This range of Primary Production values agree with recent data obtained in the Cap Ferret region during five ECOFER campaigns: 0.7 - 1.2 g C/m^2/day in spring (May 1990 and 1991) and 0.3 g C/m^2/day in autumn (October 1990; Laborde et al., 1999). Total annual Primary Production in the Bay of Biscay has been estimated between 145 and 170 gC/m^2/yr (Laborde et al., 1999).

Material and methods

At each station of our study area, cores were collected with a classical Barnett multitube corer (Barnett, 1984). At station B, we used 15 cores collected between October 1997 and April 2000. Live foraminiferal faunas of all investigated cores have already been studied by Fontanier et al. (2002, 2003a, 2003c). Most cores were cut down to 10 cm depth for faunal analysis. Sampling and storage protocols are presented in Fontanier et al. (2002, 2003a). Foraminiferal faunas were stained with rose Bengal (Walton, 1952). Limitations of this coloration technique in our study area are more fully commented by Fontanier et al. (2002). In this study, we refer to bottom water and pore water oxygenation measurements performed after sampling and sample processing described in Chaillou et al. (2002)

Isotopic measurements were realized on individuals belonging to 6 dominant taxa of the >150 µm size fraction (*Cibicidoides pachydermus*, *Hoeglundina elegans*, *Uvigerina mediterranea*, *Uvigerina peregrina, Melonis barleeanus, Globobulimina* spp.). Only two isotopic analyses were successfully performed on benthic foraminifera belonging to the 63-150 µm size fraction. Table 2 presents the investigated material (numbers of specimens analyzed) and the results of the isotopic measurements. The stable isotopic composition of live (stained) benthic foraminifera was determined with a Finnigan MAT 251 isotope ratio gas mass spectrometer directly coupled to an automated carbonate prepararion device (Kiel I) and calibrated via NBS 19 to the PDB scale. All values are given in δ–notation versus VPDB (Vienna Pee Dee Belemnite). The overall precision of the measurements based on repeated analysis of a laboratory standard over a one-year-period was better than ±0.06 and ±0.08‰ for carbon and oxygen, respectively.

In order to get $\delta^{13}C$ of dissolved inorganic carbon in bottom water ($\delta^{13}C_{DIC}$), we used the same method as McCorkle et al. (1997). We used Kroopnick's equation linking apparent oxygen utilization (AOU) in bottom water to $\delta^{13}C_{DIC}$ (Kroopnick, 1985):

$$\delta^{13}C_{DIC} = 1.54 - 0.0074 \times AOU$$

AOU is defined as the difference between the saturation dissolved oxygen concentration in bottom water and the measured dissolved oxygen concentration (O_2(meas.)):

$$AOU = O_2(sat) - O_2(meas.)$$

For each core, we calculated AOU with bottom water oxygenation measured 5 mm above the sediment-water interface and O_2 (sat). $\delta^{13}C_{DIC}$ values are presented in Table 1. As described by McCorkle et al. (1997), $\delta^{18}O$ of calcite in equilibrium with bottom water for a given temperature T (°K) (= δ^{18}Oe.c.) can be calculated with the following equation:

$$\delta^{18}Oe.c.(SMOW) = \left(e^{((2.78\times10^3 / T^2)-(2.89/10^3))} \times \left(\delta^{18}Ow + 1000\right)\right) - 1000,$$

where δ^{18}Ow is the oxygen isotopic composition of bottom water on the SMOW scale. This equation is derived from the expression for the calcite-water fractionation factor determined by O'Neil et al. (1969), incorporating a revised estimate of the CO_2-water fractionation factor (1.0412 rather than 1.0407) as discussed by Friedman and O'Neil (1977). The SMOW-PDB conversion is calculated according the equation (Friedman and O'Neil, 1977):

$$\delta^{18}O(PDB) = \left(0.97006 \times \delta^{18}O(SMOW)\right) - 29.94$$

Bottom water δ^{18}Ow of the different water masses from our study area was calculated using a North Atlantic mixing equation (δ^{18}O/S) with a slope of 0.61 and a zero salinity water isotopic signature of -21‰ (Craig and Gordon, 1965). We suppose that Mediterranean Waters (MW) in our study area are strongly mixed with surrounding water masses (NACW and NADW). Therefore, as a first approximation, bottom water δ^{18}Ow at station A is calculated following the North Atlantic mixing equation.

Table 2 (see on two next pages) Isotopic measurements for all foraminiferal taxa studied in our study area (Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Melonis barleeanus and Globobulimina spp.). Numbers of individuals used for measurements are also presented. Asterisks indicate duplicate cores available at station B. Shaded boxes correspond to isotopic measurements performed on individuals belonging to 63-150 µm size fraction. Values between parentheses are related to isotopic measurements performed on doubtfully stained individuals that are not considered alive at the time of sampling, and which may have died several weeks to months before.

Taxa Depth in the sediment (cm)	Nbr of individuals	*Aboglundina elegans* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Cibicidoides pachyderma* $\delta^{13}C$	$\delta^{18}O$	Nbr of individuals	*Uvigerina mediterranea* $\delta^{13}C$	$\delta^{18}O$
Station D, October 1997									
0-0.25									
0.25-0.75									
1-2.5									
Station B, October 1997									
0-0.25				14	0.13	1.08	15	-0.60	1.91
0-0.50							30	-1.09	1.85
0.25-0.5									
1-1.5									
Station B, January 1998									
0-0.25				10	0.29	1.03	10	-0.57	1.75
0.5-0.75									
0.75-1									
1-1.5									
Station B, June 1998									
0-1				10	0.21	1.28	10	-0.48	1.79
1.5-1.75									
Station B, July 1998									
0-0.25				10	0.42	1.21	15	-0.46	1.97
0.5-0.75									
3-3.5									
Station B, October 1998									
0-0.25				9	0.38	1.31	10	-0.55	1.77
0.25-0.5				6	0.37	1.07			
1-1.5									
3-3.5									
Station B, December 1998									
0-0.25							12	-0.71	1.75
0-0.75									
0-1				5	0.23	0.90			
0.75-1							10	-0.51	1.74
1-1.5							10	-0.41	1.88
2-2.5									
4-5									
Station B, January 1999									
0-0.25				10	0.53	1.31	13	-0.63	2.00
1-1.5									
4-5									
Station B, April 1999									
0.25-0.5									
0.75-1							15	-0.48	2.05
0-2									
1-2									
Station B, April 1999'									
0.25-0.5							13	-0.54	1.94
0.25-0.75									
1-1.5				1	0.24	1.07			
1.5-2									
2-2.5									
Station B, June 1999									
0-0.25							14	-0.53	1.97
0-0.50				11	0.36	1.23			
0.25-0.5							15	-0.49	2.00
0.75-1							14	-0.49	2.11
1-1.5							14	-0.34	2.13
1.5-2							6	-0.40	1.93
2-2.5									
Station B, June 1999'									
0-0.25							15	-0.57	2.05
0-1				8	0.31	1.16			
0-1.5									
1-1.5									
1.5-2.5									
Station B, April 2000									
0-0.25							15	-0.56	1.93
0.25-0.5							17	-0.41	2.00
0.5-0.75							14	-0.49	2.03
0.75-1							15	-0.57	1.99
1-1.5							15	-0.43	2.00
1.5-2							15	-0.40	2.10
2-2.5							11	-0.59	1.92
Station B, April 2000'									
0-0.25							16	-0.43	1.94
0-0.50				8	0.18	1.33			
1-1.5									
1-2.5									
Station A, October 1997									
0-0.25							6	-0.08	2.07
0-0.75				6	0.56	1.28			
0.25-0.5							12	-0.17	1.93
0.5-0.75							10	-0.09	2.17
0.5-1									
0.75-1	10	1.77	2.57				10	-0.25	2.07
1-1.5	7	1.78	2.49						
1.5-2									
5.5-6.5									
Station F, January 1998									
0-0.25									
0.5-0.75	6	1.79	2.69						
4-5									
Station H, October 1998									
0-0.25	12	1.89	3.48						
0.25-0.5	14	1.73	3.48						
0.5-0.75	15	1.90	3.66						
5-7									

Taxa Depth in the sediment (cm)	Nbr of individuals	Uvigerina peregrina $\delta^{13}C$	 $\delta^{18}O$	Nbr of individuals	Melonis barleeanus $\delta^{13}C$	 $\delta^{18}O$	Nbr of individuals	Globobulimina affinis $\delta^{13}C$	 $\delta^{18}O$
Station D, October 1997									
0-0.25	15	-1.78	1.66						
0.35-0.75							3	-2.26	1.83
1-2.5							6	-2.06	1.83
Station B, October 1997									
0-0.25	20	-1.51	1.65						
0-0.50	30	-1.69	1.72	10*	-1.44	1.32			
0.25-0.5				15	-1.35	1.28			
1-1.5							15	-1.52	1.98
Station B, January 1998									
0-0.25									
0.5-0.75	10	-1.38	1.74						
0.75-1							9	-1.39	1.24
1-1.5				12	-1.39	1.24			
Station B, June 1998									
0-1	12	-1.15	1.63	12	-1.71	1.12			
1.5-1.75							11	-1.68	1.84
Station B, July 1998									
0-0.25	10	-1.20	1.55						
0.5-0.75				3	-1.36	0.90			
3-3.5							6	-1.78	1.99
Station B, October 1998									
0-0.25	6	-1.41	1.22						
0.25-0.5	10	-1.35	1.31						
1-1.5				16	-1.54	1.26			
3-3.5							4	-1.49	1.94
Station B, December 1998									
0-0.25									
0-0.75	10	-1.18	1.81						
0-1									
0.75-1									
1-1.5	10	-1.08	1.75						
2-2.5				10	-1.58	1.08			
4-5							10	-1.40	2.06
Station B, January 1999									
0-0.25	9	-1.32	1.59						
1-1.5				10	-1.53	1.26			
4-5							16	-1.53	1.92
Station B, April 1999									
0.25-0.5				5	-1.61	1.26			
0.75-1									
0-2	12	-1.11	1.75						
1-2							12	-1.61	2.14
Station B, April 1999'									
0.25-0.5									
0.25-0.75	11	-1.24	1.84						
1-1.5									
1.5-2				15	-1.48	1.31			
2-2.5							13	-1.37	2.14
Station B, June 1999									
0-0.25									
0-0.50	12	-1.05	1.83						
0.25-0.5									
0.75-1									
1-1.5									
1.5-2									
2-2.5							14	-1.54	2.11
Station B, June 1999'									
0-0.25									
0-1									
0-1.5	10	-1.30	1.77						
1-1.5				14	-1.54	1.32			
1.5-2.5							11	-1.49	2.00
Station B, April 2000									
0-0.25	18	-1.24	1.78						
0.25-0.5									
0.5-0.75									
0.75-1									
1-1.5									
1.5-2				15	-1.65	1.33			
2-2.5							12	-1.49	2.09
Station B, April 2000'									
0-0.25	13	-1.19	1.78						
0-0.50									
1-1.5				15	-1.67	1.42			
1-2.5							10	-1.69	2.07
Station A, October 1997									
0-0.25									
0-0.75									
0.25-0.5									
0.5-0.75									
0.5-1	18	-0.83	1.89						
0.75-1									
1-1.5	15	-0.93	1.98						
1.5-2	13	-0.86	1.87						
5.5-6.5							20	-1.16	2.23
Station F, January 1998									
0-0.25	10	-0.58	2.24						
0.5-0.75	14	-0.63	2.18						
4-5							(4)	(-1.32)	(2.97)
Station H, October 1998									
0-0.25									
0.25-0.5	15	-0.63	3.03						
0.5-0.75									
6-7							5	-2.28	3.43

Results

$\delta^{18}O$ and $\delta^{13}O$ of oceanic bottom waters: relation to environmental parameters

Between 140 and 1993 m depth, theorical bottom water $\delta^{18}O_{e.c.}$ (PDB) increases by 1.83‰ (Table 1); the $\delta^{18}O_{e.c.}$ ranges from +1.47 to +3.30‰. This gradient in $\delta^{18}O_{e.c.}$ corresponds to a temperature decrease of 8.5°C and thus, to about -0.22‰ $°C^{-1}$. $\delta^{13}C_{DIC}$ (PDB) ranges from +0.89 to +1.20‰ with the lower value recorded at station A (1000 m deep) for the Mediterranean Waters and the heavier value recorded at station D (140 m deep) for the Northern Central Atlantic Waters (Table 1).

$\delta^{18}O$ signatures of foraminiferal taxa along the bathymetric transect

For foraminiferal taxa for which isotopic measurements were performed at least in two stations along our bathymetric transect, we can observe a systematical trend of $\delta^{18}O$ increase with depth (Fig. 2). *Hoeglundina elegans* presents the heaviest $\delta^{18}O$ isotopic signature of all our taxa (Table 2, Fig. 2). Its signature is systematically higher than theoretical $\delta^{18}O_{e.c.}$ with a roughly constant shift of about +0.17‰ ($\Delta\delta^{18}O = \delta^{18}O_{H.\ elegans} - \delta^{18}O_{e.c}$). From 140 to 1993 m depth, *Globobulimina* spp. and *Uvigerina peregrina* $\delta^{18}O$ increase respectively by 1.60‰ and 1.37‰. *Globobulimina* spp. $\delta^{18}O$ values are very close to $\delta^{18}O_{e.c.}$ (except at station D). The average offset between its signature and equilibrium calcite ($\Delta\delta^{18}O$) is only +0.10‰. The $\delta^{18}O$ of *U. peregrina* is lower than $\delta^{18}O_{e.c.}$ with a mean offset of –0.23‰. Rather surprisingly, at station D, the $\delta^{18}O$ both of *Globobulimina* spp. and *U. peregrina* are higher than $\delta^{18}O_{e.c.}$. *Uvigerina mediterranea* presents an isotopic signature close to calcite at equilibrium with bottom water. *Melonis barleeanus* and *Cibicidoides pachydermus* have the lowest isotopic values of all species with respective offsets of about -0.55‰ and -0.91‰ compared to $\delta^{18}O_{e.c.}$.

Seasonal changes of the $\delta^{18}O$ signatures of foraminiferal taxa at station B

Seasonal changes of $\delta^{18}O$ signatures of *C. pachydermus*, *U. mediterranea*, *U. peregrina*, *M. barleeanus* and *Globobulimina spp.* at station B are depicted in Figure 3. There

is no obvious seasonal change of $\delta^{18}O$. When compared to a putatively constant $\delta^{18}O_{e.c.}$ at station B (1.90‰), we observe that *Globobulimina* spp. and *U. mediterranea* signatures are close to $\delta^{18}O_{e.c.}$. *Globobulimina* spp presents $\delta^{18}O$ signatures slightly heavier than calcite at equilibrium (average offset of about 0.11 ±0.03‰) whereas the average offset between *U. mediterranea* $\delta^{18}O$ and $\delta^{18}O_{e.c.}$ is almost zero. *U. peregrina, M. barleeanus* and *C. pachydermus* have isotopic signature lower than $\delta^{18}O_{e.c.}$ with respective offsets of bout –0.24 ±0.05‰, -0.69 ±0.04‰ and –0.74 ±0.04‰.

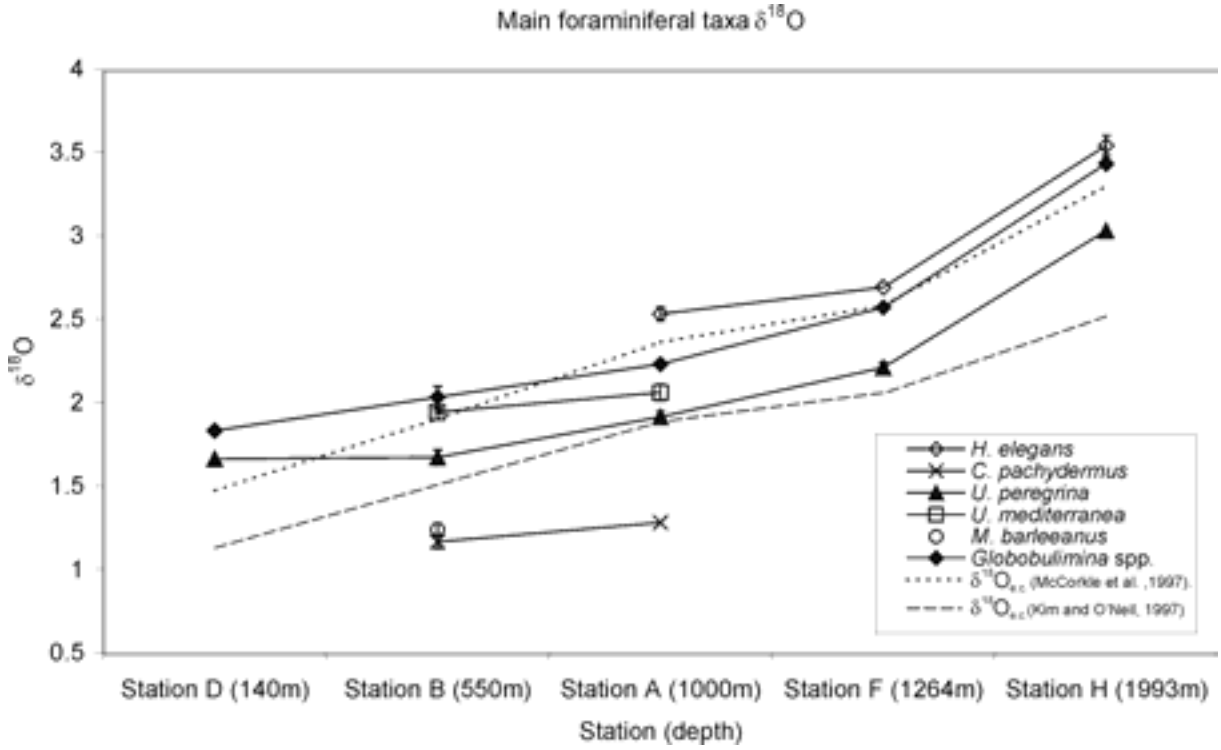


Fig. 2 $\delta^{18}O$ isotopic signatures of main foraminiferal taxa (Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Melonis barleeanus and Globobulimina spp.) along our 5 stations bathymetric transect. The dotted line represents the $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) calculated with the method of McCorkle et al. (1997). The dashed line represents the $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) calculated with the method of Kim and O'Neil (1997) (see in discussion). Vertical bars represent standard errors calculated when several isotopic measurements are available for the same station.

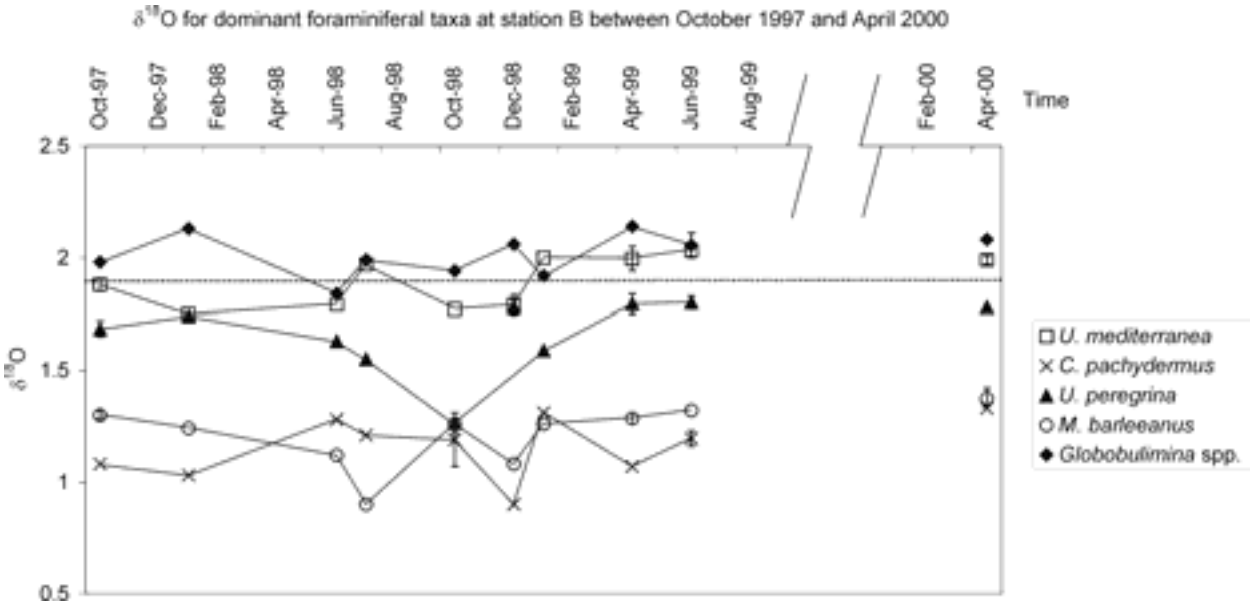


Fig. 3 Seasonal changes of the $\delta^{18}O$ for the main foraminiferal taxa (Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Melonis barleeanus and Globobulimina spp.) at station B (~550 m depth). Vertical bars represent standard errors calculated when duplicate cores and/or several isotopic measurements are available for the same sampling date. The dotted line represents the $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) calculated with method of McCorkle et al. (1997).

$\delta^{13}C$ signatures of foraminiferal taxa along the bathymetric transect

H. elegans, C. pachydermus, U. mediterreanea and U. peregrina present a $\delta^{13}C$, which shows an increasing tendancy with depth (Fig. 4). *H. elegans* has an isotopic signature ranging from 1.77 to 1.84‰. The $\delta^{13}C$ of *C. pachydermus* and *U. mediterreanea* range respectively from +0.30 to +0.56‰ and from –0.53 to –0.15‰ between 550 and 1000 m depth. Along the complete bathymetric transect, the signature of *U. peregrina* decreases from –1.78 to about -0.62‰. Only *Globobulimina* spp. exhibits a different trend. Its isotopic signature increases from -2.16 to -1.16‰ between 140 and 1000 m depth and then decreases again progressively to –2.28‰ down to 1993 m. For most taxa there is no constant offset between their $\delta^{13}C$ isotopic signature and the theoretical bottom water $\delta^{13}C_{DIC.}$ Only the isotopic difference between the isotopic signature of *H. elegans* and $\delta^{13}C_{DIC}$ is more or less constant with an average value of +0.83‰ (±0.04‰). Between 550 and 1000 m depth, $\Delta\delta^{13}C$ between *C. pachydermus* and bottom water $\delta^{13}C_{DIC}$ and between *U. mediterranea* and bottom

water $\delta^{13}C_{DIC}$ decrease significantly. This is roughly the same for $\Delta\delta^{13}C$ between *U. peregrina* and bottom water $\delta^{13}C_{DIC}$ along the total bathymetric transect. For *Globobulimina* spp., $\Delta\delta^{13}C$ ($\Delta\delta^{13}C = \delta^{13}C_{Globobulimiona\ spp.} - \delta^{13}C_{DIC}$) is about –3.36‰ at stations D and H and is minimum at station A (-2.05‰).

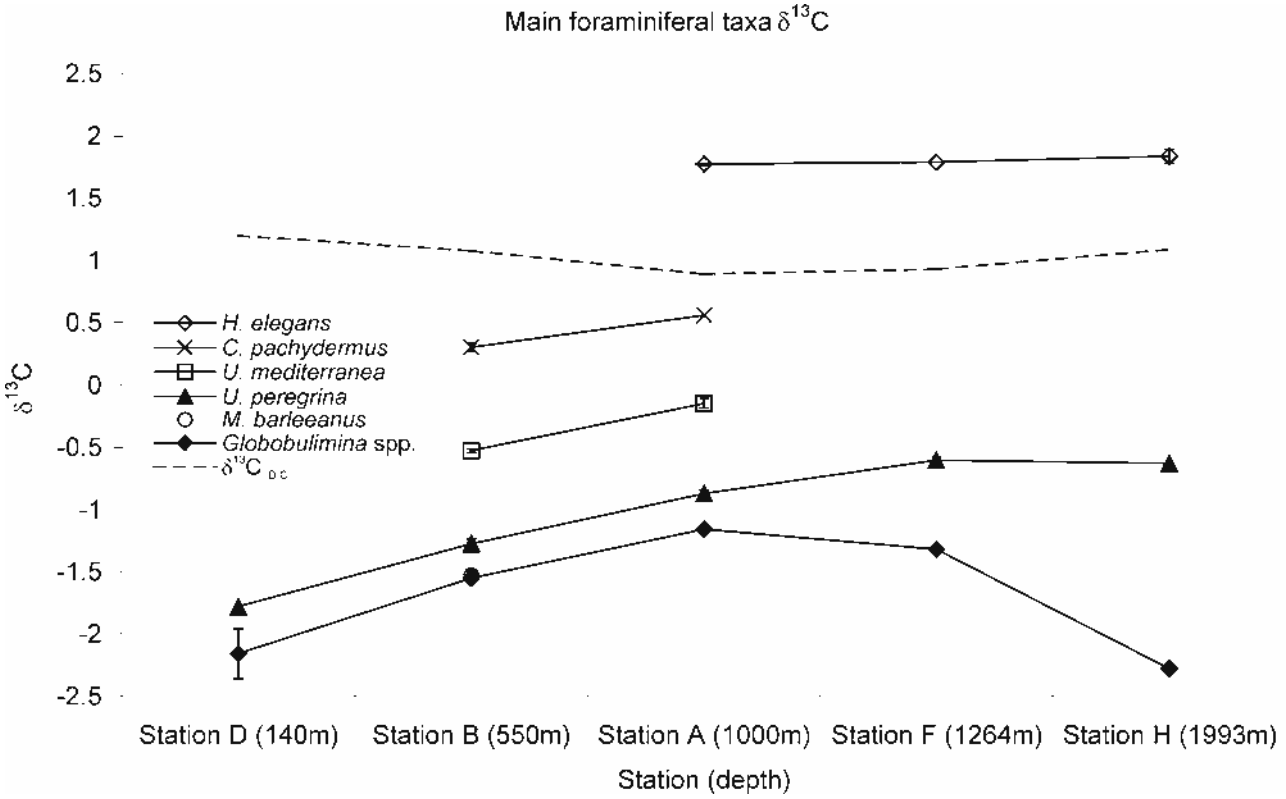


Fig. 4 $\delta^{13}C$ isotopic signatures of the main foraminiferal taxa (Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Melonis barleeanus and Globobulimina spp.) along our 5 stations bathymetric transect. The dotted line represents the hypothetical $\delta^{13}C$ of dissolved inorganic carbon of bottom water. Vertical bars represent standard errors calculated when several isotopic measurements are available for the same station.

Seasonal changes of $\delta^{13}C$ signatures of foraminiferal taxa at station B

At station B, there is no marked $\delta^{13}C$ seasonal change for any of the foraminiferal taxa (Fig. 5). Shifts between foraminiferal isotopic signatures and $\delta^{13}C_{DIC}$ (= $\Delta\delta^{13}C$) are rather constant throughout the 2.5 years of study. Average $\Delta\delta^{13}C$ is lowest for *C. pachydermus* (-

0.79 ±0.04‰). Average $\Delta\delta^{13}C$ are –1.64 ±0.04‰ for *U. mediterranea,* –2.36 ±0.05‰, -2.61 ±0.04‰ and –2.64 ±0.04‰ for *U. peregrina*, *M. barleeanus* and *Globobulimina* spp.

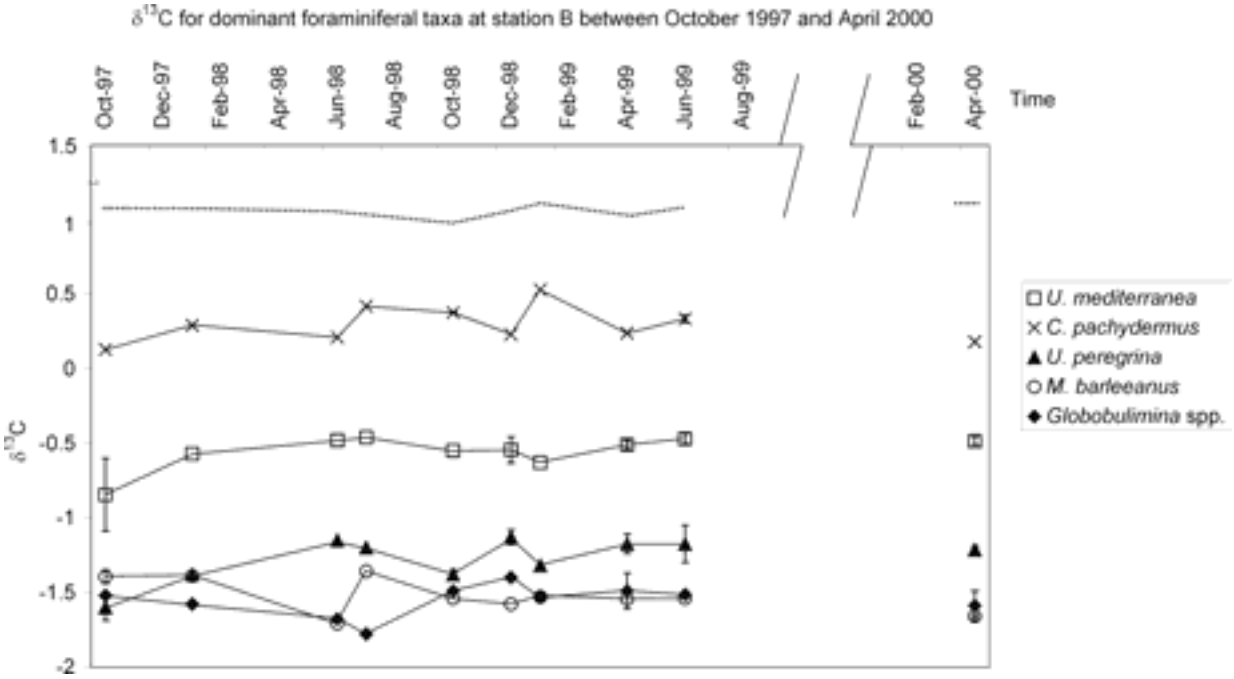


Fig. 5 Seasonal changes of the $\delta^{13}C$ for the main foraminiferal taxa (Hoeglundina elegans, Cibicidoides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Melonis barleeanus and Globobulimina spp.) at station B (~550 m depth). Vertical bars represent standard errors calculated when duplicate cores and several isotopic measurements are available for the same sampling date. Dotted line represents the hypothetical $\delta^{13}C$ of dissolved inorganic carbon of bottom water.

$\delta^{18}O$ and $\delta^{13}O$ changes in relation to vertical distribution of main foraminiferal taxa

Figures 6a-b show the foraminiferal isotopic signatures at stations A and B in relation to the sediment interval where the foraminiferal individuals have been sampled. Also the density profiles of foraminiferal taxa are presented in order to appreciate the foraminiferal vertical distribution in relation to the sediment-water interface and the zero oxygen boundary. The description of the foraminiferal microhabitat is more fully presented in Fontanier et al. (2002, 2003a). *C. pachydermus* and *H. elegans* live in very shallow infaunal and oxic microhabitats close to the sediment-water interface (Fig. 6a-b). *U. mediterranea* and *U. peregrina* occupy shallow infaunal niches. *Melonis barleeanus* lives in an intermediate

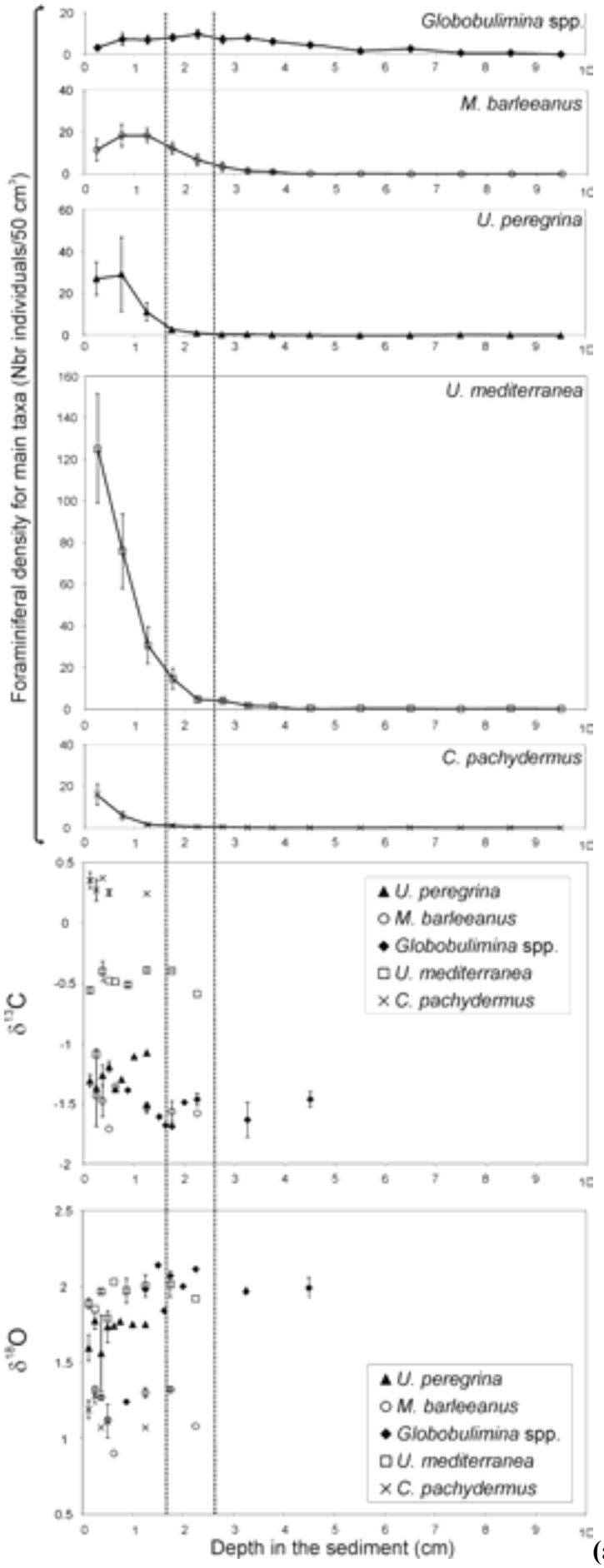
infaunal niche just above the zero oxygen boundary (Fig. 6a). *Globobulimina* spp. is a deep infaunal taxon that preferentially lives around and below the zero oxygen boundary (Fig. 6a-b). To sum up, Table 3 presents average living depth (ALD) for all taxa for the 5 stations of our bathymetric transect. Methods of calculation of ALD and results have been already described in Fontanier et al. (2002, 2003a).

At station B, where an important isotopic data set is available, none of the investigated taxa presents a significant change of $\delta^{18}O$ and $\delta^{13}C$ with depth in the sediment. For example, *U. mediterranea* shows surprisingly stable $\delta^{18}O$ and $\delta^{13}C$ values with depth (Fig. 6a). At station A, we can observe the same pattern, although isotopic measurement are less numerous than at station B. When we consider all stations, deep and intermediate infaunal taxa (*Globobulimina* spp. and *M. barleeanus*) exhibit systematically lower $\delta^{13}C$ signatures. Very shallow infaunal taxa (*H. elegans* and *C. pachydermus*) present the heaviest values. *U. mediterreanea* and *U. peregrina* have intermediate $\delta^{13}C$ values. There are no obvious changes in the $\delta^{18}O$ signature of foraminiferal taxa in relation to microhabitat preferences.

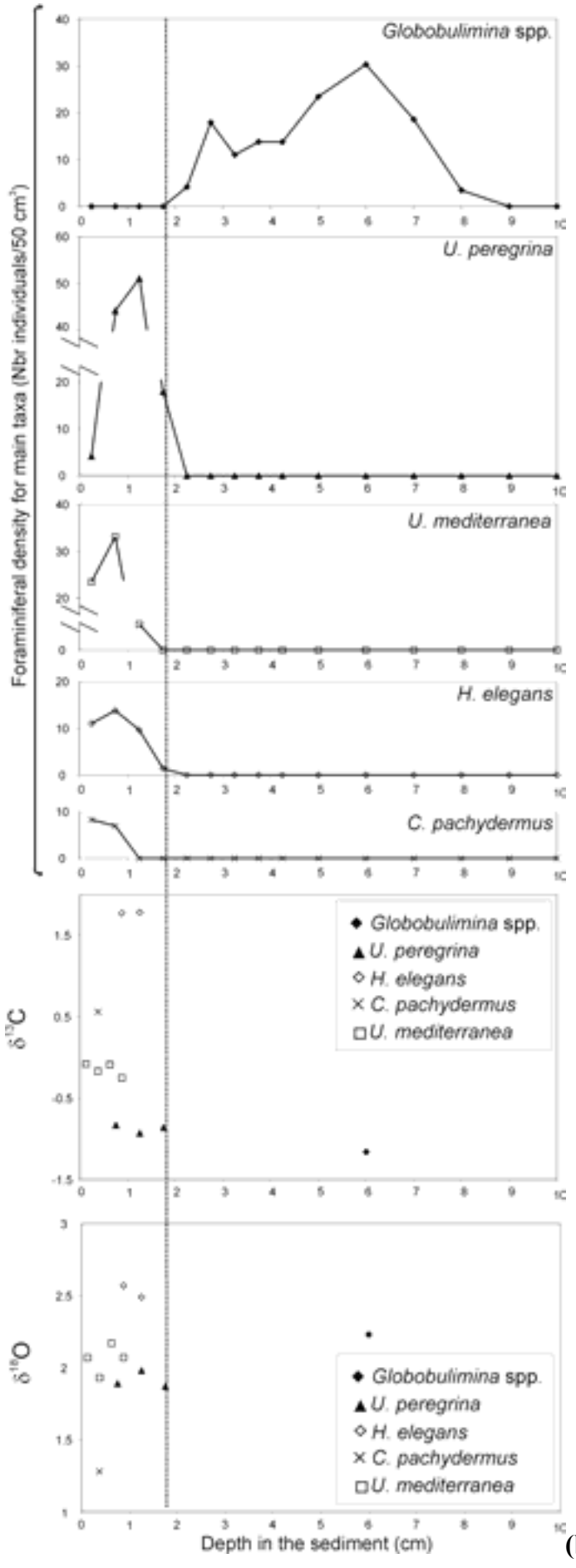
Taxa	Stations, ALD_{10}					Microhabitat
	Station D	Station B	Station A	Station F	Station H	
Cibicidoides pachydermus		0.5	0.4		1.4	SI
Globobulimina spp.	2.2	2.8	4.7		6.1	DI
Hoeglundina elegans			0.8	0.5	0.6	SI
Melonis barleeanus		1.3	1.7	1.4		II
Uvigerina mediterranea		0.8	0.6			SI
Uvigerina peregrina	0.4	0.8	1.1	0.9	0.7	SI/II
Oxygen penetration depth (cm)	0.8	1.7-2.6	2	6.4	6.3	

Table 3 Average Living Depth (ALD_{10}) calculated for all present foraminiferal taxa along the bathymetric transect. Values at station D, A, F and H are presented in Fontanier et al. (2002). At station B, ALD are average weighed values for 13 cores (Fontanier et al., 2003a).

Fig. 6; 6a $\delta^{13}C$ and $\delta^{18}O$ isotopic signatures for the main foraminiferal taxa at station B. Foraminiferal densities in the sediment are expressed as numbers of individuals per 50 cm^3 per sediment interval. 6b. Same, station A. The dotted line depicts the zero oxygen boundary in the sediment. For station B, All values for foraminiferal densities are the average of 12 cores. The two dotted lines indicating the zero oxygen boundary represent the minimum and maximum values observed during the 12 samplings. For isotopic values, vertical bars represent standard errors calculated when several isotopic measurements for the same depth interval are available.


Globobulimina spp.
M. barleeanus
U. peregrina
U. mediterranea
C. pachydermus
Foraminiferal density for main taxa (Nbr individuals/50 cm³)
δ¹³C
δ¹⁸O
▲ U. peregrina
○ M. barleeanus
◆ Globobulimina spp.
□ U. mediterranea
× C. pachydermus
Depth in the sediment (cm)

(a)


Globobulimina spp.
U. peregrina
U. mediterranea
H. elegans
C. pachydermus
Foraminiferal density for malin taxa (Nbr individuals/50 cm³)
δ13C
δ18O
Globobulimina spp.
U. peregrina
H. elegans
C. pachydermus
U. mediterranea
Depth in the sediment (cm)

(b)

Discussion

Foraminiferal $\delta^{18}O$ isotopic signatures

Intergeneric $\delta^{18}O$ variability along the bathymetric transect

Our results suggest that all calcitic benthic foraminiferal taxa investigated in this study (*Cibicidoides pachydermus*, *Uvigerina mediterreanea*, *Uvigerina peregrina*, *Melonis barleeanus* and *Globobulimina* spp.) biomineralise their test close to isotopic equilibrium with bottom waters, with a rather constant offset. This is very clear when we compare the $\delta^{18}O$ of *U. peregrina* and *Globobulimina* spp. with equilibrium calcite $\delta^{18}O$ ($\delta^{18}O_{e.c.}$) (Fig. 2). $\Delta\delta^{18}O$ is significantly constant with depth suggesting that both taxa calcify their test following a temperature dependant fractionation. However, it is also evident that significant shifts exist between isotopic signatures of all taxa. "Vital effects" may explain these rather constant differences (Urey et al., 1951). A vital effect, which is independent of environmental parameters, was already suggested by McCorkle et al. (1990; 1997) to explain the significant shift of the $\delta^{18}O$ of *Cibicidoides pachyderma* (= *C. pachydermus*) and *Melonis barleeanum* (= *M. barleeanus*) in comparison to bottom water $\delta^{18}O_{e.c.}$.

In figure 7, we present the average $\Delta\delta^{18}O$ between the $\delta^{18}O$ of each taxon and bottom water $\delta^{18}O_{e.c.}$ in our study area. The $\delta^{18}O$ of *U. mediterranea* is closest to perfect equilibrium calcite $\delta^{18}O$. As demonstrated by McCorkle et al. (1990; 1997), the $\delta^{18}O$ of *Globobulimina* spp. is slightly higher than bottom water $\delta^{18}O_{e.c.}$ with an average $\Delta\delta^{18}O$ of +0.08‰. *C. pachydermus* presents the lightest isotopic signature with a $\Delta\delta^{18}O$ of about –0.75‰ in comparison to bottom water. This shift is equal to the $\Delta\delta^{18}O$ average value determined by McCorkle et al. (1997). *M. barleeanus* presents a significant shift of about -0.65‰, which is close to the value of about –0.50‰ measured by McCorkle et al. (1990). *U. peregrina* presents a shift of about –0.25‰, which is close to the value of –0.30‰ determined by Rathburn et al. (1996) and in the range of $\Delta\delta^{18}O$ determined by McCorkle et al. (1990) (between -0.15 and –0.25‰).

As demonstrated by Rathburn et al. (1996), who performed isotopic measurements on live benthic foraminifera from Sulu and South China Seas, the different microhabitat preferences of foraminiferal taxa from our study area do not have an impact on stable oxygen isotopes in foraminiferal carbonate. This is in agreement with the assumption that pore water

and bottom water present the same $\delta^{18}O$ isotopic signal. However, it is noticeable that significant differences exist between species belonging to the same genus. This is the case between *U. mediterranea* and *U. peregrina* for which we note an average shift of about 0.25‰. This difference can not be explained by a putative microhabitat effect since both taxa occupy roughly the same sediment depth interval. Therefore, they must be due to "vital effects". Our data confirm the suggestion of Woodruff et al. (1980) that the use of *Uvigerina* spp. for oxygen isotope stratigraphic framework and paleoceanographic studies without any precise identification at the species-level is irrelevant and can induce significant errors. In Table 4, we propose correction factors that may be used to correct isotopic data from our foraminiferal taxa in comparison to *U. mediterranea*, which constructs its tests in equilibrium with bottom water $\delta^{18}O$.

Complications about the $\delta^{18}O$ of calcite in equilibrium with bottom water

In this paper, our calculations of $\delta^{18}O$ of calcite in equilibrium with bottom water are based on the method used by McCorkle et al. (1997). We decided to use another method of calculation of δ^{18}Oe.c., which is described by Kim and O'Neil (1997), in order to make a simple comparison between both methods and also to precise the relevance of our interpretations. The equation of Kim and O'Neil (1997) is:

$$\delta^{18}Oe.c.(PDB) = (-0.2004 \times T) + (\delta^{18}O_w - 0.27),$$

where temperature (T) is expressed in Celsius degrees and $\delta^{18}O_w$ is the oxygen isotopic composition of bottom water on the SMOW scale. The conversion of $\delta^{18}O$ of calcite in equilibrium with bottom water to PDB scale in this equation is carried out by subtracting 0.27‰ (Hut, 1987).

Surprisingly, the δ^{18}Oe.c signatures calculated with the method of Kim and O'Neil (1997), are significantly lower than the values we calculated with the method of McCorkle et al. (1997). They range from 1.13 to 2.53‰ along our bathymetric transect (Fig. 2). By taking account of these values, the $\delta^{18}O$ of *Uvigerina peregrina* is slightly higher to the δ^{18}Oe.c signature whereas other taxa exhibit more significant offsets (Fig. 7). It is very difficult to assume our method gives more reliable δ^{18}Oe.c than the method of calculation of Kim and

O'Neil (1997). However, it seems more relevant to use the method of McCorkle et al. (1997) if we want to compare our results with their consistent data.

Moreover, the calculations of $\delta^{18}O$ of calcite in equilibrium with bottom are also widely dependent on accurate calculations of the bottom water $\delta^{18}O$ as well as on precise temperature measurements of bottom water. Different North Atlantic mixing equations ($\delta^{18}O/S$) exist to determine bottom water $\delta^{18}O$, what can generate marked difference of $\delta^{18}O_w$ calculation for a same water mass. Although we use a commonly used North Atlantic mixing equation, the uncertainty about our calculations of $\delta^{18}O$ of calcite in equilibrium with bottom could be significant.

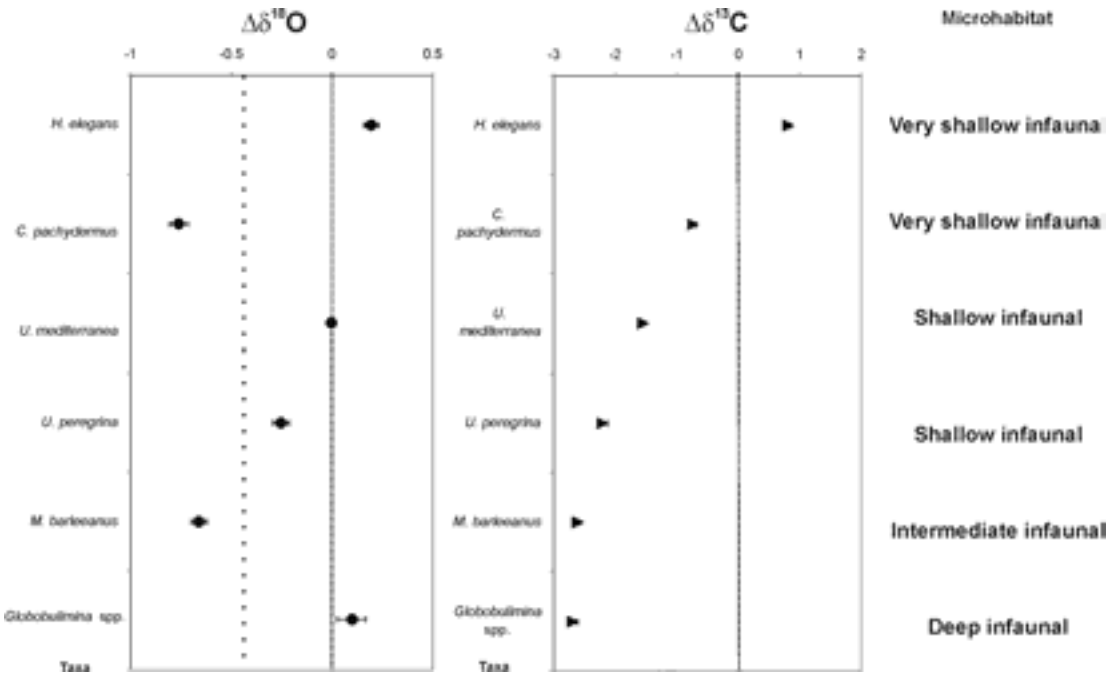


Fig. 7 $\Delta\delta^{18}O$ between foraminiferal taxa and $\delta^{18}O_{e.c.}$ ($\Delta\delta^{18}O = \delta^{18}O_{benthic\ foraminifera} - \delta^{18}O_{e.c.}$). $\Delta\delta^{13}C$ between foraminiferal taxa and $\delta^{13}C_{DIC}$ in our study area ($\Delta\delta^{13}C = \delta^{13}C_{benthic\ foraminifera} - \delta^{13}C_{DIC}$). The microhabitat description of the six foraminiferal taxa is added on the right side of the figure. See Fontanier et al. (2002; 2003a) for complementary explanation about foraminiferal microhabitat. Vertical bars represent standard errors calculated on the basis of all measurements performed on foraminiferal material in our study area. The $\delta^{18}O$ of calcite in equilibrium with bottom water ($\delta^{18}O_{e.c.}$) was calculated with the method of McCorkle et al. (1997). The dotted line represents the putative $\Delta\delta^{18}O$ between foraminiferal taxa and $\delta^{18}O_{e.c.}$ calculated with method of Kim and O'Neil (1997), which is equal to zero (see in discussion).

^{18}O between *Uvigerina mediterranea* and XXX	Correction factor
Hoeglundina elegans	-0.20
Cibicidoides pachydermus	0.76
Uvigerina peregrina	0.25
Melonis barleeanus	0.66
Globobulimina spp.	-0.09

Table 4 $\Delta\delta^{18}O$ between Uvigerina mediterranea and other dominant foraminiferal taxa in our study area. $\Delta\delta^{18}O$ values may be used as correcting factors for future paleoceanographic studies in order to construct, a complete and improve oxygen isotope stratigraphic frameworks.

Foraminiferal $\delta^{13}C$ isotopic signatures

Intergeneric $\delta^{13}C$ variability related to microhabitat

It is well known that pore water $\delta^{13}C_{DIC}$ within the sediment is not constant and varies from a value close to bottom water $\delta^{13}C_{DIC}$ at the sediment-water interface to much lighter values in the deeper sediments. Pore water $\delta^{13}C_{DIC}$ decreases downwards as a result of progressive degradation of organic matter buried in deeper sediments and the related release of ^{12}C by aerobic and anaerobic bacterial degradation. (e.g. Grossman, 1984a; Grossman, 1987; McCorkle et al., 1985; McCorkle and Emerson, 1988; Sackett, 1989; McCorkle et al., 1990). Unfortunately, we have no pore water $\delta^{13}C_{DIC}$ profiles for our cores. However, our results suggest that benthic foraminiferal $\delta^{13}C$ is closely related to pore water $\delta^{13}C_{DIC}$ and much less to bottom water $\delta^{13}C_{DIC}$. Therefore, $\delta^{13}C$ in foraminiferal carbonate shells seems directly affected by a "microhabitat effect" (e.g. Woodruff et al., 1980; Belanger et al., 1981; Grossman, 1987; McCorkle et al., 1990, Rathburn and Corliss, 1996; McCorkle et al., 1997). Microhabitat effects refer to carbonate precipitation in isotopically distinct growth environments. Because *C. pachydermus* and *U. mediterranea* live in shallow infaunal niches (Fontanier et al., 2002, 2003a), they both present heavy isotopic signatures close to bottom water $\delta^{13}C_{DIC}$ (Fig. 7). Heavier isotopic signatures for *C. pachyderma* (= *C. pachydermus*) relative to other shallow and deep infaunal species are also observed in cores from the Sulu

and China Seas by Rathburn et al. (1996). Identical observations were realized on foraminiferal faunas from the North Carolina continental margin where *C. pachyderma* presents a higher $\delta^{13}C$ than shallow infaunal *U. peregrina* and deep infaunal *M. barleeanum* and *Globobulimina* spp. (McCorkle et al., 1990 ; 1997). The $\delta^{13}C$ of *U. peregrina* is surprising since this taxon presents a relatively light $\delta^{13}C$ signature despite its shallow infaunal microhabitat close to *U. mediterranea* (Table 3). Three phenomena can explain this offset in comparison to *U. mediterranea*. On the one hand, *U. peregrina* may occupy microhabitat slightly deeper than that of *U. mediterranea* (Fontanier et al., 2002). However, our recent data do not confirm this idea but rather show an identical microhabitat for both taxa (Fontanier et al., 2003a). Despite the rather similar microhabitat, it is possible that *U. peregrina* calcifies deeper in the sediment than *U. mediterranea.* On the other hand, *U. peregrina* may biomineralise a large part of its test in eutrophic periods when its shallow infaunal niche is temporarily enriched in ^{12}C by the rapid degradation of phytodetritus in a shallow bioturbation zone. *U. peregrina* is indeed commonly described as an opportunistic taxon that would preferentially reproduce and show rapid growth during eutrophic periods (spring and autumn bloom) (Fontanier et al., 2003a, 2003c). Finally, it is also feasible that complex vital effects influence the $\delta^{13}C$ signature of *U. peregrina* just as it is commonly described for other species (e.g. Rathburn et al., 1996). *M. barleeanus* and *Globobulimina* spp., which generally occupy deeper infaunal microhabitats, close to the zero oxygen boundary (Fontanier et al. 2002; 2003a), have generally the lowest $\delta^{13}C$ of all our data set (Fig. 7). Very low $\delta^{13}C$ for deep infaunal *Globobulimina* species have observed in numerous other studies (e.g. Grossman, 1984a; Grossman, 1987). Our results underline the importance of microhabitat effects on both taxa.

At stations A and B, where we have a relavant data set, all investigated species present rather constant $\delta^{13}C$ values throughout the depth interval in the sediment where they are found (Fig. 6a-b). As suggested by Rathburn et al. (1996), it is conceivable that each taxon will "record" pore water $\delta^{13}C_{DIC}$ of a rather narrow sediment layer where it performs the major part of its metabolic activity and related calcification. However, it can also be envisaged that the final isotopic signal is a composite of the life history of the individual and presents an average value of much wider depth interval in which the foraminifera lives and calcifies.

Intergeneric $\delta^{13}C$ variability along the bathymetric transect

Our study suggests that the $\delta^{13}C$ of most superficially living benthic foraminiferal taxa investigated along our bathymetric transect (*Cibicidoides pachydermus*, *Uvigerina mediterreanea* and *Uvigerina peregrina*) is directly controlled by the annually exported organic carbon flux from the surface waters. As already demonstrated by McCorkle et al. (1997), there is a clear relation between the $\Delta\delta^{13}C$ between *U. peregrina* and bottom water $\delta^{13}C_{DIC}$ to the exported organic carbon flux (Jz) along our bathymetric transect. A simple linear regression between the both variables shows a rather good correlation ($y = -0.0471x - 1.5609$, $r^2 = 0.8625$) (Fig. 8).

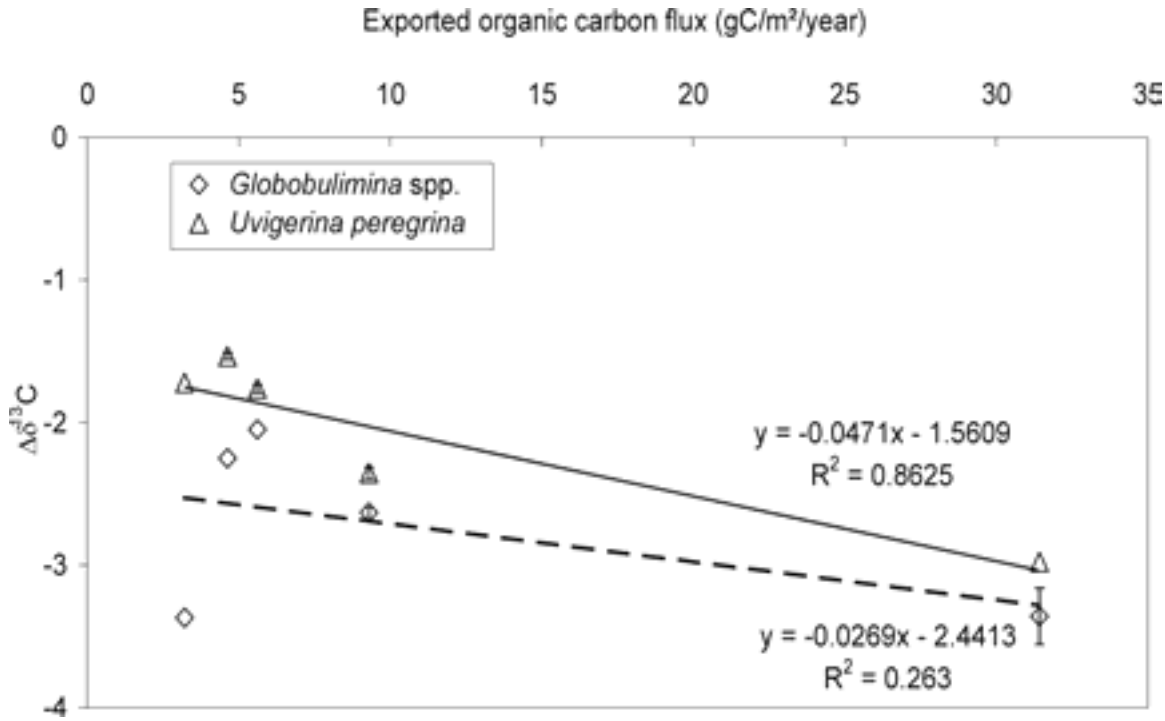


Fig. 8 $\Delta\delta^{13}C$ between the $\delta^{13}C$ of Uvigerina peregrina and the $\delta^{13}C_{DIC}$ bottom water versus exported organic carbon flux. $\Delta\delta^{13}C$ between the $\delta^{13}C$ of Globobulimina spp. and the $\delta^{13}C_{DIC}$ bottom water versus exported organic carbon flux. Vertical bars represent standard errors calculated when we have duplicate cores at the same station and several isotopic measurements for the same depth interval are available. Simple linear regressions were systematically performed. For each regression, the equation and the "r²" are presented.

Estimated exported organic carbon supplies along our bathymetric transect decrease with water depth causing a significant decrease of intensity of organic degradation on and within the topmost oxic sediments with water depth. This results in steep pore water $\delta^{13}C_{DIC}$ profiles

in shallow environments and much less marked $\delta^{13}C_{DIC}$ profiles in deeper and more oligotrophic settings (McCorkle et al., 1985; McCorkle and Emerson, 1988; Loubere et al., 1995; McCorkle et al., 1997). In other words, the organic carbon flux at the sediment-water interface plays a fundamental role controlling the shallow infaunal foraminiferal $\delta^{13}C$, since it may induce drastic $\delta^{13}C_{DIC}$ changes in the upper sediment layers of areas with a high labile organic matter input. On the contrary, the $\Delta\delta^{13}C$ between *Globobulimina* spp and bottom water $\delta^{13}C_{DIC}$ appears not to be correlated with Jz (Fig. 8).

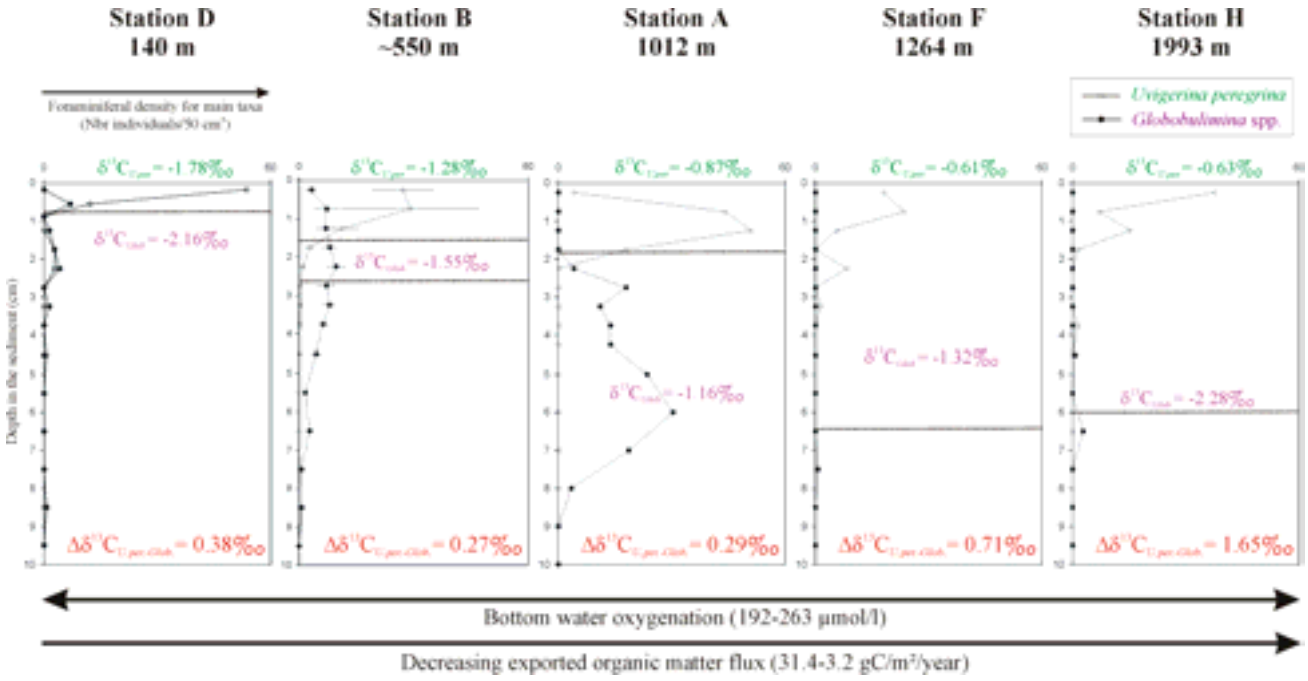


Fig. 9 Synthetic scheme showing the carbon isotopic signatures of Globobulimina spp. and Uvigerina peregrina along a bathymetric transect in the Bay of Biscay. Both foraminiferal taxa are supposed to record pore water $\delta^{13}C_{DIC}$ of the sediment interval where they preferentially live (microhabitat effect) (see text for further explanation). The vertical density profiles of Globobulimina spp. and Uvigerina peregrina are added. Foraminiferal densities are expressed in number of individuals per 50 cm³. The $\delta^{13}C$ of Uvigerina peregrina and Globobulimina spp. and the $\Delta\delta^{13}C$ between both taxa are presented for the 5 stations

Figure 9 shows the vertical distribution of *Uvigerina peregrina* and *Globobulimina* spp. in cores collected along our bathymetric transect, the average $\delta^{13}C$ signature of both taxa and the $\Delta\delta^{13}C$ between *Uvigerina peregrina* and *Globobulimina* spp. for each station. Both foraminiferal taxa are supposed to calcify their test in close equilibrium with pore water $\delta^{13}C$

of the sediment interval in which they preferentially live (assuming a dominant microhabitat effect). *U. peregrina* thrives in shallow infaunal niches in the first cm of sediment whereas *Globobulimina* spp. lives around and below the zero oxygen boundary (Fontanier et al. 2002) (Table 3, Fig. 4a-b). As previously explained, the $\delta^{13}C$ of *U. peregrina* decreases along our bathymetric transect as a direct result of the decrease of the exported organic matter flux with water depth. At station D, where the exported organic carbon input is much higher, $\delta^{13}C$ depletion is strong in the first cm as a direct result of the elevated release of ^{12}C-enriched CO_2 by aerobic degradation. Downslope, pore water $\delta^{13}C$ depletion in the first cm of sediment will become weaker as a result of the decreasing organic carbon flux. The decrease of organic matter remineralization in the oxic surficial sediments with water depth is probably accompanied by a relative increase (with respect to the oxic degradation at the sediment surface) of the anaerobic degradation of more refractory organic carbon deeper in the sediment. As a consequence, in these more oligotrophic areas, the $\delta^{13}C$ profile will be much less steep in the uppermost sediment. But since a major part of the scarce organic carbon is degraded in dysoxic and anoxic sediment layers, most ^{12}C will be released deeper in the sediment, where we will find a gradual $\delta^{13}C$ pore water shift over a much larger depth interval. Such a scenario can explain why the $\Delta\delta^{13}C$ between shallow infaunal *U. peregrina* and deep infaunal *Globobulimina* spp. is minimal in eutrophic areas, but shows an important increase towards oligotrophic areas. If true, this could mean that the $\Delta\delta^{13}C$ can give us information about the relative importance of aerobic and anaerobic degradation of organic matter.

Paleoceanographic applications

In view of the rather good correlation between $\Delta\delta^{13}C$ of some shallow infaunal foraminifera and the exported organic carbon flux at our well-oxygenated stations, it appears that isotopic chemistry of foraminiferal test can be useful to reconstruct paleoproductivity from surface waters on the basis of a past sedimentary record. The use of $\Delta\delta^{13}C$ between *U. peregrina* and a hypothetical strictly epifaunal taxon that would biomineralise its test in close equilibrium with bottom water $\delta^{13}C$ would surely be a very good proxy to appreciate the variation of exported organic carbon paleoflux ("paleo-Jz") at the sediment-water interface (McCorkle et al., 1997). *Cibicides wuellerstorfi*, which is considered in many papers as such a purely epifaunal taxon, is generally used as a relevant "paleo-recorder" of bottom water $\delta^{13}C$.

However, many papers show that *C. wuellerstorfi* is not exclusively living at the sediment surface, but spreads also in shallow infaunal microhabitats (e.g. Jorissen et al., 1998, Fontanier et al., 2003c). Next, if its $\delta^{13}C$ signature is indeed influenced by exported organic matter flux (Mackensen et al., 1993), *C. wuellerstorfi* should no longer be the ideal proxy of bottom water $\delta^{13}C$.

We think that the use of $\Delta\delta^{13}C$ between *Uvigerina peregrina* and *Globobulimina* spp. may be a relevant tool to shed light on the relative importance of aerobic and anaerobic remineralisation of organic matter in the top sediment. As far as we assume that most infaunal foraminifera calcify their test following microhabitat effects, the use of other taxa, such as intermediate infaunal and purely epifaunal species, could help to reconstruct paleo-profiles of pore water $\delta^{13}C_{DIC}$ in oxygenated sediment, and this to better understand the fate of organic carbon transported to the sea-floor in the past.

Seasonal changes of benthic foraminifera $\delta^{18}O$ and $\delta^{13}C$

Our seasonal study at station B confirms that benthic foraminifera biomineralise their test in close equilibrium with bottom water $\delta^{18}O$. For each taxon, $\delta^{18}O$ stays constant throughout the year, suggesting that bottom water values do not vary seasonally. More surprisingly, $\delta^{13}C$ signatures of foraminiferal taxa do not exhibit any seasonal changes. Mackensen et al. (1993) suggested that *Fontbotia wuellerstorfi* (=*Cibicides wuellerstorfi*) would respond to exported productivity changes at the sediment water interface. Similarly, Corliss et al. (2001) suggested that also the $\delta^{13}C$ of *H. elegans* reflects phytodetritus seasonal deposits in North Atlantic. Therefore, we would expect to observe a lower $\delta^{13}C$ in eutrophic periods for our opportunistic taxa living close to the sediment-water interface (like *U. peregrina* and *U. mediterranea*) as a direct result of a temporal ^{12}C enrichment of surficial niches. Samplings in October 1997, April 1999, June 1999 and April 2000 correspond to bloom events in surface waters (Fontanier et al., 2003a). High benthic foraminiferal standing stocks in shallow infaunal niches are generally recorded in cores collected at those sampling dates. If we assume that temporal ^{12}C enrichment of surficical niches is effective when phytodetritus is intensively degraded in shallow infaunal microhabitats, the absence of a clear response in adult individuals suggests that temporal ^{12}C enrichment will predominantly affect isotopic chemistry of newly recruited juveniles tests (*U. peregrina*, *U. mediterranea*) and of small opportunistic taxa (*Epistominella exigua*, *Nuttallides pusillus*), all belonging to the 63-

150 µm size fraction. At the moment, we performed only two isotopic measurements on juvenile foraminifera belonging to *U. mediterranea* and *U. peregrina* species (Table 2). It appears that the $\delta^{13}C$ of these juveniles picked in October 1997 at station B (-1.09‰ and –1.69‰) are markedly lower than adult $\delta^{13}C$ signatures, which would be in agreement with our previous opinion. We think that isotopic measurements performed on *U. peregrina* and *U. mediterranea* individuals belonging to the >150 µm fraction will reflect a long-term averaged calcification process that is not strongly based towards the eutrophic periods. It is evident that complementary isotopic measurements on individuals from the 63-150 µm are necessary to confirm these ideas and to better appreciate seasonal changes of the $\delta^{13}C$ of benthic foraminifera.

Hoeglundina elegans: an aragonitic taxon

Hoeglundina elegans is an aragonitic taxon, which is enriched in ^{18}O relative to calcite equilibrium values as well as other calcitic taxa by several tenths per mil (e.g. Sommer and Rye, 1978; Grossman, 1984a; Ganssen, 1983; Dunbar and Wefer, 1984; Grossman and Ku, 1986; Grossman, 1987; Rathburn et al., 1996). Grossman and Ku (1986) showed that the $\delta^{18}O_w$-corrected $\delta^{18}O$ values (PDB) for *H. elegans* (enrichment between *H. elegans* and *bottom water*) are dependent on temperature, describing a temperature dependency of the aragonite-water fractionation similar to that of the calcite-water fractionation. ^{18}O enrichment of *Hoeglundina elegans* relative to calcitic *Uvigerina peregrina* is rather constant and not temperature dependant. In our study area, this offset ranges from +0.48 to +0.61 at stations A, F and H without any trend to increase or decrease along our thermo-bathymetric transect. This is in agreement with enrichment values ranging from +0.4 to +0.6‰ between *H. elegans* related to *U. peregrina* calculated in previous studies (e.g. Grossman and Ku, 1986; McCorkle et al., 1990, Rathburn and Corliss, 1996). Thus, as already demonstrated by Grossman and Ku (1986), there is no significant temperature dependence in *Hoeglundina elegans-Uvigerina peregrina* ^{18}O fractionation precluding its use as a paleothermometer.

Surprisingly, there are no drastic changes of the $\delta^{13}C$ of *H. elegans* along our bathymetric transect. The values ranges from +1.77 to +1.84‰, from station A to station H. Moreover, ^{13}C enrichment of *Hoeglundina elegans* relative to dissolved inorganic carbon for station A, F and H ranges from 0.75 to 0.88 with a small relation with temperature decrease. We do not observe a 0.10‰ decrease per 1°C increase of temperature, which was suggested by Grossman and Ku (1986). Our results show a only 0.02‰ increase per 1°C increase of

temperature. The temperature range we investigated in our study area, from station A to H (~6°C), may be too small and the number of investigated samples is surely too low to appreciate the potential impact of temperature on bicarbonate-aragonite fractionation.

Acknowledgements

We would like to thank the French national program PROOF (INSU-CNRS) for sponsoring the OXYBENT and the FORAMPROX programs. We have special and kind thoughts for the crews and the captains of the Côte de la Manche, our scientific ship during all campaigns. We thank Günter Meyer and Katrin Blancke for their precious technical help to perform isotopic measurements in Bremerhaven (AWI).

SYNTHESE ET CONCLUSION

Rappel des objectifs initiaux de la thèse

Comme énumérés dans l'introduction, les objectifs de cette thèse intitulée « Ēcologie des foraminifères benthiques du Golfe de Gascogne : études de la variabilité spatiale et temporelle des faunes de foraminifères benthiques et de la composition isotopique ($\delta^{18}O$, $\delta^{13}C$) de leurs tests. » peuvent être déclinés en 5 grands points :

1. Ētudier la répartition bathymétrique des peuplements des foraminifères benthiques dans le Golfe de Gascogne en fonction du niveau trophique et du niveau d'oxygénation de diverses stations, en précisant notamment les facteurs limitants majeurs contrôlant la densité, la composition et les microhabitats des faunes de foraminifères benthiques, et en éprouvant le modèle TROX (Jorissen et al., 1995).
2. Préciser la dynamique saisonnière et inter-annuelle des communautés de foraminifères benthiques en réponse aux dépôts saisonniers de phytodétritus et des changements supputés de la diagenèse précoce.
3. Apprécier la structure des communautés de foraminifères benthiques dans les zones dépôts centres d'accumulation préférentielle de matière organique réfractaire telles que les environnements de canyon.
4. Appréhender les variations chimiques $\delta^{13}C$ et $\delta^{18}O$ du test d'espèces dominantes de foraminifères benthiques en fonction des paramètres environnementaux afin de calibrer des outils paléo-océanographiques.
5. Déterminer la justesse de l'utilisation de certaines taxa de foraminifères benthiques en tant qu'outils de reconstruction qualitative et quantitative de paramètres paléo-environnementaux (proxies).

Pour se faire, les 6 chapitres de ce travail ont permis de préciser les caractéristiques écologiques majeures des faunes de foraminifères benthiques de 7 stations de la marge continentale aquitaine du Golfe de Gascogne. Dans le synthèse qui suit, sont résumés les principales réponses apportées par cette thèse aux interrogations scientifiques précédemment décrites ainsi que les points d'interrogation non résolus et méritant, semble-t-il, des investigations poussées dans le futur. Une conclusion générale permet d'apprécier le(s) rôle(s) des foraminifères benthiques au sein de l'écosystème benthique profond, leur place dans la biocénose et les contraintes imposées par le biotope.

1. Distribution bathymétrique des faunes de foraminifères benthiques dans le Golfe de Gascogne

Densité et composition des peuplements de foraminifères benthiques: l'impact majeur du carbone organique exporté

L'étude des faunes de foraminifères benthiques le long du transect bathymétrique défini dans le chapitre 1 montre le rôle prépondérant que joue le flux de carbone organique, exporté depuis la production primaire des eaux de surface, sur la densité et la composition des faunes benthiques (Fontanier et al., 2002). Comme illustré dans de nombreux travaux, les flux élevés de carbone organique associés à des stations peu profondes (bordure et haut de pente) soutiennent des communautés benthiques denses alors que dans les parties plus profondes des bassins des flux moindres de carbone organique ne peuvent entretenir que des faunes de faible densité. Le niveau d'eutrophisation de l'écosystème benthique est largement tributaire de cette manne organique d'origine pélagique constituant une source de nourriture indispensable à l'immense majorité des foraminifères benthiques organohétérotrophes.

Dans notre zone d'étude, la composition des peuplements de foraminifères échantillonnés permet de réaliser la différentiation entre environnements benthiques eutrophes de la plateforme externe, environnements mésotrophes du haut de pente et environnements oligotrophes de milieu et bas de pente (Fig. 1). Alors que certaines espèces dites eutrophes n'apparaissent qu'à partir de certaines valeurs élevées de flux exporté, d'autres espèces plus oligotrophes marquent systématiquement des environnements moins pourvus en détritus phytodétritiques. Nos résultats montrent que *Uvigerina mediterranea* et *Uvigerina peregrina*, par exemple, espèces dominantes aux stations B et A (550 et 1000 m), sont des taxa ayant des exigences trophiques plus élevées que celles d'*Hoeglundina elegans* ou de *Gyroidina orbicularis* (espèces dominantes de la station H à 1993 m) (Fontanier et al., 2002). L'existence de limite de tolérance en terme d'apport en carbone organique pélagique a été démontrée d'une façon pertinente dans cette étude, ce qui confirme les données préliminaires de la Mer Méditerranée où la plupart des espèces de foraminifères benthiques se répartissent le long des pentes des divers bassins étudiés en suivant scrupuleusement des isoflux remarquables de carbone organique exporté, et cela indépendamment de la profondeur et des autres conditions physico-chimiques des masses d'eau associées (température, salinité et pression) (De Rijk et al., 1999; 2000).

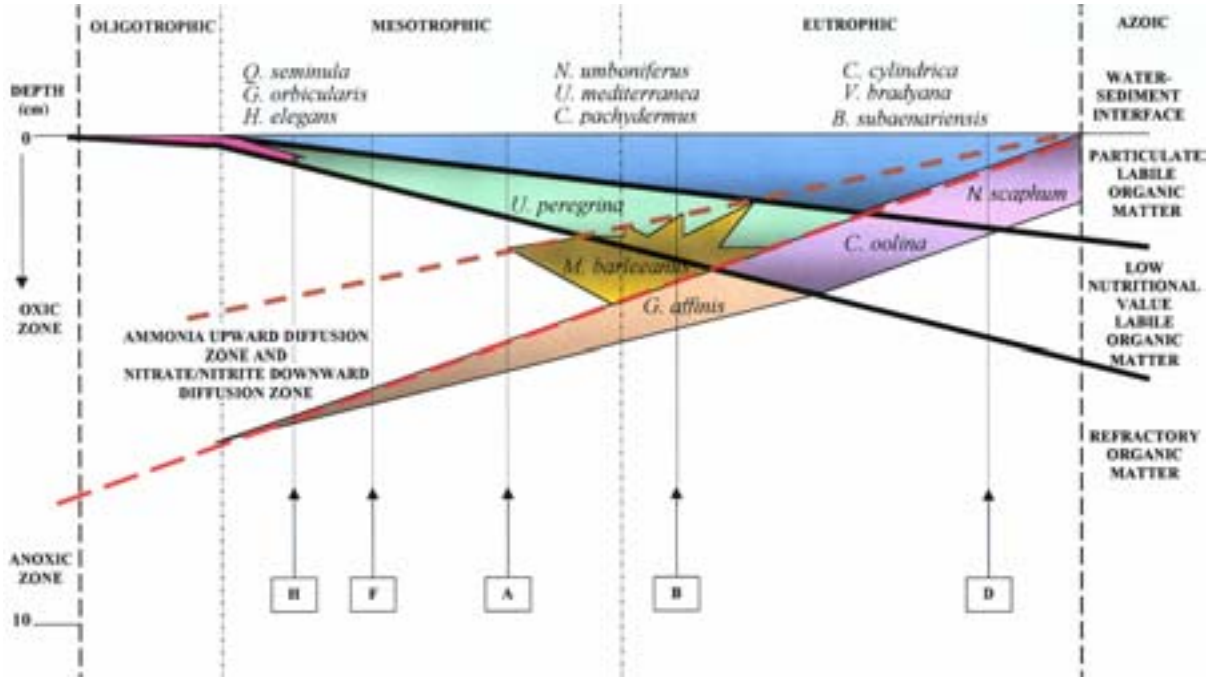


Fig. 1 Microhabitat et composition au niveau spécifique des faunes de foraminifères benthiques le long du transect bathymétrique dans le Golfe de Gascogne; la position approximative des 5 stations étudiées dans le chapitre 1 est indiquée (voir chapitre 1).

Le rôle mineur de l'oxygénation des eaux de fond le long du transect bathymétrique

L'impact de l'oxygénation des eaux de fond sur la densité et la composition des communautés de foraminifères benthiques de notre transect bathymétrique ne peut pas être correctement éprouvé du fait de la bonne oxygénation générale des masses d'eau et de la gamme limitée de variations des concentrations d'oxygène des eaux de fond (138-263 µmol/l). De plus, les variations saisonnières de l'oxygénation des eaux de fond aux stations A et B sont trop modérées pour permettre d'apprécier l'impact d'une hypothétique dysoxie épisodique sur la dynamique des faunes de foraminifères benthiques (Chapitres 2 et 3). Cela n'enlève en rien le rôle limitant qu'exercent les sous-oxygénations marquées (sévère dysoxie ou suboxie) dans certains environnements benthiques profonds d'autres zones d'étude où seules les espèces de foraminifères tolérant des concentrations basses en oxygène dissous peuvent proliférer (e.g. Sen Gupta et Machain-Castillo, 1993; Bernhard et Sen Gupta, 1999).

Les microhabitats : une illustration du modèle TROX

L'étude des relations existant entre la distribution verticale des communautés de foraminifères benthiques et les conditions diagénétiques dans les sédiments du Golfe de Gascogne est en accord quasi-parfait avec les prévisions du modèle TROX (Jorissen et al., 1995). Dans notre zone d'étude, le flux exporté de matière organique et l'oxygénation des eaux porales sont les deux paramètres majeurs qui déterminent le microhabitat des espèces dans le sédiment (Fig. 1). Dans les écosystèmes profonds oligotrophes, la majorité des taxa de foraminifères benthiques rencontrés, subordonnés semble-t-il aux faibles apports de détritus organiques, vivent très proches de l'interface eau-sédiment, dans des microhabitats endopéliques peu profonds et bien oxygénés. Certaines espèces (e.g. *Cibicides wuellerstorfi* et *Cibicidoides* spp.) adoptent même des positions épibiotes sur des foraminifères branchus (*Hyperammina* spp. et *Rhizammina* spp.) émergeant au-dessus du sédiment pour profiter vraisemblablement des moindres particules organiques en suspension voire de la matière organique dissoute dans les eaux de fond (Planche 6, annexe 1). Dans les environnements du haut de pente, les apports de matière organique ont une incidence plus forte sur les processus diagénétiques. Les gradients chimiques entretenus par la décomposition importante de la matière organique réactive sont marqués. Les premiers centimètres du sédiment, enrichis en détritus organiques labiles, dépolymérisés ou solubilisés, et vraisemblablement occupés par des consortia bactériens organohétérotrophes et chimiolithotrophes, constituent autant de niches idéales pour les taxa de foraminifères benthiques endopéliques. Ainsi, alors que certaines espèces vivent dans des microhabitats profonds en relation très proche avec la zone oxygène zéro (*Globobulimina* spp. *Melonis barleeanus*), d'autres espèces présentent des populations très denses dans le premier centimètre oxygéné du sédiment en tirant un bénéfice trophique immédiat des apports organiques phytodétritiques en voie de décomposition (*Uvigerina mediterranea*, *Uvigerina peregrina*). La ségrégation entre des microhabitats endopéliques peu profonds, intermédiaires et profonds dépend à priori de la disponibilité de nourriture dans les niches correspondantes, des besoins trophiques des foraminifères qui les peuplent, et des degrés de tolérances des différentes espèces à la sous-concentration en oxygène dissous des eaux interstitielles. A la station de bordure de plate-forme (station D), les apports importants de phytodétritus ont une répercussion considérable sur les processus diagénétiques et la répartition des foraminifères benthiques. L'essentiel de la communauté des foraminifères benthiques vit dans l'étroite portion de sédiment oxygéné et tend à se concentrer sous l'interface eau-sédiment, et cela malgré une disponibilité vraisemblable de

détritus organiques labiles plus en profondeur. Seules certaines espèces tolérantes à l'anoxie peuvent s'étaler dans des niches endopéliques intermédiaires (*Chilostomella oolina*, *Nonion scaphum*). Ces premières sont sûrement plus à même de tirer un avantage trophique de la présence de matière organique labile enfouie en profondeur dans le sédiment par rapport aux espèces endopéliques intermédiaires moins opportunistes enregistrées aux stations plus profondes. Dans cette situation eutrophe, l'oxygénation des eaux interstitielles, directement corrélée aux apports de détritus organiques, limite la profondeur de vie de nombreuses espèces et semble jouer de ce fait un rôle majeur sur la distribution verticale de la communauté des foraminifères benthiques (Fontanier et al., 2002).

2. Dynamique saisonnière des faunes de foraminifères benthiques du Golfe de Gascogne

Les blooms de printemps et d'automne : une dynamique pélagique saisonnière

Dans les eaux de surface du Golfe de Gascogne se produisent chaque année deux événements saisonniers remarquables d'augmentation de production phytoplanctonique. Il s'agit du bloom de printemps s'étalant de mars en mai et parfaitement visible sur des photos satellites traitant des concentrations en Chlorophylle-a des eaux de surface. Et il s'agit également du bloom d'automne, rarement observé et peu documenté dans le Golfe de Gascogne. Ces deux blooms entraînent des dépôts massifs et épisodiques de phytodétritus labiles dans les premiers centimètres bioturbés des sédiments des environnements marins benthiques profonds.

La variabilité spatiale des faunes de foraminifères benthiques : impact de l'hétérogénéité spatiale des dépôts de détritus organiques

La distribution des dépôts de détritus organiques à l'interface eau-sédiment n'est pas uniforme et répond le plus souvent aux contraintes imposées (1) par les processus de resuspension, (2) par les phénomènes de concentration préférentielle dans des dépressions micro-topopographiques et (3) par la nature même particulaire des détritus organiques (Thiel et al., 1990). Les « patchs » de détritus organiques, tels des oasis de nourriture, sont rapidement colonisés par des organismes des plus opportunistes. Cette hétérogénéité dans la

distribution spatiale des détritus organiques les plus labiles est responsable de l'hétérogénéité spatiale des communautés benthiques et favorise une importante diversité des écosystèmes benthiques (Grassle et Morse-Porteous, 1987; Grassle, 1989; Snelgrove et al., 1996).

Dans les stations A (1000 m) et B (550 m), où des duplicata de carottes ont permis d'éprouver l'hétérogénéité des faunes de foraminifères benthiques au cours de divers échantillonnages, la variabilité spatiale des communautés benthiques à petite ou moyenne échelle (1-100 mètres) demeure inférieure à la variabilité saisonnière maximale, trouvée dans l'ensemble de prélèvements (Chapitre 2 et 3). Cependant, les variations spatiales de composition faunistique sont souvent effectives et d'autant plus marquées que les duplicata correspondent à des prélèvements réalisés en périodes eutrophes (Fontanier et al., 2003a ; 2003b). Cela suggère un « patchiness » des communautés de foraminifères benthiques en relation directe avec des dépôts hétérogènes de phytodétritus.

Ces interprétations demeurent cependant discutables du fait du nombre réduit de réplicata utilisés pour éprouver l'hétérogénéité spatiale des faunes.

La réponse saisonnière des faunes de foraminifères benthiques : le couplage pelagos-benthos

Les foraminifères benthiques hétérotrophes peuvent répondre de deux façons aux apports épisodiques de phytodétritus assimilables. Soit l'énergie tirée de l'assimilation de la matière organique détritique est utilisée dans des processus rapides de reproduction de certaines espèces, soit elle permet d'améliorer temporairement la croissance des individus.

Aux apports saisonniers de détritus organiques, les faunes de foraminifères benthiques des stations B (550 m) et A (1000 m) répondent par une augmentation significative de la densité globale des faunes et par l'apparition d'espèces typiquement opportunistes qui occupent exclusivement la partie superficielle du sédiment (Fig. 2 et 3). *Epistominella exigua, Nuttallides pusillus* et *Reophax guttiferus* appartiennent à la fraction fine (63-150 µm) et montrent des augmentations drastiques d'effectif en périodes eutrophes. Ils sont, semble-t-il, des exemples typiques de stratèges-r à développement rapide, à reproduction précoce, de petite taille et à durée de vie apparemment courte. *E. exigua* et *N. pusillus* ont été plusieurs fois décrits comme des espèces ultra-opportunistes des environnements marins profonds (e.g. Gooday, 1988, Gooday et Hughes, 2002). Il est à peu près certain que ces taxa colonisent efficacement le phytodétritus fraîchement déposés et en tirent un bénéfice trophique aussi

promptement que les bactéries aérobies organohétérotrophes. *Uvigerina mediterranea* et *Uvigerina peregrina* sont deux espèces de la fraction >150 µm qui montrent également des augmentations significatives de leur densité durant ces périodes eutrophes. Leur microhabitat endopélique peu profond leur permet de tirer rapidement un bénéfice des apports organiques labiles phytodétritiques injectés dans leur niche par bioturbation. Leur dominance relative durant les périodes oligotrophes (été, hiver) semble cependant illustrer un taux de renouvellement moins rapide et un cycle de vie beaucoup plus long que les petites espèces de foraminifères les plus opportunistes. Il est fort possible que les apports saisonniers de phytodétritus ne favorisent qu'une accélération de croissance chez les juvéniles d'*Uvigerina mediterranea* et *Uvigerina peregrina* déjà recrutés depuis plusieurs mois et ne provoquent que des événements reproductifs limités.

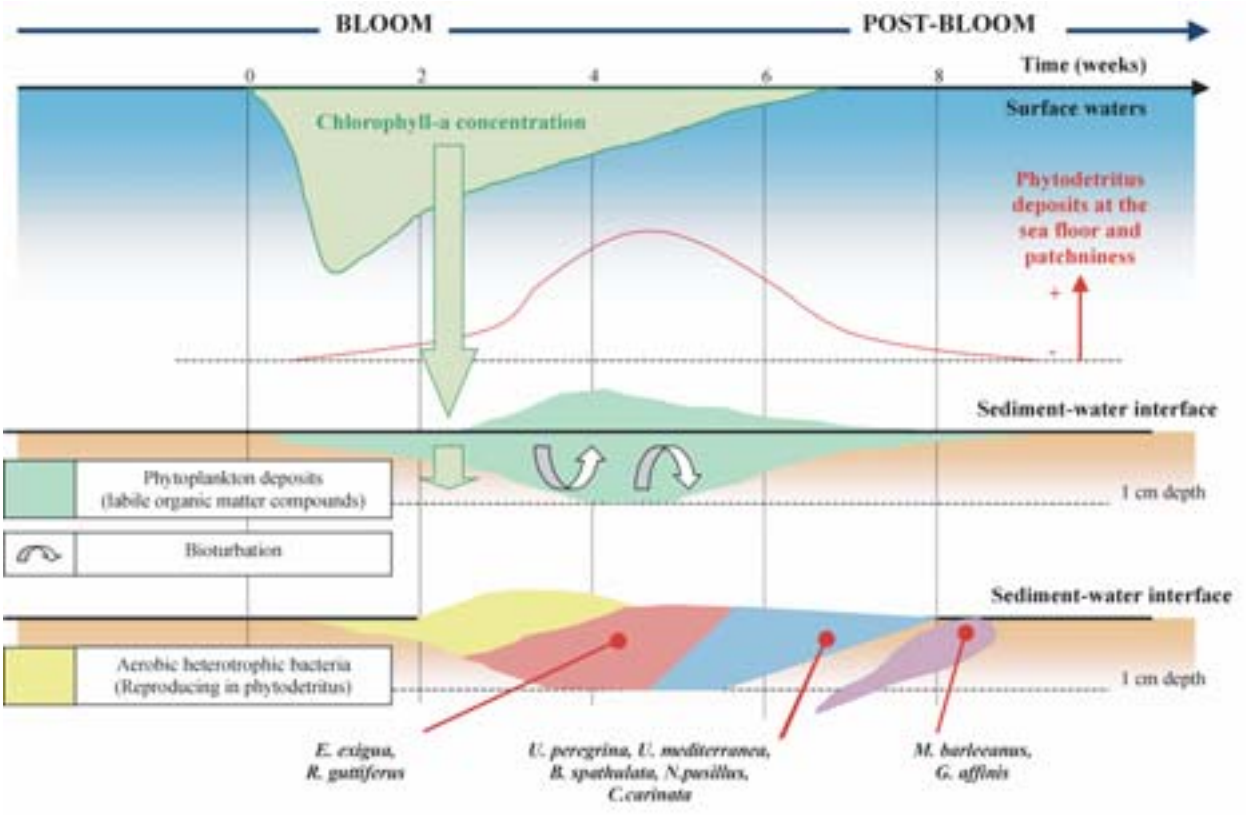


Fig. 2 Couplage entre la production pélagique phytoplanctonique et le benthos: réponse de l'écosystème benthique aux apports saisonniers de phytodétritus (voir chapitre 2).

Les apports de phytodétritus n'altèrent que modérément les processus diagénétiques inhérents au sédiment. Uniquement en avril 2001 et à la station A (1000 m), l'oxygénation des eaux de fond et des eaux interstitielles est substantiellement modifiée par les apports hypothétiques de

détritus organiques. Les apports et la minéralisation des phytodétritus étant circonscrits par bioturbation aux deux premiers centimètres du sédiment, les conditions géochimiques du sédiment profond sont peu perturbées et les populations de foraminifères endopéliques intermédiaires et profonds (*Melonis barleeanus*, *Globobulimina* spp.) apparaissent comme stables et beaucoup moins réactives que les espèces endopéliques superficielles. A ce titre, les taxa correspondants peuvent être considérés sommairement comme des stratèges-K, très compétitifs dans leur microhabitat limitant. Il est vraisemblable que ces individus ont des développements lents, des reproductions tardives et des durées de vie relativement longues (une année ou plus). Nos résultats suggèrent que *Globobulimina* spp. et *Melonis barleeanus* se reproduiraient une fois dans l'année dans des périodes oligotrophes succédant au bloom de printemps

Comparaison des dynamiques saisonnières des foraminifères benthiques entre les stations B et A

La dynamique saisonnière enregistrée à la station B est en phase avec celle enregistrée à la station A mais diffère tant sur le plan de l'amplitude des variations (moins marquée à la station plus profonde) que sur le plan de la composition des espèces les plus opportunistes. Aussi, la différence quantitative entre les flux saisonnièrement exportés aux deux stations semble-t-elle discriminer des faunes opportunistes de périodes de forte eutrophisation du sédiment (riche en *E. exigua et R. guttiferus*) de faunes opportunistes d'épisodes d'eutrophisation plus modérée (riche en *N. pusillus* et *U. peregrina*) (Fig. 3).

3. La structure des faunes de foraminifères benthiques d'un environnement profond de canyon dans le Golfe de Gascogne

Dans le chapitre 4, sont décrites les faunes de foraminifères benthiques collectées dans la partie inférieure du Canyon de Cap-Ferret. A près de 3000 mètres de profondeur, à la station I, les conditions oligotrophes prévalent. Les apports saisonniers de phytodétritus depuis les eaux de surface sont sûrement mineurs en comparaison de ceux enregistrés aux stations A et B. Seuls les apports latéraux de matière organique, accrus dans le Canyon de Cap-Ferret par des processus de resuspension-concentration, contribuent en un enrichissement important en carbone organique du sédiment profond et superficiel des carottes étudiées.

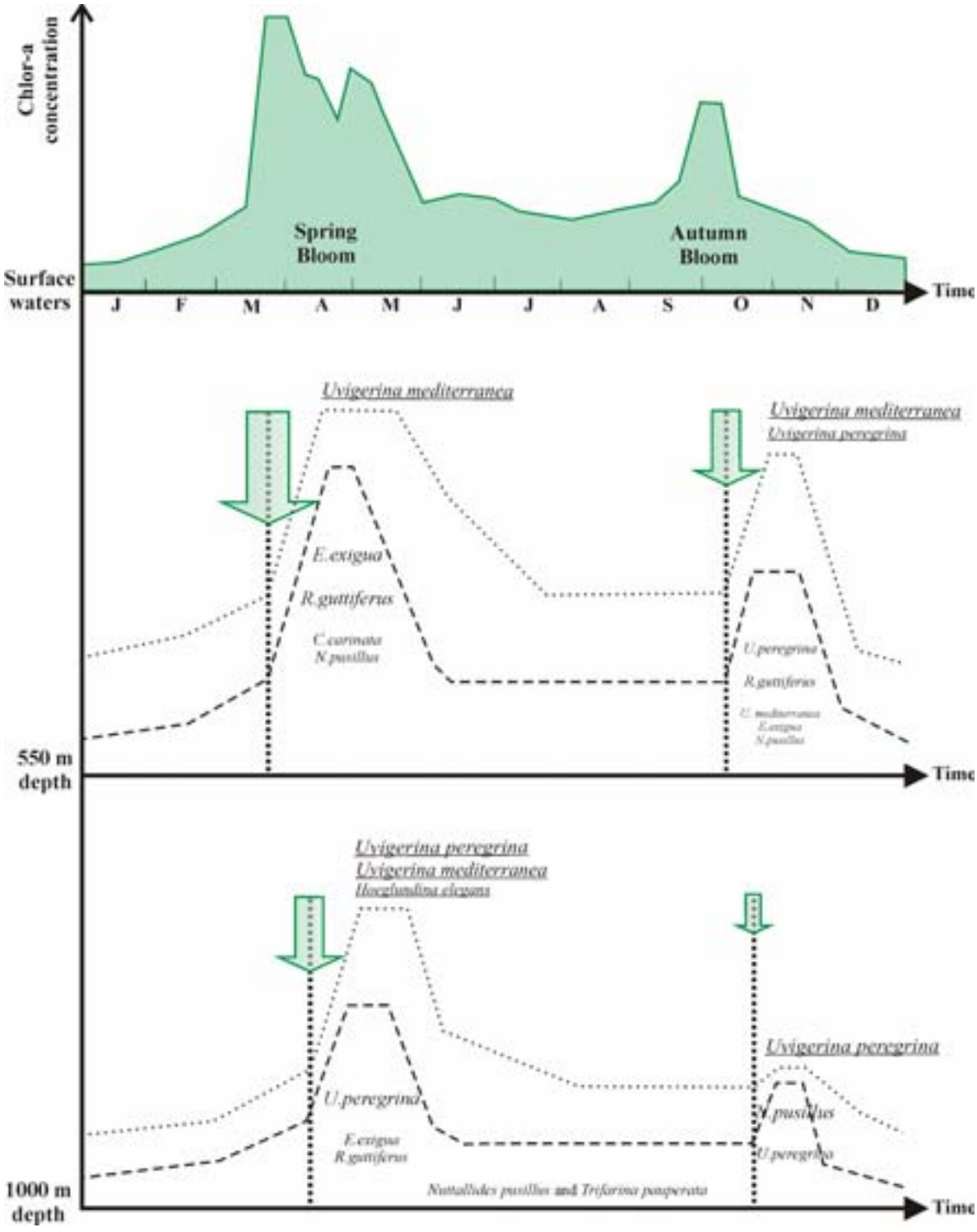


*Fig. 3 Couplage entre la production pélagique phytoplanctonique et la dynamique des faunes opportunistes de foraminifères benthiques à la station B (550 mètres de profondeur) et la station A (1000 mètres de profondeur)**:** le modèle ODYSSEY (Opportunist DYnamics along a Slope tranSEct in the (B)ay of (B)iscaY) (voir chapitre 3).*

D'une façon très surprenante, les faunes de foraminifères benthiques sont dominées par des espèces occupant des microhabitats endopéliques intermédiaires et profonds (Fontanier et al., 2003c). Il s'agit de *Melonis barleeanus*, *Chilostomella oolina* et *Globobulimina* spp. Ces populations représentent, semble-t-il, des communautés plutôt stables et associées le plus souvent à des gradients géochimiques remarquables (Fig. 4). Aussi, de toutes les stations échantillonnées dans le Golfe de Gascogne, la station I présente-t-elle les endofaunes de foraminifères benthiques les plus importantes. L'existence de ces populations de foraminifères benthiques dans les niches où l'oxygène est en faible concentration voire absent et où la disponibilité de détritus phytodétritiques labiles est très limitée, est énigmatique. Elle pose le problème des stratégies métaboliques adoptées par ces organismes pour survivre dans des microhabitats aux caractéristiques si adverses.

Pour partiellement répondre à cette interrogation et, de fait, proposer une piste de réflexion, il est argumenté dans ce chapitre que ces populations endopéliques profondes et intermédiaires de foraminifères benthiques pourraient vivre en intime relation avec les consortia bactériens impliqués dans la dépolymérisation de l'importante quantité de dépôts organiques remaniés déposés dans le bas du canyon, ou participant à des processus chimiosynthétiques. Différents scénarii quant à la dépendance trophique des différentes espèces composant l'endofaune sont envisagés. Soit les foraminifères endopéliques intermédiaires et profonds sont capables de se nourrir de la matière organique en voie de dépolymérisation (détritivores), soit ces espèces, au sein de boucles trophiques dysaérobies et anaérobies, sont à même de se nourrir de bactéries organohétérotrophes inféodée à la dégradation des détritus organiques résistants, soit les foraminifères benthiques sont capables d'entretenir des liens mutualistes avec les bactéries chimiolithotrophes que l'on sait capable d'entretenir des réactions remarquables d'oxydation dans le sédiment profond. A ce titre, la corrélation existant notamment entre les maxima d'abondance de *Globobulimina* spp. et les pics de précipitation d'oxyhydroxydes de fer, sans relation claire avec la profondeur de la « limite oxygène zéro », nous laisse supposer qu'une relation symbiotique mutualiste forte pourrait exister entre ce taxon et des bactéries chimiolithotrophes responsables de l'oxydation du fer dissout.

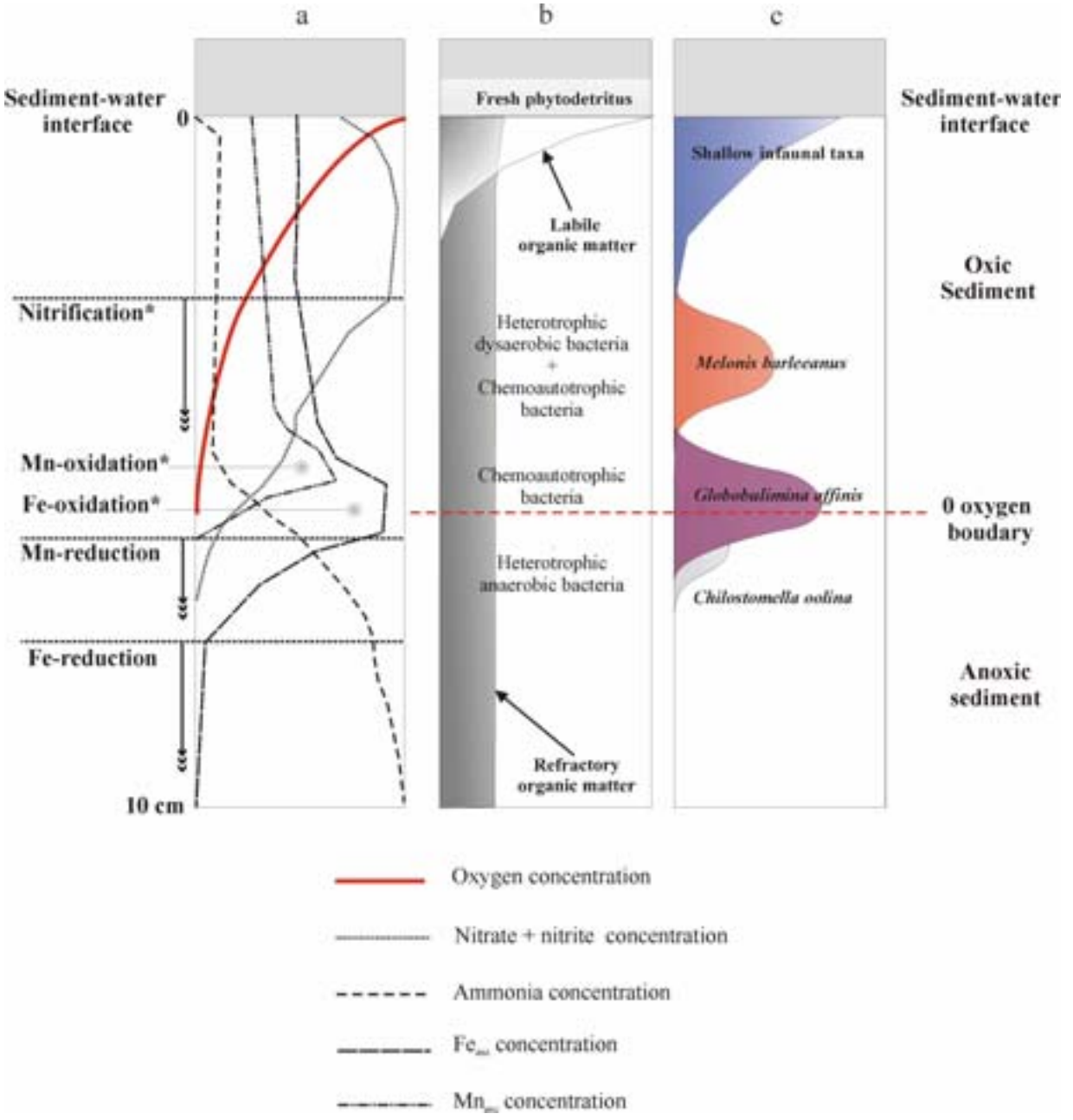


Fig. 4; 4a Principales zones redox dans les 10 premiers centimètres d'une carotte virtuelle représentative des caractéristiques biogéochimiques majeures des carottes de sediment collectées à la station I en janvier et juin 1999; 4b Distribution supputée de la matière organique labile et réfractaire ainsi que le carbone organique labile produit en profoundeur lors de la conversion bactérienne; 4c Distribution verticale et profils de densité des foraminifères benthiques endopélique peu profonde (comme un unique groupe) ainsi que Melonis barleeanus, Chilostomella oolina et Globobulimina affinis (voir chapitre 4).

Les résultats de cette étude suggèrent que les endofaunes de foraminifères benthiques présentent une dynamique et des besoins trophiques découplés des apports directs de phytodétritus labiles. Les espèces endopéliques intermédiaires et profondes tirent, semble-t-il, un bénéfice beaucoup plus certain de la quantité importante de matière organique de mauvaise qualité enfouies en profondeur et dont la dégradation entretient un ensemble de processus biogéochimiques exacerbés (e.g. stratification bactérienne, « labilisation des détritus organiques », gradients géochimiques marqués).

5. La composition isotopique ($\delta^{18}O$ et $\delta^{13}C$) des faunes de foraminifères benthiques du Golfe de Gascogne

L'effet de microhabitat

Le microhabitat a un effet direct sur la signature $\delta^{13}C$ des espèces de foraminifères benthiques. Il semble que les foraminifères biominéralisent leur test en équilibre plus ou moins juste avec le carbone inorganique dissous dans les eaux interstitielles du sédiment où il vit. La signature est d'autant plus lourde que les taxa étudiés présentent un microhabitat proche de l'interface eau-sédiment comme un effet direct de l'alourdissement relatif du $\delta^{13}C$ du carbone inorganique dissous dans les niches superficielles.

Variations du $\delta^{13}C$ des faunes de foraminifères benthiques le long du transect bathymétrique

Le long du transect bathymétrique étudié dans le chapitre 1, l'état d'eutrophisation des niches superficielles du sédiment peut être déterminé, semble-t-il, via la signature $\delta^{13}C$ des tests des espèces de microhabitat endopélique peu profond tels qu'*Uvigerina peregrina.* Ce taxon présente des valeurs $\delta^{13}C$ d'autant plus basses que la minéralisation des détritus organiques dans le premier centimètre de sédiment où il vit est intense. Dans les environnements profonds et oligotrophes, la décomposition de faibles quantités de détritus organiques dans les premiers centimètres de sédiment libère peu de ^{12}C, engendrant des signatures $\delta^{13}C$ du test d'*Uvigerina peregrina* relativement plus lourde que les environnements peu profonds. Dans les sédiments dysoxiques et anoxiques profonds des zones oligotrophes, la dégradation plus avancée et plus lente des détritus organiques semble

ralativement plus importante que dans stations eutrophes peu profondes. Aussi, le gradient du $\delta^{13}C$ du carbone inorganique dissous dans les eaux porales s'étale-t-il plus en profondeur dans les stations profondes oligotrophes que dans les stations eutrophes. Le gradient $\Delta\delta^{13}C$ entre *Uvigerina peregrina* et *Globobulimina* spp. (dont la microhabitat est largement inféodé à la « limite oxygène zéro ») permet alors d'estimer l'intensité des processus de dégradation de la matière organique dans la partie habitée du sédiment (Fig. 5).

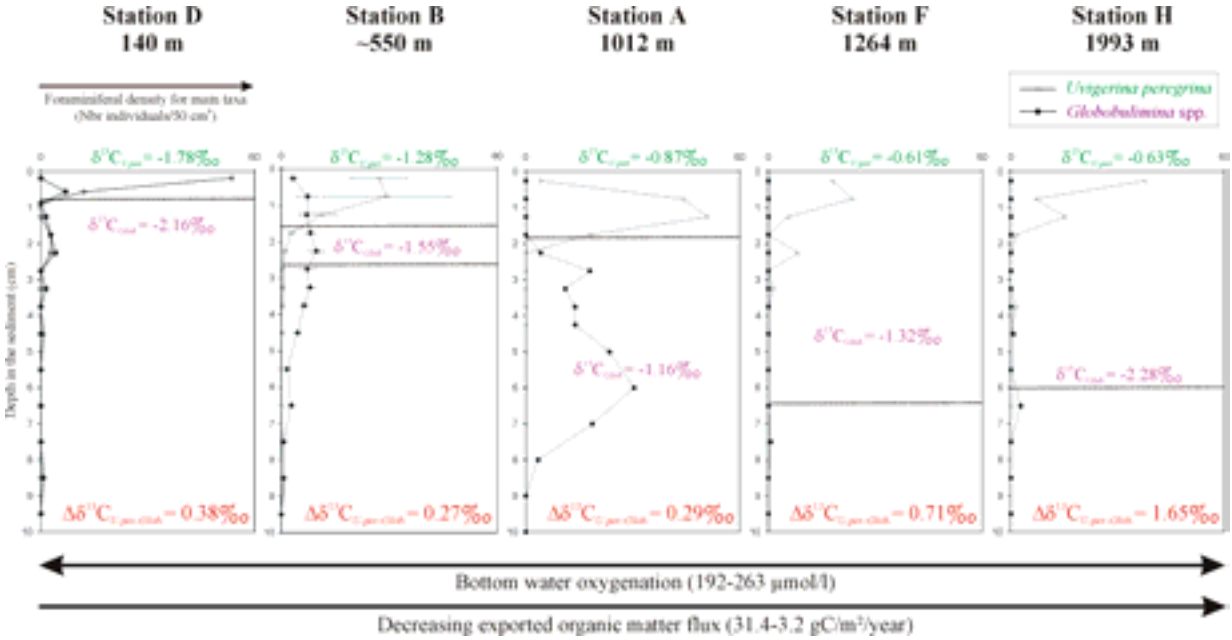


Fig. 5 Schéma synthétique montrant les signatures isotopiques $\delta^{13}C$ de Globobulimina spp. et d'Uvigerina peregrina le long du transect bathymétrique dans le Golfe de Gascogne. Ces deux espèces sont supposées enregistrer le $\delta^{13}C_{DIC}$ des eaux porales où elles vivent (effet de microhabitat). Les profiles verticaux de densités de ces deux espèces sont également présentés. Les densités sont exprimées en nombre d'individus par 50 cm^3. Le $\Delta\delta^{13}C$ entre les deux espèces est calculé pour chaque station. Les lignes en pointillés représentent la profondeur de la « limite oxygène zéro ». A la station B, les deux lignes en pointillés sont associées aux valeurs maximales et minimales de pénétration de l'oxygène enregistrées lors de 12 échantillonnages (voir chapitre 6).

Le rôle de la température: signature isotopique $\delta^{18}O$ des tests de foraminifères benthiques

Il a été largement commenté et statistiquement prouvé qu'à la différence du flux exporté de carbone organique, les paramètres physico-chimiques tels que la température, la salinité et la pression n'exerce aucune limitation probante sur les communautés de foraminifères benthiques des environnements profonds (e.g. Loubere et Fariduddin, 1999; De Rijk et al, 2000). Dans notre zone d'étude, la température ne joue apparemment aucun rôle sur la dynamique et la structure des faunes de foraminifères benthiques (Chapitre 1, 2, 3 et 4). La relation existant entre la température des eaux de fond et certaines espèces calcitiques de foraminifères benthiques n'est visible qu'au travers de la signature isotopique $\delta^{18}O$ de leur test dans la mesure où la température et le gradient exprimé le long du transect bathymétrique (entre la station D et la station H) contrôlent les coefficients de fractionnement des isotopes de l'oxygène lors de la calcification du test des foraminifères. A ce sujet, il apparaît que la plupart des espèces étudiées d'un point de vue isotopique (chapitre 6) biominéralise leur test en proche équilibre isotopique avec les eaux de fond. Ceci est particulièrement claire pour *U. peregrina* et *Globobulimina* spp. dont les signatures isotopiques $\delta^{18}O$ le long du transect bathymétrique suivent les tendances du $\delta^{18}O$ de la calcite précipitée à l'équilibre avec les eaux de fond.

Les variations saisonnières de la composition isotopique $\delta^{13}C$ des faunes de foraminifères benthiques à la station B

En ce qui concerne les isotopes stables du carbone chez les espèces dominantes étudiées à la station B (>150 μm), les signatures $\delta^{13}C$ restent relativement constantes durant l'année. Les apports épisodiques de phytodétritus ainsi que leur reminéralisation accrue dans les microhabitats superficiels du sédiment ne trouvent apparemment aucun écho saisonnier dans la chimie isotopique des espèces endopéliques peu profondes, même en ce qui concerne les taxa à comportement supposé opportuniste tels qu'*U. peregrina* et *U. mediterranea*. Il est supputé que ces espèces n'enregistrent les changements épisodiques de $\delta^{13}C$ des eaux porales qu'au travers des tests des juvéniles qui croissent durant les périodes eutrophes dans la fraction 63-150 μm pas encore étudiée.

6. Relations entre les faunes de foraminifères benthiques, les détritus organiques et l'oxygénation des eaux interstitielles

Rapport à la qualité de la matière organique

Au travers de notre étude, les foraminifères benthiques apparaissent comme des organismes détritivores majeurs de l'écosystème benthique dont la dynamique saisonnière est couplée à la production pélagique phytoplanctonique. Alors que certaines espèces suspensivores sont vraisemblablement adaptées à se nourrir de particules surnageant dans les eaux de fond, la majeure partie des taxa, dépositivores, ne peuvent apparemment s'accommoder que de détritus organiques sédimentés.

L'importance des populations opportunistes dans certaines stations en réponse aux dépôts épisodiques de phytodétritus montre la préférence de certains foraminifères pour une matière organique labile riche en lipides et acides aminés hydrolysables facilement assimilables. Elle suggère également le rôle prépondérant que jouent les foraminifères, au même titre que les bactéries hétérotrophes aérobies, dans la consommation primaire de la matière organique pélagique et sur sa minéralisation partielle de celle-ci. Au travers de phénomène de bioturbation, des composés organiques labiles détritiques sont vraisemblablement disponibles dans les microhabitats endopéliques peu profonds pour répondre également aux besoins trophiques des populations du sédiment superficiel.

Plus en profondeur dans le sédiment, l'injection de détritus organiques labiles n'est sûrement associée qu'à la présence très ponctuelle de terriers macrofaunaux. Suivant le modèle de Carney, il est plus probable que la matière organique détritique enfouie dans les parties profondes du sédiment soit le plus souvent de moindre qualité par rapport aux phytodétritus déposé à l'interface et en voie de « labilisation » par le jeu de la dégradation bactérienne organohétérotrophe. Les espèces de foraminifères occupant les niches endopéliques intermédiaires et profondes (*Melonis barleeanus*, *Uvigerina elongatastriata*, *Globobulimina* spp.) sont soit capables de se nourrir d'une matière organique de moins bonne qualité en voie de dépolymérisation, soit capables de se nourrir directement de bactéries organohétérotrophes. Il est également possible que certains taxa comme *Globobulimina* spp. vivent en symbiose avec des bactéries chimiolithotrophes (Chapitres 4 et 5). Ces dernières pourraient fournir à leur hôte, par translocation, des composés organiques nouvellement synthétisés grâce à l'énergie chimique de réaction d'oxydation. Les associations symbiotiques

« bactéries myxotrophes-foraminifères benthiques » ont été plusieurs fois observées dans des environnements benthiques profonds sous-oxygénés (e.g. Bernhard, 2003). Il est également envisageable que la matière organique dissoute dans les eaux interstitielles joue un rôle trophique non négligeable sur les diverses populations de foraminifères benthiques.

L'essentiel des résultats de cette thèse suggère un vaste ensemble d'interactions possibles existant entre les populations de foraminifères benthiques supposées détritivores et bactériophages, le matériel organique détritique et les divers consortia bactériens. Cependant, l'absence de donnée quantitative et qualitative sur les détritus organiques enfouis dans le sédiment et sur les bactéries doit préserver les lecteurs de toutes conclusions hâtives.

Rapport à la concentration en oxygène dissous des eaux interstitielles

Notre étude montre que les diverses espèces de foraminifères benthiques possèdent des limites de tolérance très variées vis à vis du degré d'oxygénation des eaux porales. L'oxygène, en tant qu'accepteur final d'électron lors des phénomènes respiratoires en aérobie est indispensable à la réalisation et l'entretien de l'activité métabolique (catabolisme et anabolisme) de certains organismes benthiques dits aérobies. Il est vraisemblable que les foraminifères benthiques occupant les microhabitats endopéliques superficiels, indépendamment de leur exigence en matière organique fraîchement déposée, demandent également des concentrations élevées en oxygène dissous pour répondre d'une façon optimale à leurs besoins énergétiques. En ce qui concerne les espèces de foraminifères benthiques occupant les microhabitats endopéliques intermédiaires et profonds, le problème est tout autre. Les microhabitats de ces espèces correspondent le plus souvent à des conditions de sévère dysoxie, de suboxie voire d'anoxie. Ainsi, il semble que *Melonis barleeanus* traque systématiquement des gradients de concentration en oxygène compris entre 1 et 50 µmol/l (Chapitres 2 et 4). *Globobulimina* spp. présente des populations adultes strictement inféodées à la zone où l'oxygénation devient nulle (Chapitres 1, 2, 3, 4, 5). Cela semble témoigner de stratégie d'organismes capables de vivre sous des concentrations très limitées en oxygène dissous. Comme certaines bactéries, il est possible que ces deux taxa puissent se comporter comme des organismes micro-aérophiles, capables d'avoir des activités métaboliques optimales sous des concentrations très faibles en oxygène (1-5 µmol/l). Il est également possible que ces espèces de foraminifères utilisent d'autres oxydants que l'oxygène comme accpeteur final d'électron lors de leur respiration. *Globobulimina* spp. pourrait parfaitement utiliser le nitrate comme accepteur d'électron lors de processus respiratoires anaérobies.

7. Applications de l'étude des faunes actuelles des foraminifères benthiques en paléo-océanographie

Les nombreuses interprétations et conclusions apportées par cette thèse traitant de l'écologie des foraminifères benthiques de la marge aquitaine du Golfe de Gascogne trouvent un écho plus qu'important dans les utilisations multiples qu'il est possible d'en faire en paléo-océanographie. Aussi, les foraminifères benthiques, rares éléments fossilisables des biocénoses benthiques des plates-formes continentales et des pentes océaniques, constituent-ils des outils incontournables de reconstructions des conditions paléo-environnementales benthiques. Ce travail de thèse constitue une amorce primordiale et essentielle au projet FORAMPROX (FORAMinifères et PROXies), actuellement en cours. Le but ultime du programme FORAMPROX est de calibrer, avec la plus grande des justesses et cela à partir de l'étude des faunes actuelles de foraminifères benthiques, des « proxies » efficaces en paléo-océanographie.

Reconstruction de la paléo-productivité exportée au sédiment

Dans la mesure où la composition des peuplements de foraminifères benthiques de notre zone d'étude est fortement asservie aux conditions d'eutrophisation du sédiment via la productivité exportée, l'analyse d'assemblages fossiles de foraminifères benthiques constitue une étape essentielle afin d'apprécier qualitativement les conditions d'eutrophisation des paléo-environnements benthiques et les variations d'apports de matière organique originaire de la production primaire. Travailler sur les faunes fossiles de la fraction >150 µm permet notamment d'envisager d'une façon assez fidèle les larges variations de paléo-productivité exportée. A titre d'exemple, dans notre zone d'étude, alors que les assemblages riches en *Uvigerina mediterranea* et en *Uvigerina peregrina* témoignent de conditions eutrophes de haut de pente, des faunes riches en *Hoeglundina elegans* ont un caractère beaucoup plus oligotrophe de bas de pente. Il est alors possible, à partir de succession de divers assemblages de foraminifères benthiques dans un enregistrement sédimentaire donné, de préciser les variations relatives de la paléo-productivité exportée. Connaissant les seuils actuels de tolérance de certaines espèces-clés par rapport au flux de carbone organique exporté, il est même possible de quantifier sommairement la paléo-productivité exportée et, par conséquent,

de calculer des valeurs annuelles de paléo-production exportée. L'étude des faunes fossiles appartenant à la fraction 63-150 μm est, quant à elle, un formidable outil écologique pour préciser qualitativement la nature plus ou moins saisonnières des dépôts de matière organique phytodétritique. Des espèces opportunistes remarquables telles qu'*Epistominella exigua*, *Nuttalides pusillus*, *Uvigerina peregrina* apparaissent, dans notre zone d'étude, comme des garants indiscutables de conditions d'eutrophisation saisonnière du haut de pente. Des assemblages fossiles dominés par de telles espèces peuvent alors se révéler être de très bons outils de reconstruction qualitative de la saisonnalité des dépôts phytodétritiques. Les résultats isotopiques de ce travail de thèse suggèrent, quant à eux, qu'il est également possible d'utiliser la signature $\delta^{13}C$ de certaines espèces endopéliques peu profondes afin d'estimer les variations de productivité exportée. C'est semble-t-il le cas d'*U. peregrina.* La différence entre sa signature $\delta^{13}C$ et celle des eaux de fond est bien corrélée avec le flux exporté de carbone organique. Comme suggéré par McCorkle et al. (1997), il suffit de déterminer un $\Delta\delta^{13}C$ entre *U. peregrina* et une espèce enregistrant préférentiellement la signature des eaux de fond le long d'un enregistrement sédimentaire, pour pouvoir évaluer les variations relatives de paléo-productivité exportée. L'avantage d'*U. peregrina* est que ce taxon apparaît dans les faunes de foraminifères benthiques s'étalant dans une très large gamme bathymétrique, entre 140 et 2800 mètres de profondeur. Ce qui n'est malheureusement pas le cas de *C. wuellerstorfi*.

Reconstruction des conditions de dégradation des détritus organiques dans le sédiment superficiel

Notre étude isotopique a conduit à la suggestion que le $\Delta\delta^{13}C$ entre *Uvigerina peregrina* et *Globobulimina spp.* peut être un outil très intéressant pour reconstruire le long d'un enregistrement sédimentaire les variations des conditions de dégradation aérobique et anaérobique des détritus organiques dans le sédiment superficiel.

Calibration des courbes stratigraphiques isotopiques $\delta^{18}O$

Les signatures isotopiques $\delta^{18}O$ des foraminifères benthiques sont communément utilisées à la construction des charpentes stratigraphiques isotopiques des enregistrements sédimentaires marins à comparer avec les enregistrements glaciaires et continentaux. Les

analyses isotopiques des espèces dominantes des stations étudiées dans le Golfe de Gascogne montrent que ces espèces de foraminifères benthiques présentent des signatures $\delta^{18}O$ plus ou moins proches de celles de la calcite à l'équilibre avec les eaux de fond. Les différences isotopiques des signatures des diverses espèces par rapport à la calcite et des espèces entre elles sont relativement invariables suggérant que des courbes stratigraphiques isotopiques complètes peuvent être réalisées à partir de mesures isotopiques réalisés sur des ensembles composites de plusieurs espèces (e.g. *Cibicides pachydermus, Uvigerina peregrina, Uvigerina mediterranea, Melonis barleeanus, Globobulimina* spp.) et en tenant compte de facteurs correctifs qui sont proposés en chapitre 6.

Conclusion générale : Le rôle des foraminifères dans l'écosystème benthique profond

La compréhension d'un écosystème et de sa dynamique ne peut se limiter à l'étude d'un seul groupe d'organismes dans la mesure où les structures des diverses populations de la biocénose sont imbriquées dans un réseau complexe d'interactions biotiques fortes. Cependant, les environnements marins profonds sont vraisemblablement l'exemple d'écosystèmes les plus sous-échantillonnés et consécutivement les plus mal connus des sciences de la Vie et de la Terre et lorsqu'il s'agit d'envisager l'étude complète de leur dynamique, des problèmes de logistique et de compétence se posent très rapidement. Seule une succession d'études pluridisciplinaires ciblées sur les différents groupes d'organismes peut permettre de décortiquer les entremêlements biotiques et abiotiques complexes liant biotope et biocénose. Cette thèse dresse la vision actuelle des relations existant entre les faunes de foraminifères benthiques de divers environnements benthiques profonds et certains paramètres abiotiques majeurs. Elle tente de préciser au mieux les limitations qu'exercent certaines variables abiotiques majeures des écosystèmes benthiques profonds sur les diverses populations de foraminifères benthiques dans le but de mieux préjuger de leur rôle dans l'écosystème benthique.

La conclusion principale de ce travail est que la matière organique détritique d'origine pélagique joue un rôle majeur sur la structure et la dynamique des diverss peuplements de foraminifères benthiques des environnements marins profonds du Golfe de Gascogne. Non seulement elle structure la distribution spatiale verticale et horizontale des faunes, mais aussi elle asservit la dynamique saisonnière des diverses populations des foraminifères benthiques.

Les foraminifères benthiques, en tant qu'organismes détritivores et potentiellement bactériophages, constituent vraisemblablement un pool de consommateurs primaires et secondaires de première importance dans l'écosystème benthique. La figure 6 montre combien le couplage entre la production pélagique phytoplanctonique et la structure des peuplements de foraminifères benthiques est forte. Cette figure synthétique insiste notamment sur les incidences des apports de phytodétritus sur la structure spatiale et la dynamique saisonnière des communautés de foraminifères benthiques, via les changements bathymétriques et saisonniers de densité, de composition, de microhabitat et de composition isotopique ($\delta^{18}O$ et $\delta^{13}C$) dans le Golfe de Gascogne. Le rôle des foraminifères benthiques dans la fixation et dans la minéralisation partielle de la matière organique pélagique exportée ne laisse, semble-t-il, aucun doute. Les espèces les plus opportunistes répondent très rapidement aux apports soudains et éphémères de phytodétritus par des reproductions accrues et une colonisation très rapide du sédiment très superficiel alors que les espèces de foraminifères benthiques plus compétitives, aux cycles de vie plus longs et aux comportements trophiques variés, vivent dans les parties profondes du sédiment ou à l'interface eau-sédiment lors des périodes oligotrophes. Aussi, les foraminifères benthiques, comme les consortia bactériens organohétérotrophes impliqués dans la décomposition des détritus organiques, peuvent-ils être considérés comme un maillon essentiel des boucles trophiques aérobies et anaérobies des écosystèmes benthiques profonds. Ils participent aux transferts de matière et d'énergie au sein des écosystèmes benthiques ainsi qu'aux cycles biogéochimiques impliqués dans la minéralisation de la matière organique.

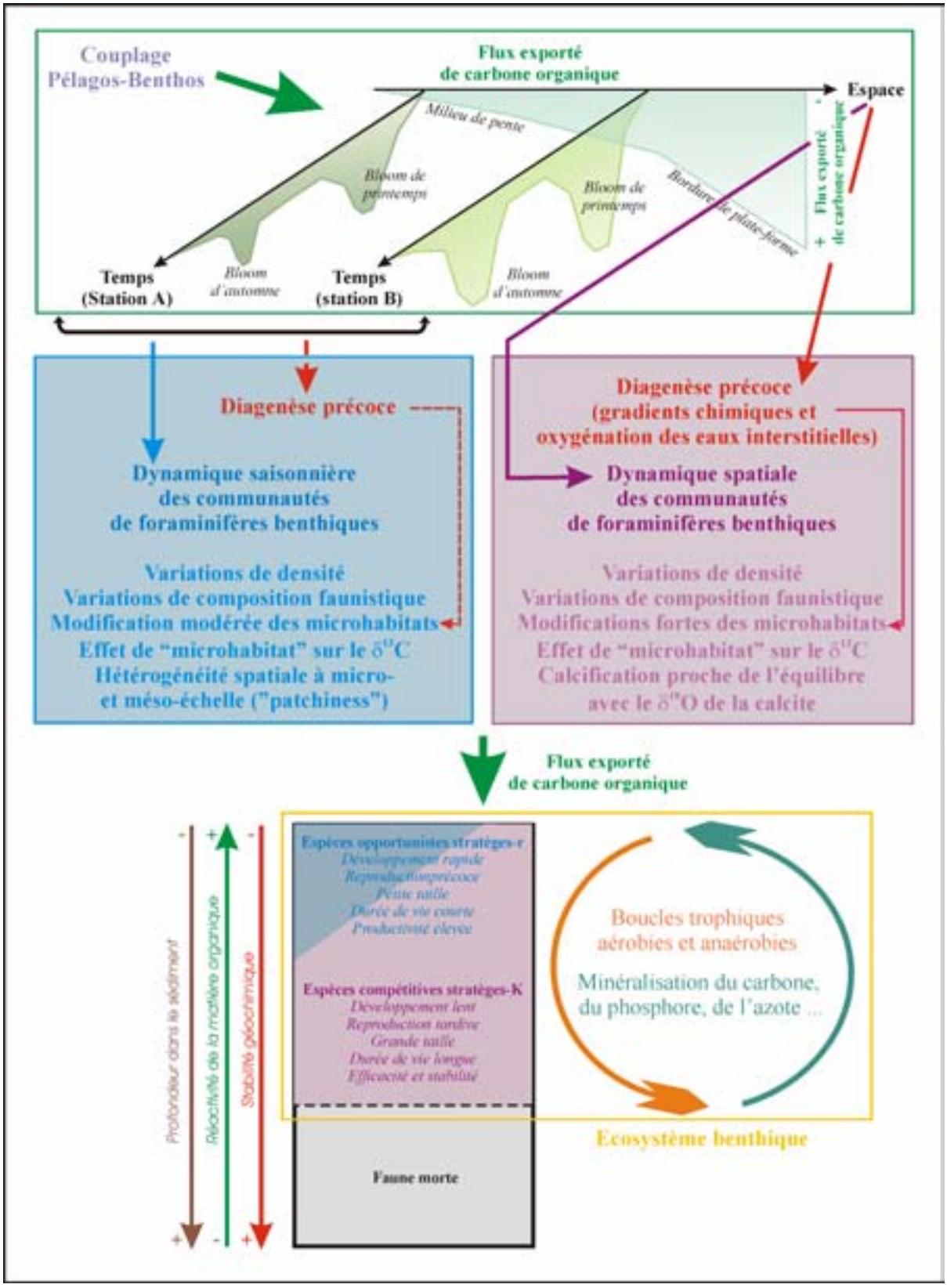


Fig. 6 Couplage pélagos-benthos et incidence sur la dynamique spatiale et saisonnière des communautés de foraminifères benthiques (densité, composition, microhabitat, isotopes stables du carbone et de l'oxygène) dans le Golfe de Gascogne.

Les perspectives d'étude

A l'issu de ce travail de thèse, de nombreuses interrogations demeurent concernant l'écologie des peuplements de foraminifères benthiques des environnements du Golfe de Gascogne. Parmi ces questions, certaines nécessiteraient des investigations complémentaires ou des travaux précurseurs. Aussi, voici présentée une liste succincte de différentes problématiques qui pourraient dans un futur proche comme lointain faire l'objet de nombreuses études :

- La relation existant entre la matière organique détritique et la structure des faunes de foraminifères benthiques semble indubitable. Cependant, à la lumière des résultats de cette thèse, il semble maintenant nécessaire de mieux préciser les relations trophiques existant entre les différentes espèces de foraminifères et les détritus organiques dont la composition et la nature restent très spéculatives. Des analyses biochimiques précises sur le contenu organique du sédiment ainsi que les analyses poussées concernant les consortia bactériens (taxonomie, biomasse, distribution verticale) présents dans des carottes de sédiment prélevées in situ à diverses périodes de l'année pourraient être maintenant nécessaires si les relations existant entre détritus organiques, bactéries, et foraminifères benthiques veulent être précisément comprises.
- Des cultures expérimentales menées sur des faunes de foraminifères d'environnements profonds est en cours dans certains laboratoires européens (Université d'Angers, d'Utrecht et de Tübingen). Nombreuses sont les observations et les interprétations qui ont été réalisées dans le cadre de ces études. Il serait cependant intéressant d'éprouver certaines suggestions avancées dans cette thèse. Parmi celles-ci, les relations trophiques et symbiotiques entre les bactéries et certaines espèces de foraminifères semblent des plus énigmatiques. Des observations ultratructurales de foraminifères « cultivés » en présence de consortia bactériens correctement choisis seraient de première importance pour confirmer certaines hypothèses.
- En outre, des observations des ultrastructures de divers individus d'espèces dominantes fraîchement collectées in situ seraient également très utiles pour apprécier les adaptations métaboliques de ces espèces, via la présence/l'absence de certaines organelles, à certains environnements benthiques profonds particuliers. Il serait notamment important de cibler les foraminifères benthiques collectés dans les

sédiments suboxiques ou anoxiques de zone à oxygène minimum ou les faunes si particulières des environnements hydrothermaux.

- La variabilité spatiale des faunes en relation avec la distribution hétérogène de la matière organique est amplement suggérée dans cette thèse. Cependant il semble qu'une étude exhaustive à partir d'un jeu complet de 8 carottes prélevées lors d'un même tir de multitube en période eutrophe serait très pertinente. Alternativement, il serait très simple d'un point de vue logistique et très porteur d'un point de vue scientifique de stimuler en mésocosme des dépôts hétérogènes de matière organique phytodétritique afin d'apprécier à partir de sous-échantillons la variabilité spatiale des faunes de foraminifères benthiques.
- Peut-être, une étude précise des faunes de foraminifères benthiques le long d'un transect bathymétrique dans l'axe d'un canyon « passif » tel le canyon de Cap-Ferret serait intéressante, notamment pour apprécier les différences fondamentales (densités, microhabitats, compositions) entre de telles communautés et celles étudiées le long du transect présenté dans cette thèse.
- Afin de compléter les résultats de cette thèse, il serait intéressant de réaliser les mesures de $\delta^{13}C$ et $\delta^{18}O$ sur les espèces dominantes prélevées lors des enregistrements saisonniers de la station A. L'accent pourrait être porté sur les espèces dominantes de la fraction 63-150 µm dont le signal $\delta^{13}C$ serait plus sensible aux apports saisonniers de phytodétritus.

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ANNEXES

ANNEXE 1 :

12 planches photos sur les foraminifères benthiques du Golfe de Gascogne.

ANNEXE 2 :

Recent turbidite deposition in the eastern Atlantic: Early diagenesis and biotic recovery.

Anschutz P., Jorissen F.J., Chaillou G., Abu-Zied R. and C. Fontanier (2002) dans *Journal of Marine Research*, **60**.

ANNEXE 3 :

Circulation changes and nutrients concentrations in the late Quaternary Aegean Sea: A nonsteady state concept for sapropel formation.

Casford J.S.L., Rohling E.J., Abu-Zied R., Cooke S., Fontanier C., Leng M.J. et V. Lykousis (2002) dans *Paleoceanography*, **17**, no 2.

A dynamic concept for eastern Mediterranean circulation and oxygenation during sapropel formation.

Casford J.S.L., Rohling E.J., Abu-Zied R., Fontanier C., Jorissen F.J., M.J. Leng, Schmiedl G. et J. Thomson (2003) dans *Palaeogeography*, *Palaeoclimatology and Palaeoecology,* **190**.

Annexe 1

PLANCHE 1

Figures A et B *Adercotryma glomerata* (station I)

Figures C et D *Ammobaculites agglutinans* (station I)

Figure E *Lagenammina pseudodifflugiformis* (Station A)

Figure F *Clavulina cylindrica* (station D)

Figure G *Cribrostomoides subglobosus* (station B)

Figures H et I *Clavulina cylindrica* (stations D et B)

Figure J *Bigenerina nodosaria* (station B)

Figures K, L et M *Cribrostomoides subglobosus* (stations I et B)

Figure N *Cystammina argentea* (station A)

Figure O *Cyclammina* sp.2 (station B)

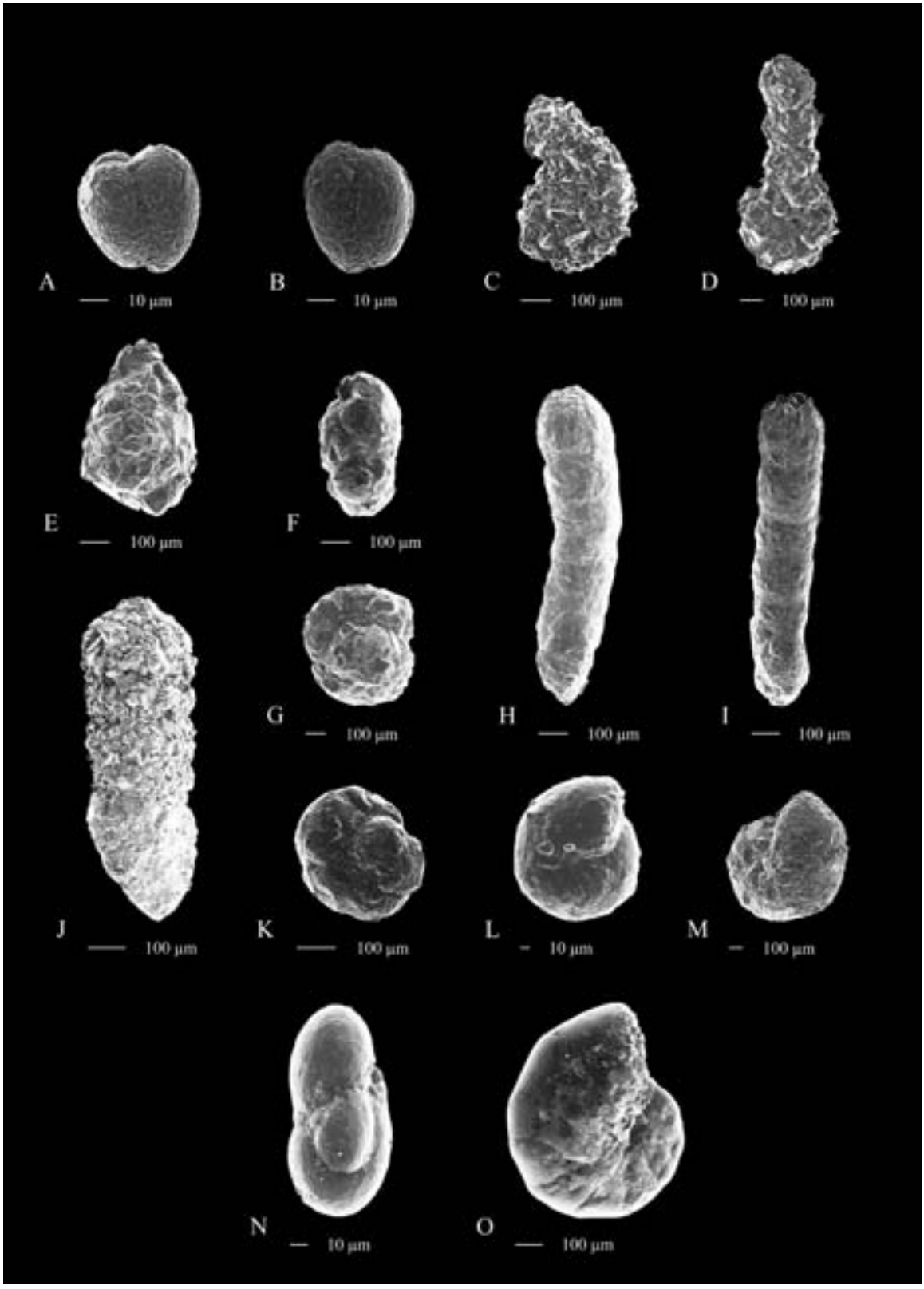
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PLANCHE 2

Figures A, B et C *Eggerella bradyi* (stations A et I)

Figure D *Eggerella scabra* (station B)

Figure E *Glomospira gordialis* (station B)

Figure F *Glomospira charoides* (station I)

Figure G *Karreriella* sp. (station I)

Figures H et I *Karreriella bradyi* (station A)

Figure J Agglutiné sp.22 (station A)

Figures K et L ?*Miliammina* sp. (station A)

Figure M *Pseudoclavulina cylindrica* (station B)

Figure N Agglutiné sp.46 (station A)

Figures O et P Agglutiné sp.11 (station A)

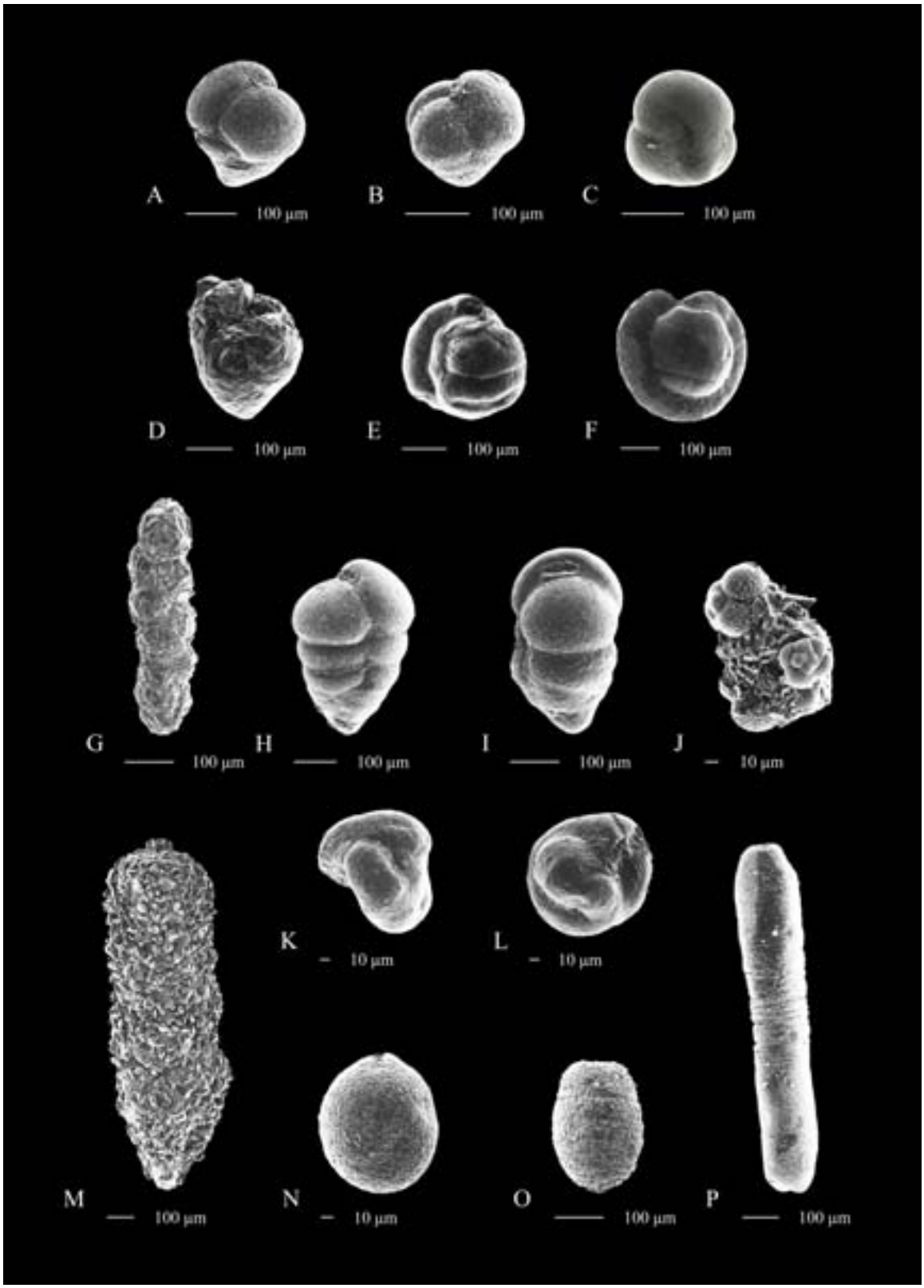
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PLANCHE 3

Figures A, B et C *Reophax bilocularis* (station I)

Figure D *Reophax dentaliniformis* (station I)

Figures E, F et G *Reophax guttiferus* (stations B et I)

Figures H et I *Reophax micaceus* (station A)

Figures J, K, L, M, N, O, P et Q *Reophax scorpiurus* (station A et I)

Figures R *Reophax* sp.3 (station I)

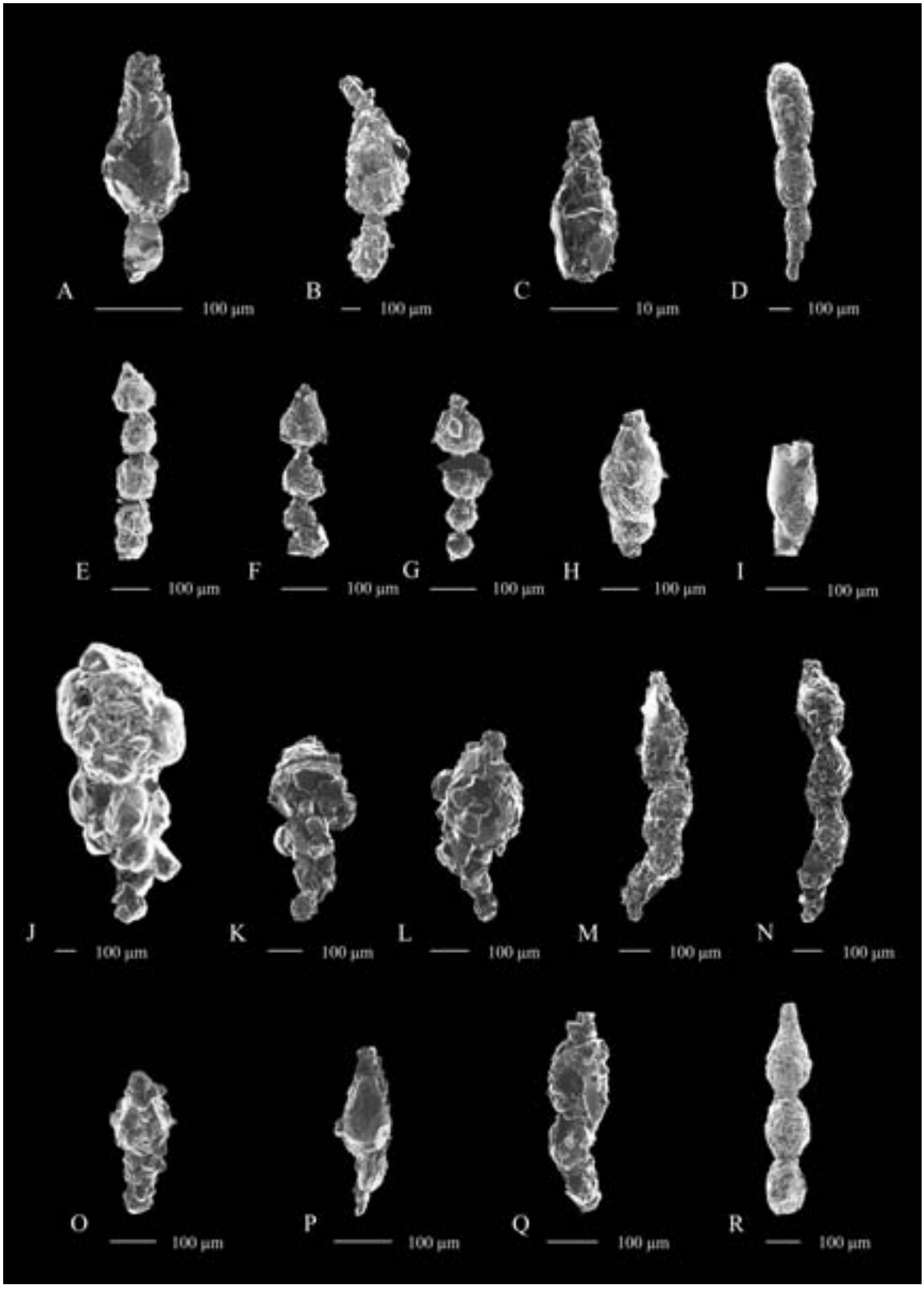
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PLANCHE 4

Figure A *Recurvoides* sp. (station I)

Figures B et C ?*Siphotextularia* sp. et détails des coccolithes constitutifs du test (station I)

Figures D et E *Spiroplectammina* sp. (station I)

Figure F ?*Textularia* sp. (station A)

Figure G *Technitella legumen* (station A)

Figure H *Thurammina albicans* (station A)

Figures I et J *Trochammina* sp.1 (station I)

Figures K et L *Trochammina* sp.103 (station A)

Figure M *Trochammina* sp.5 (station A)

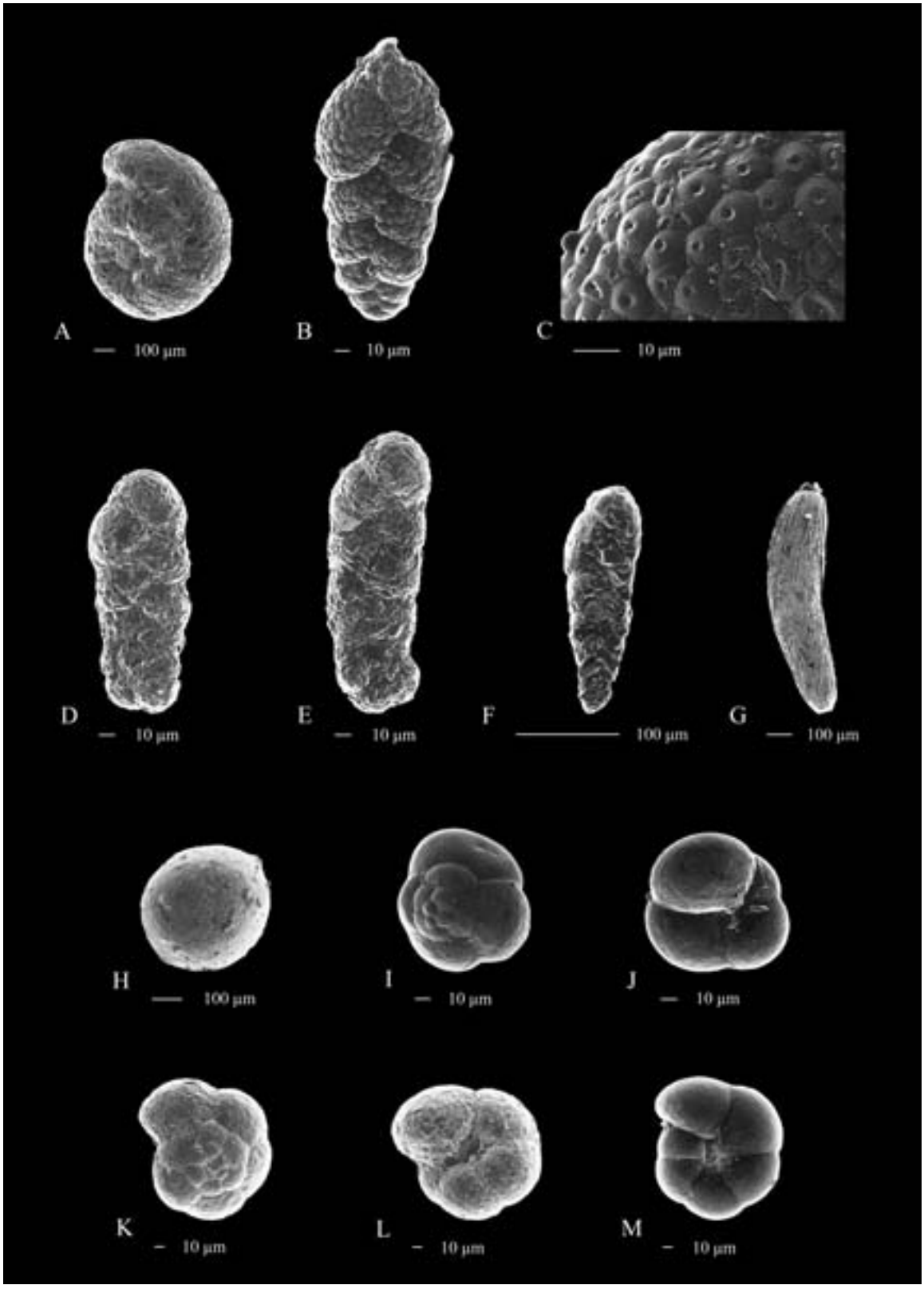
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PLANCHE 5

Figure A *Amphicoryna scalaris* (station A)

Figures B et C *Bolivina pseudoplicata* (station I)

Figure D ?*Bolivina* sp. (station I)

Figure E *Bolivina spathulata* (station B)

Figure F *Bolivina alata* (station D)

Figure G *Bolivina subaenariensis* (station D)

Figure H *Bolivina albatrossi* (station A)

Figure I *Bolivinita quadrilatera* (station B)

Figures J et K *Bulimina alazanensis* (station I)

Figure L *Bulimina inflata* (station A)

Figure M ?*Bulimina inflata* (station I)

Figure N *Bulimina marginata* (station B)

Figures O et P *Bulimina* sp.1 (station I)

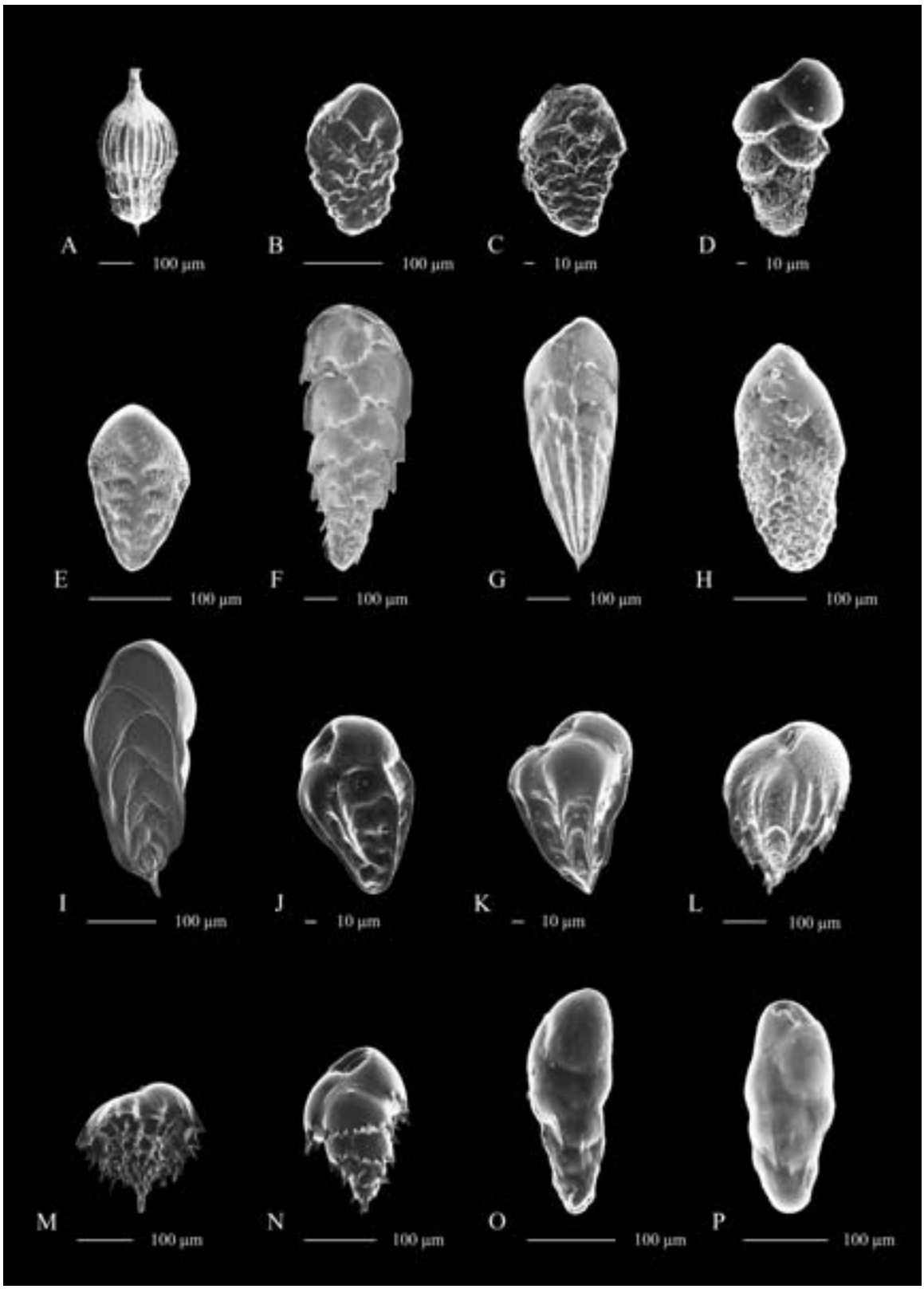
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PLANCHE 6

Figure A *Cassidulina crassa* (station I)

Figure B ?*Cassidulina oblonga* (station I)

Figure C *Ceratobulimina* sp. (station A)

Figures D, E et F *Chilostomella oolina* (stations I et D)

Figure G *Cibicides wuellerstorfi* sur foraminifère branchu indéterminé (station I)

Figures H et I *Cibicidoides pachydermus* (station B)

Figure J *Cibicidoides ungerianus* (station A)

Figure K *Cibicidoides robertsonianus* (station A)

Figures L et M *Coryphostoma* sp. (station D)

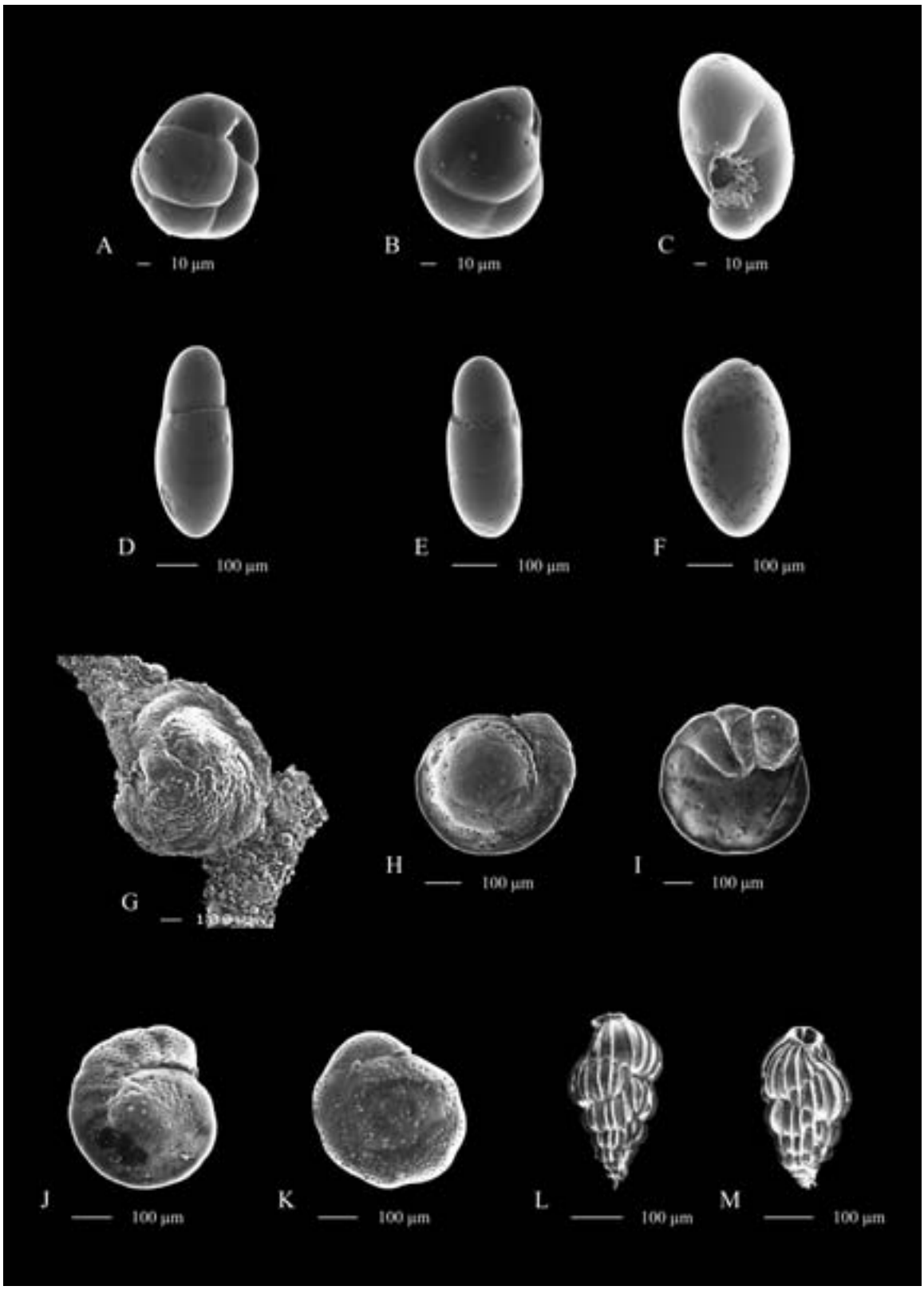
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PLANCHE 7

Figure A *Dentalina subemaciata* (station B)

Figures B, C, D et E *Epistominella exigua* (station I et B)

Figure F *Fissurina* sp. (station A)

Figures G et H *Globocassidulina subglobosa* (station I)

Figures I, J et K *Gyroidina altiformis* (station B)

Figures L et M *Gyroidina orbicularis* (station A)

Figures N et O *Gyroidina umbonata* (station I)

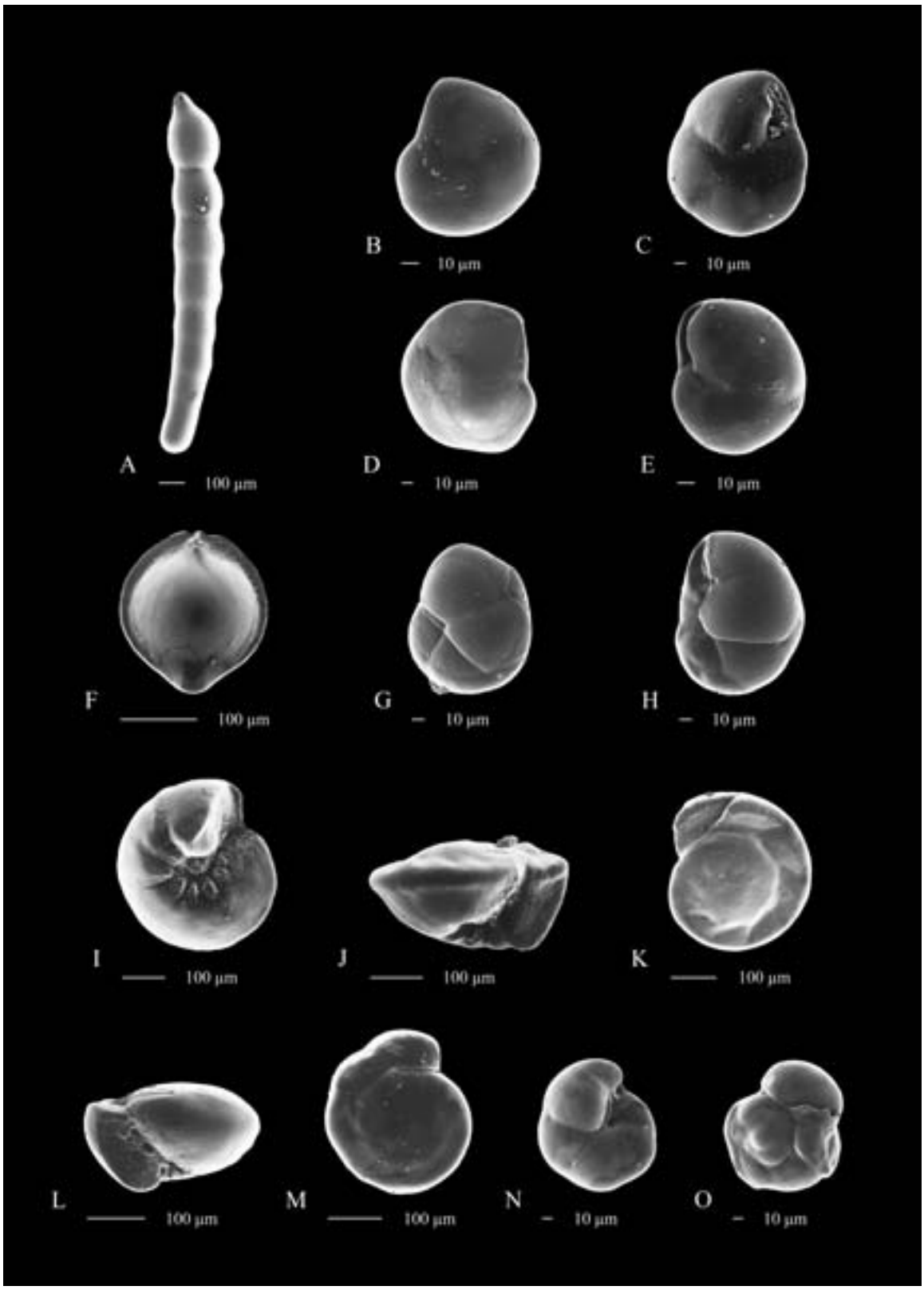
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PLANCHE 8

Figures A, B, C, D et E *Hoeglundina elegans* (stations A et I)

Figure F *Hyalinea balthica* (station D)

Figure G *Lagena* sp. (station A)

Figures H, I, J et K *Melonis barleeanus* (stations A et I)

Figures L et M *Nonion scaphum* (station D)

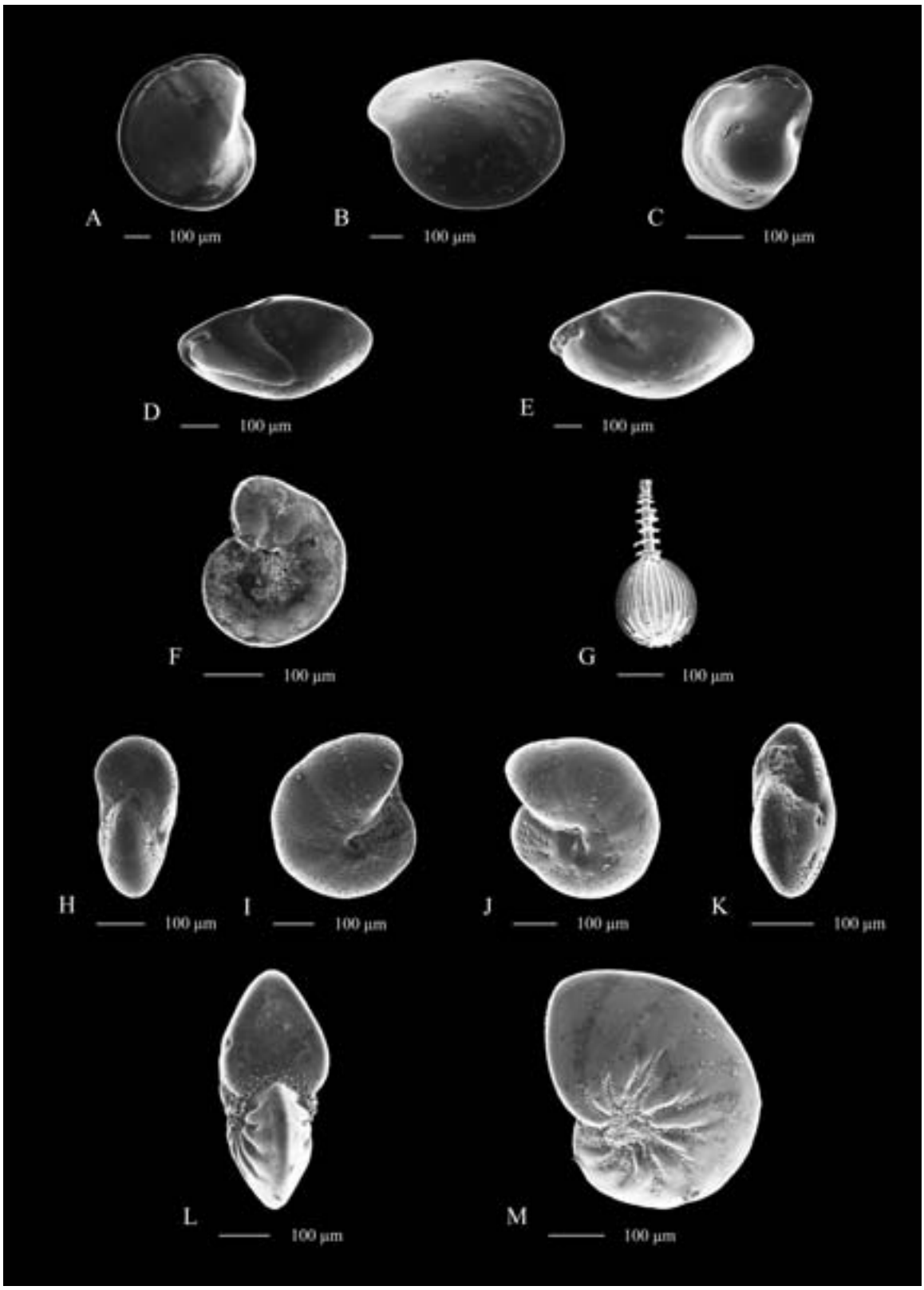
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PLANCHE 9

Figures A, B, C et D *Nuttallides pusillus* (stations A et I)

Figures E, F et G *Nuttallides umboniferus* (station A)

Figures H et I ?*Pseudononion* sp. (station I)

Figures J et K *Pullenia* sp.1 (station I)

Figures L et M *Pullenia bulloides* (station I)

Figures N et O *Pullenia quinqueloba* (station I)

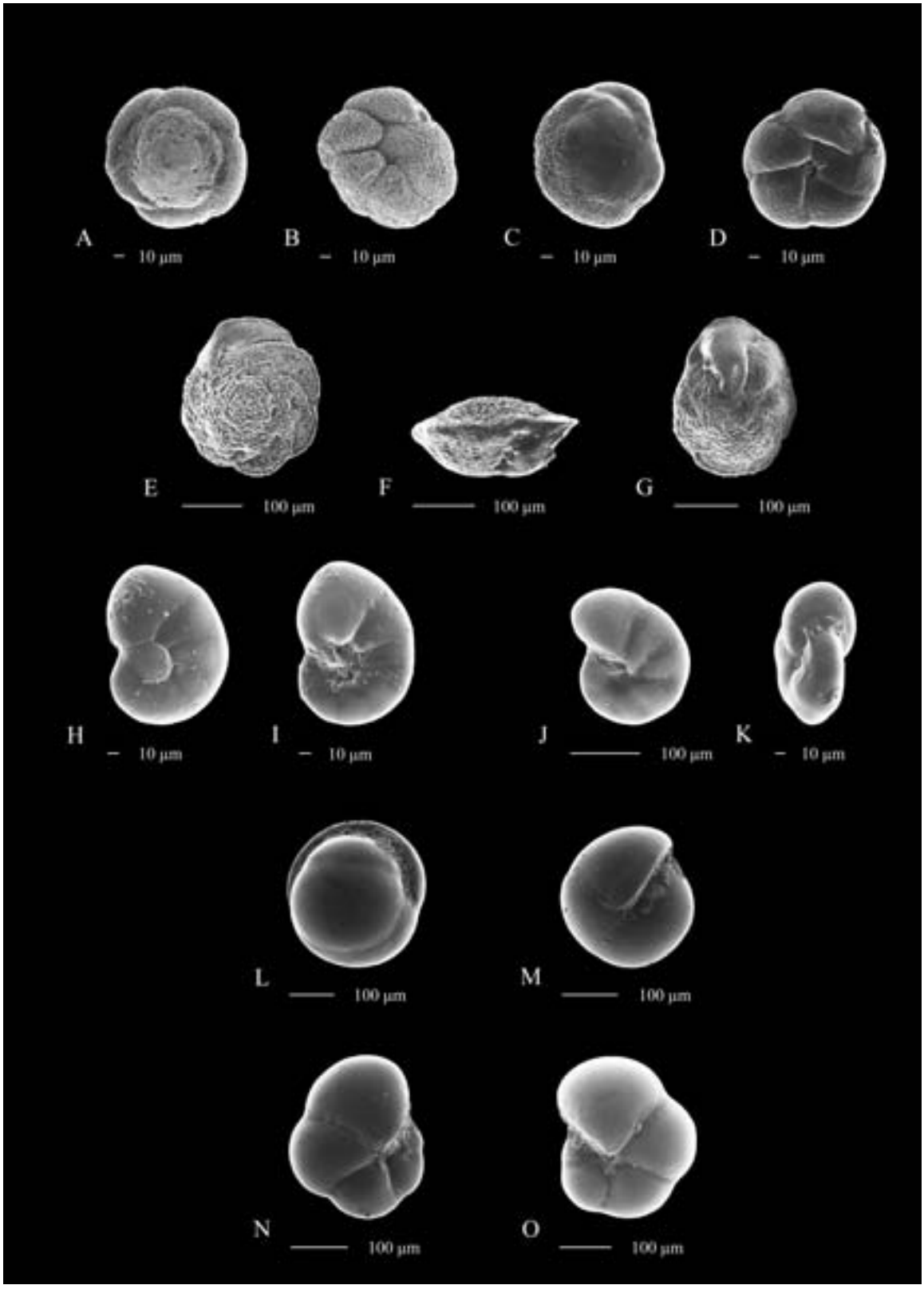
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PLANCHE 10

Figure A *Rectuvigerina phlegeri* (station D)

Figure B *Robertinoides bradyi* (station A)

Figures C et D ?*Rotamorphina involuta* (station A)

Figure E *Siphogenerina columellaris* (station B)

Figures F et G *Trifarina bradyi* (stations A et B)

Figures H et I *Trifarina pauperata* (station A)

Figures J, K et L *Uvigerina elongatastriata* (station B)

Figures M et N *Uvigerina mediterranea* (stations A et B)

Figures O et P *Uvigerina peregrina* (stations A et I)

Figures Q et R *Uvigerina mediterranea* (stations A et B)

Figures S et T *Uvigerina peregrina* (station A)

Figure U *Valvulineria bradyana* (station D)

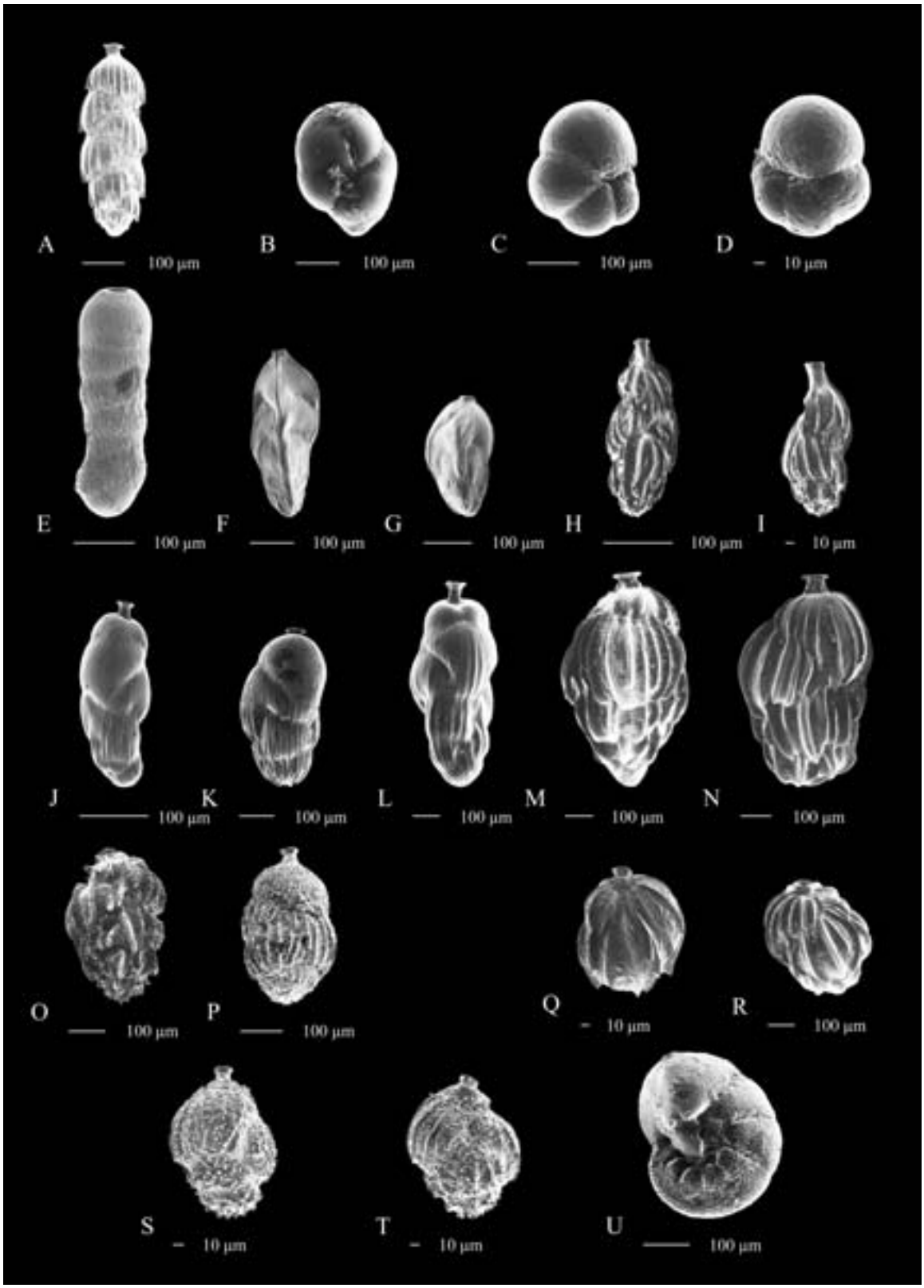
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PLANCHE 11

Figure A *Biloculinella irregularis* (station A)

Figure B *Cornuspira involvens* (station A)

Figure C *Cornuspira foliacea* (station B)

Figure D *Pyrgo elongata* (station I)

Figure E *Pyrgo depressa* (station I)

Figure F *Pyrgo murrhina* (station I)

Figure G *Pyrgo subsphaerica* (station I)

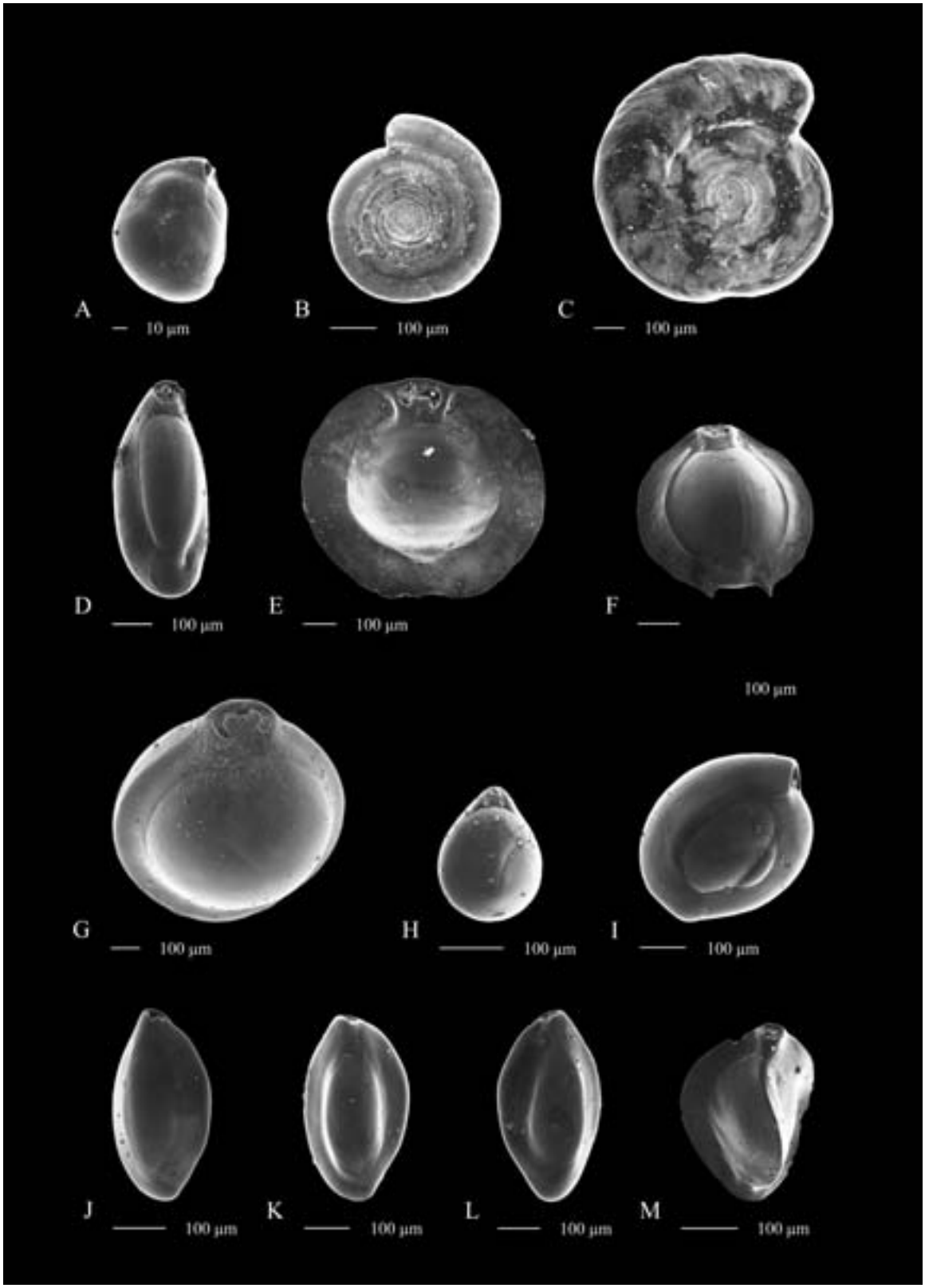
Figure I *Pyrgoella sphaera* (station A)

Figure J *Quinqueloculina seminula* (station I)

Figure K *Quinqueloculina* sp.1 (station I)

Figures L et M *Quinqueloculina* sp.2 (station I)

Figure N *Triloculina tricarinata* (station A)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Annexe 2

Les canyons constituent des environnements sédimentaires très intéressants à étudier à plus d'un titre. Alors que les canyons dits passifs se comportent le plus souvent comme des zones de dépôt centre pour la matière organique détritique, les canyons dits actifs sont le siège de processus d'érosions-dépôts de plus ou moins grande amplitude soulignés par les évênements turbiditiques souvent récurrents. L'article qui suit fait part de l'étude d'une carotte de carottier multitube prélevée en Mai 2000 dans l'axe du Canyon de Capbreton (station K), et dans laquelle des courtes séquences turbidites sont enregistrées (Anschutz et al., 2002). La turbidite la plus récente, liée vraisemblablement à la tempête de décembre 1999, constitue la partie supérieure des dépôts sédimentaires ; elle fait l'objet d'une étude biogéochimique exhaustive. Il est notamment suggéré que la faune de foraminifères bentiques échantillonnés dans le premier décimètre de la carotte, au sommet de la turbidite, corresponde à un stade de recolonisation précoce d'un sédiment superficiel turbiditique fraîchement déposé.

Journal of Marine Research, 60, 835–854, 2002

Recent turbidite deposition in the eastern Atlantic: Early diagenesis and biotic recovery

by P. Anschutz[1], F. J. Jorissen[1,2], G. Chaillou[1], R. Abu-Zied[3] and C. Fontanier[1]

ABSTRACT

An interface core taken in Capbreton canyon shows a succession of sedimentary facies interpreted as classical Bouma turbiditic sequences. Activities of ^{234}Th and ^{210}Pb suggest that the deposition of the most recent turbidite was triggered by the violent storm that affected the Atlantic coast of southern France on the 27th of December 1999, about four months before the sampling of the core. This turbidite allows us to study the ongoing diagenesis of the new sediment layer and of the previous sediment-water interface, which has been buried and only slightly eroded. A study of benthic foraminiferal populations informs us about the rate of benthic ecosystem recovery after such a major ecosystem disturbance event. The composition of the benthic foraminiferal fauna suggests that the benthic ecosystem in Capbreton canyon remains in an early stage of colonization. The rare agglutinant taxon *Technitella melo* appears to be the first colonizing species. It is suggested that *Technitella melo* is advantaged by the food-impoverished conditions in the days following turbidite deposition. Almost all of the turbidite layer and the previous oxic sediment-water interface contain reduced dissolved metal species and were anoxic. The buried interface contains Fe- and Mn-oxides inherited from its recent oxic past. The reduction of manganese oxides was in progress at the time of core collection. The reduced Mn remained trapped in the sediment as Mn-containing carbonates. Iron-oxides did not undergo significant reductive dissolution. The top of the newly deposited turbidite formed an oxic layer, which was rapidly enriched in metal-oxides. The enrichment of manganese oxides was mostly due to the oxidation of dissolved Mn^{2+}, which diffused from below. The enrichment of iron oxides is explained both by the oxidation of the upward flux of dissolved Fe^{2+}, and by the input of detrital iron oxide after, or as a result of the turbidite deposition.

1. Introduction

The deposition of turbidites in marine environments results from gravity flows triggered by mass wasting events, during which several centimeters or meters of new sedimentary material can be rapidly deposited on top of autochthonous sediments (Bouma, 1962; Mulder and Cochonat, 1996). The gravity flow may either erode the previous sediment-

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water interface, or preserve it below the newly deposited sediments. In both cases the ongoing biogeochemical and biological processes will be strongly disturbed. The aim of this paper is to study these changes, especially those affecting the redox state of the dominant elements, and the biological response to the disturbance, evidenced by benthic foraminifera, a dominant element of deep-sea meiofauna (Gooday *et al.,* 1992).

One of the major biogeochemical changes accompanying turbidite emplacement is the isolation of the former sediment-water interface from oxygenated seawater. For example, Fe- and Mn-oxides are solid in oxic conditions, and are generally enriched in the oxic layer at the top of the sediment. In case of a rapid oxygen depletion of the sediment-water interface, the metal oxides may either dissolve and migrate through the sediment column (Mucci and Edenborn, 1992), or they may persist for years and form an oxic barrier for reduced species at depth within the sediment. The return to steady-state conditions at the fossilized interface will depend on the relative proportion of reduced and oxidized species and the kinetics of the biogeochemical processes. Several studies have described non-steady-state diagenesis linked to the deposition of turbidites. Most of these papers describe modifications of the sediment geochemistry caused by turbidite deposition on a millennial time scale (e.g. Wilson *et al.,* 1985; DeLange, 1986; Buckley and Cranston, 1988; Thomson *et al.,* 1998) or, at best, a decadal time-scale (Mucci and Edenborn, 1992). Observations of the evolution of redox-sensitive species toward a new steady state have only been described for a sediment layer deposited in Saguenay fjord after a catastrophic flash flood in 1996 (Deflandre *et al.,* 2000; 2002).

Benthic foraminiferal colonization has been studied intensively in nearshore and in laboratory settings. An excellent overview of the most significant results is given by Alve (1999). There appears to be an important difference between two types of environments. In areas with a high hydrodynamic energy (current velocities > 20 cm/s), recolonization may be nearly instantaneous, and faunas comparable to those before the disturbance event may install in a couple of days. In low energy environments (current velocities < 10 cm/s), on the contrary, it may take many months, or even years to arrive at faunas with a density, species variability and equitability comparable to the original faunas. In this case, a classical ecological succession develops, with a first colonization of a low diversity opportunistic pioneer fauna, followed by several intermediate faunas, before arriving at the highly diverse, specialized climax community (Alve, 1999). Certain negative aspects of the newly available environment, such as the presence of anoxic conditions, or strongly diminished food availability, may cause significant delays.

Few data (see Alve, 1999 for an overview) exist on foraminiferal re-colonization of deep-sea environments. Hess and Kuhnt (1996) conclude that even several years after the 1991 Mt Pinatubo ashfall, the faunas were still far from total recovery. Very little information is available about re-population after turbidite deposition. Jorissen *et al.* (1994), who studied live foraminiferal assemblages in Wilmington and South Hayes Canyon (off New Jersey, USA), conclude that the rather poor, low diversity, and surface living faunas represent a first stage of ecosystem colonization. They speculate that in these

very active canyon environments foraminiferal faunas will often remain in early colonization stages, and will not fully recover. Therefore, it is very difficult to define the characteristics of the climax community.

The top of the sedimentary sequence recovered at 650 m water depth in the canyon of Capbreton contains a turbidite, presumably deposited only a few months before sampling (Mulder *et al.,* 2001). The most probable natural event capable of triggering the turbidity current was the violent storm that affected the southern French Atlantic coast on the 27th of December 1999. The material collected on the 2nd of May 2000 gives us the opportunity to study the transient behavior of redox sensitive species in the buried sediment-water interface and the biogeochemical properties of the newly formed sediment-water interface. Furthermore, it allows us to observe the state of foraminiferal recolonization 4 months after the disturbance event, which created a more or less abiotic environment, which will subsequently be recolonized.

2. Material and methods

The studied sediment was collected with an SMBA multi-corer in the southeastern part of the Bay of Biscay, at 647 m depth (station K), in the axis of Capbreton canyon (Fig. 1), on the 2nd of May 2000, during cruise Oxybent 10. The bottom waters are North Atlantic Central Waters, with an *in situ* temperature of 10.7°C (Ogawa and Tauzin, 1973). Capbreton canyon is one of the largest European submarine valleys. The axis is a location of turbidite deposition (Nesteroff *et al.,* 1968). The SMBA multi-corer allowed us to sample the first decimeters of the sediment, the overlying bottom waters, and the undisturbed sediment-water interface, in a 10 cm diameter plexiglas tube. Overlying water samples were collected immediately after core recovery for dissolved O_2 measurements, using the Winkler titration method (Strickland and Parson, 1972). Profiles of pore water O_2 were measured on board using a cathode-type mini-electrode (Revsbech and Jørgensen, 1986; Helder and Baker, 1985; Revsbech, 1983). The measurement was performed at a 1 mm step 5 mm above the sediment-water interface, within the bottom water recovered with the multi-tube device, and 20 mm below, in the sediment. It was completed within 15 min after core recovery. Subsequently, the core used for O_2 profiling was sliced in thin horizontal sections (0.5 cm for the top 2 cm, 1 cm below, and 2 cm at the bottom) within 90 minutes. For each level a sub-sample was immediately sealed in a pre-weighed vial and frozen under inert atmosphere (N_2) for further analyses of porosity and solid fraction. Another subsample was centrifuged under N_2 at 5000 rpm during 20 min in order to collect pore waters. Two aliquots of water were filtered (0.2 μm) and frozen at −25°C for nutrient analyses, and the other aliquot was filtered and acidified with ultrapure HNO_3 for dissolved Mn and Fe analyses. This sub-sampling has been used routinely for all cores of the eleven Oxybent cruises (Anschutz *et al.,* 1999). The vertical resolution for pore water analyses is high at the top and slightly poorer below. However, our sampling procedure allowed us to extract three samples below the recent turbidite. A second tube of the same multi-core employment was brought back to the laboratory and opened (in late May 2000) for

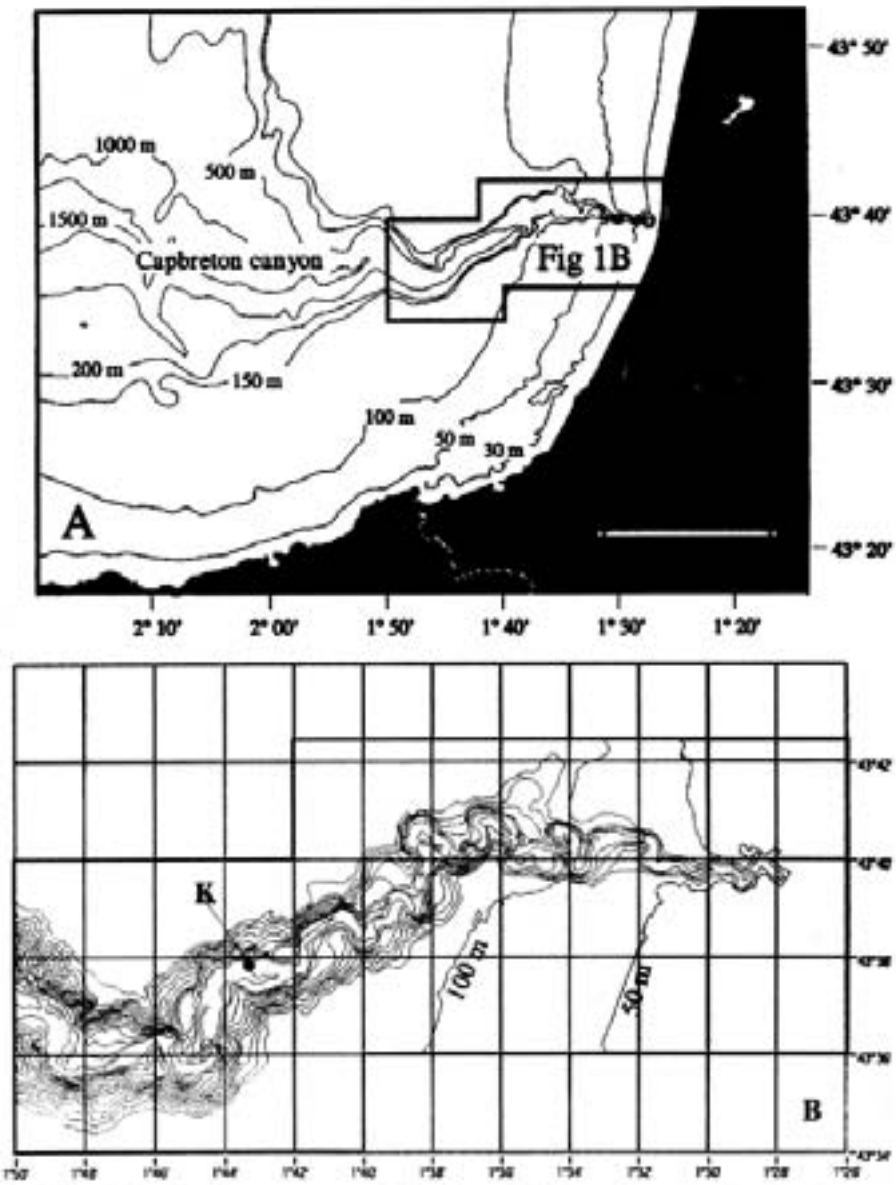

Figure 1. A. Map of the Southeastern part of the Bay of Biscay showing the Capbreton canyon. B. Detailed map of the study area showing the location of the Station K. Isobaths at 50 m intervals (from Mulder *et al.*, 2001).

sedimentological observations and high-resolution sub-sampling of the solid fraction. A third core was sampled for benthic foraminifera immediately upon retrieval. The top ten centimeters of the core were sliced, the 0–1 cm interval into 0.25 thick slices, the 2–4 cm interval into 0.5 cm slices, and the 4–10 cm interval into 1 cm thick slices. Sediment was stored in 250 ml bottles, which were filled with 95% ethanol and contained 1 g/l Rose-Bengal stain (Lutze and Altenbach, 1991). In late May 2000, the five cm below the turbidite were sampled in the second tube (see before), and underwent the same treatment.

Foraminiferal samples were sieved through 63 and 150 μm mesh screens. All sieve fractions were preserved in 95% ethanol. Foraminifera were picked from a solution of 50% ethanol, and stored in Chapman slides. When we discovered the presence of a recent turbidite, about three weeks after sampling, new samples were collected immediately below the turbidite. This paper concentrates on the foraminifera found in the >150 μ fraction. The concentration of living (stained) benthic foraminifera as well as planktonic foraminifera is expressed as the number of individuals per 50 cm^3.

The activities of ^{210}Pb and ^{234}Th were determined in freeze-dried samples by gamma counting. The excess activity of ^{210}Pb was calculated from ^{226}Ra-supported ^{210}Pb deduced from the activities of ^{214}Pb and ^{214}Bi. Porosity was determined by comparison of the weights of wet and freeze-dried sediment. The freeze-dried solid fraction was homogenized and the water content used to correct the analyses for the presence of sea salt.

Particulate sulfur (S_{tot}) and total carbon were measured on the dry sediment using a Leco C/S 125. Inorganic carbon (C_{inorg}) was measured by automated calcimetry with 6N HCl from 250 mg of powdered sample. Organic carbon (C_{org}) is calculated as the difference between total carbon and C_{inorg}. Wet samples were subjected to an extraction technique for the determination of reactive particulate Fe- and Mn-oxides. The most reducible fraction was extracted with an ascorbate solution buffered at pH 8 (Ferdelman, 1988; Kostka and Luther, 1994; Anschutz *et al.,* 1998). About 1 g of wet sample was leached with a 25 ml solution during 24 hours while shaking continuously at room temperature. Iron extracted with ascorbate (Fe_{ASC}) comes from amorphous iron oxides. Specific tests on particulate-Mn extraction with ascorbate (Mn_{ASC}) have not yet been published. It has been shown in our laboratory, however, that it represents the complete fraction of Mn-oxides. Mn_{ASC} is extracted at pH 8, which suggests that Mn-carbonates are not leached. Mn and Fe were measured by flame atomic absorption spectrometry.

Interstitial water compounds were analyzed using techniques adapted for small volumes of samples. Nitrate was measured by flow injection analysis (FIA) according to Anderson (1979). Ammonia was analyzed with the FIA method described by Hall and Aller (1992). Dissolved Fe was measured with the colorimetric method using ferrozine (Stookey, 1970). Dissolved Mn^{2+} was determined by atomic absorption spectrometry. The pH was measured onboard with an electrode calibrated using three NBS buffers and a synthetic seawater TRIS buffer solution.

3. Results

a. Core description

Macroscopic observation of the core shows three sedimentary units noted S1, S2 and S3 from top to bottom. A detailed description of these sedimentary sequences, based on an X-ray imaging system and grain size measurements, was presented earlier by Mulder *et al.* (2001). The two topmost units, S1 and S2, are separated by an erosive contact; also the contact between units S2 and S3 is rather sharp. Ocher (10YR 6/5) oxidized layers

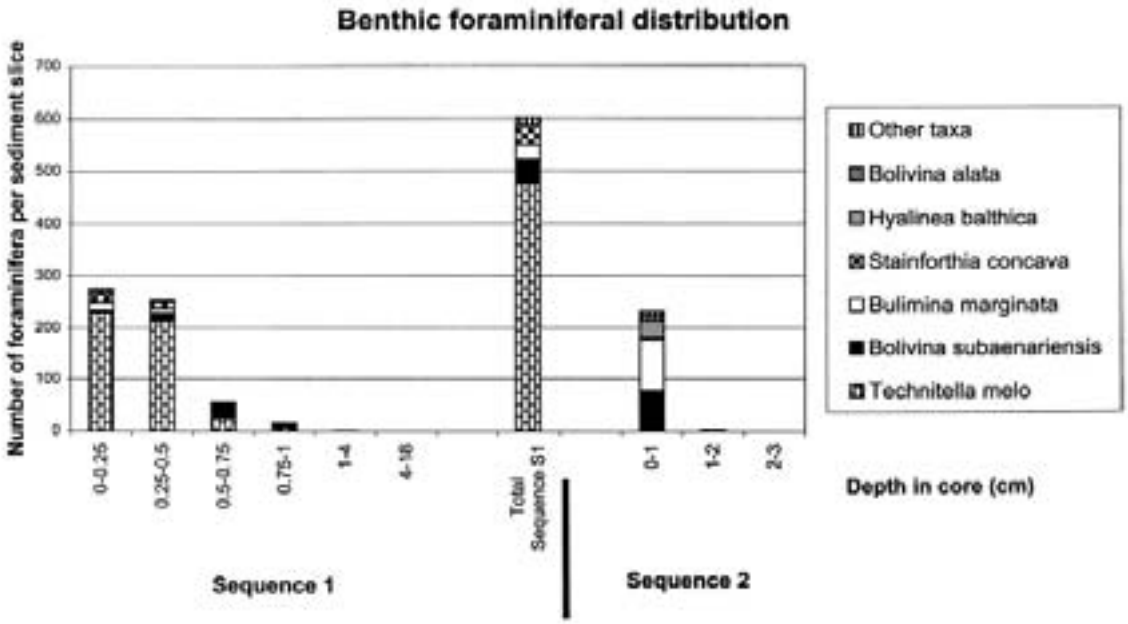

Figure 2. Vertical distribution of Rose-Bengal stained benthic foraminiferal tests. Numbers are given per 50 cm^3.

containing Rose-Bengal stained benthic foraminifera are located below the contact between S1 and S2. Sequence S3 is a fining-up sequence with its base missing due to insufficient coring depth. Grain size grades up from fine sands to clayey silts. Sequence S2 is 5 cm thick. It contains only a fine silty clay facies with slight bioturbation at its top, overlain by an oxidized layer. Sequence S1 is the most complete one. It is 18-cm-thick, fining-upward, and shows a clean sandy facies with mud clasts at the base, above an erosive basal contact. This 3 cm thick basal part is overlain by a facies with convolute laminations and by a facies with parallel laminations. The latter facies is marked by an increase of porosity. The sequence ends with a 6 cm thick silty-clay facies similar to the facies observed in S2 with slight bioturbation in the top centimeter. A 1 cm-thick oxidized facies has developed at the top of the core. The facies succession and the progressive fining-up trend suggest that the three sequences observed in core K correspond to classical Bouma sequences (Bouma, 1962; Shanmugam, 1997). The unlaminated facies at the top of the three sequences is interpreted as the composite of the finest, topmost part of the turbiditic facies and the hemipelagic, clay sedimentation in the months following turbidite deposition.

b. Foraminiferal distribution

Sequence S1 contains a fairly rich stained benthic foraminiferal fauna, which is entirely concentrated in the oxic layer (Fig. 2, Table 1). The bulk of the live specimens (88%, 528 out of 601) are even found in the first two 0.25 cm levels. The fauna is strongly dominated by *Technitella melo,* which accounts for 79% of the total. *Stainforthia concava* (6%),

Table 1. Number of Rose-Bengal stained benthic foraminifera per sediment slices and the abundance of planktonic foraminifera.

Station OB10-K	*Technitella melo*	*Bolivina subaenariensis*	*Bulimina marginata*	*Stainforthia concava*	*Hyalinea balthica*	*Bolivina alata*	Other taxa	Total benthic foraminifera	Planktonic foraminifera	Planktonic forams/10cc
0–0.25	229	3	17	18	1		7	268	51	32,38
0.25–0.5	214	14	9	14			2	251	59	37,46
0.5–0.75	24	23	3	3			3	53	46	29,21
0.75–1	7	5	1	1			2	14	47	29,84
1–4	1						0	1	32	10,16
4–18							0	0	8	1,27
0–1		78	100	1	35	8	9	222	101	16,03
1–2		1	1				1	2	77	12,22
2–3							0	0	12	1,90
Total Sequence S1	475	124	131	37	36	8	24	811	433	
Total Sequence S2	0	79	101	1	35	8	10	224	190	

Bulimina marginata (5%) and *Bolivina subaenariensis* (7.5%) are the main accompanying taxa. The former two species are mainly present in the first two 0.25 cm levels, whereas *B. subaenariensis* is found slightly deeper, and has a maximum in the 0.5–0.75 cm level. Eight rarer taxa account for the remaining part of the fauna. Planktonic foraminiferal tests (Fig. 3) are fairly abundant in the first cm (about 150 tests per 50 cc), in the second cm their density drops to about 50 tests per 50 cc, and in all deeper levels only trace quantities are found.

The top of sequence S2 was sampled in less detail. The topmost 0–1 cm level contains 231 weakly stained specimens, the 1–2 cm only 3 weakly stained specimens. The fauna is dominated by *B. marginata* (43%), *B. subaenariensis* (34%) and *Hyalinea balthica* (15%). Six other rare taxa complete the assemblage. Planktonic foraminiferal tests are relatively abundant (50–70 tests per 50 cc) in the first 2 cm; only trace quantities were found in deeper layers (Fig. 3).

c. Geochemistry

With its very short half-life of 24 days, $^{234}Th_{exc}$ should be present only at the water-sediment interface. The top of S1 has an extremely high $^{234}Th_{exc}$ activity, of 3600 Bq/kg. However, the activity remains high in the top 6 cm of the core (Fig. 4), suggesting an efficient mixing of the sediment. The preservation of the turbiditic sequences (Mulder *et al.,* 2001) suggests that the post-depositional mixing of the particles was low.

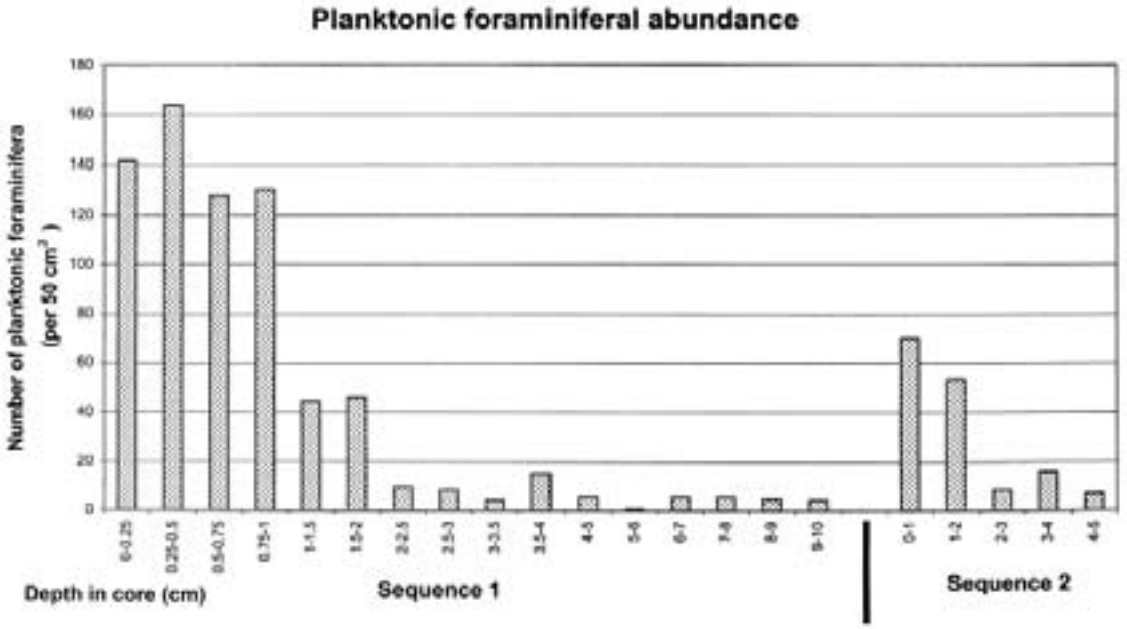

Figure 3. Vertical distribution of planktonic foraminiferal tests, standardized for a sediment volume of 50 cm^3.

The activity of $^{234}Th_{exc}$ detected below the sediment-water interface is probably a residue of the ^{234}Th, which has been trapped on the fine particles during the turbiditic event, and before their settling. The detectable activity of $^{234}Th_{exc}$ indicates that the turbidite has been deposited within less than a few months before core collection. Also the interface between S1 and S2 shows a high $^{234}Th_{exc}$ activity. This suggests that this former sediment-water

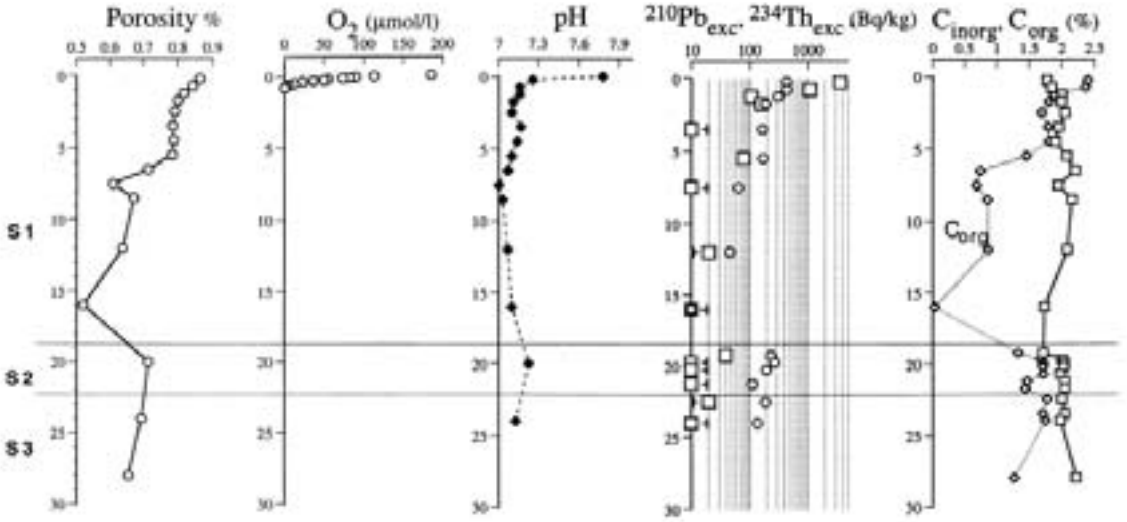

Figure 4. Vertical profiles of porosity in %, pore water O_2 in µmol/l, pH, organic carbon (C_{org}), and inorganic carbon (C_{inorg}) in weight percent of dry sediment corrected for salt content, and excess ^{210}Pb (circles) and ^{234}Th (squares) in Bq/kg in the sediment of the Station K.

interface has been covered very recently by the turbiditic sequence S1. The most probable natural event able to trigger the turbidity current is the violent storm that affected the southern Atlantic coast of France the 27th of December 1999 (Mulder *et al.,* 2001). Therefore, the time elapsed between the turbidite event and the core sampling was probably 127 days. 127 days corresponds to more than 5 half-lives of the radioactive decrease of ^{234}Th, which indicates that the activity of $^{234}Th_{exc}$ at the top of S2 was close to 1600 Bq/kg at the time of the turbidite emplacement. Such a high activity is common for the top sediments of the Capbreton canyon (Hyacinthe *et al.,* 2001). The top parts of S1 and S2 show a high $^{210}Pb_{exc}$ activity (half-life of 22.3 years) (Fig. 4). The $^{210}Pb_{exc}$ activity decreases at the bottom of S1. In a sedimentary sequence, where the grain size grades up, the $^{210}Pb_{exc}$ activity cannot be directly related to the accumulation rate and the continuous radioactive decay. The activity also depends on the $^{210}Pb_{exc}$ inventory at the moment of the sediment deposition. The grain size is a parameter, amongst others, which determines the amount of $^{210}Pb_{exc}$ adsorbed on particles. In the sequence S1, the downward decrease of the $^{210}Pb_{exc}$ activity can be related to the increase of grain size.

The dissolved O_2 concentration in the bottom water was 202 μmol/l, which corresponds to concentrations measured earlier at this water depth (Ogawa and Tauzin, 1973). Oxygen concentration decreased 2 mm above the sediment-water interface and reached the zero level at only 7 mm depth, and remained at zero deeper down. The bottom water pH was 7.78. It dropped to 7.26 in the upper part of the core and continued to decrease below to values between 7.2 and 7.0. The pH increased again to 7.23 in the sample located just below the S1–S2 interface (Fig. 4).

The organic carbon content is above 1.5 wt% at the top of S1 and S2 (Fig. 4). The concentration drops below 1 wt% in the silty and sandy facies in the lower part of S1. It was close to 0 at 16 cm depth at the bottom of unit S1. The C_{inorg} concentration of the sediment has a mean concentration of 2.0 wt%. This concentration does not vary significantly along the profile. However, values lower than 1.8% were measured at the very top of the core, at the top of the S1–S2 interface, and at the sandy bottom of S1.

The nitrate concentration was close to 15 μmol/l in the bottom water and decreased sharply within the oxic layer to values lower than 2 μmol/l (Fig. 5). We observed a peak of 5 μmol/l at the bottom of S1. The concentrations of dissolved NH_4^+ were below the detection limit in the bottom water and they increased in a regular manner in the upper part of the S1 unit. They reached a concentration above 600 μmol/l below unit S1 (Fig. 5).

Dissolved manganese became detectable in samples where the oxygen concentration reached values close to zero. Below, the Mn^{2+} concentrations increased sharply to values which stay close to 50 μmol/l. The sample located at the top of S2 had a concentration peak of 110 μmol/l (Fig. 5). The profile of dissolved Fe was more irregular than that of Mn^{2+}. Dissolved iron appears 5 mm below dissolved manganese. It increases below to concentrations up to 650 μmol/l. Dissolved iron decreases at the bottom of unit S1 but increases again to 200 μmol/l in unit S2.

The profiles of reactive metal oxides extracted with ascorbate (Fig. 5) shows maximal

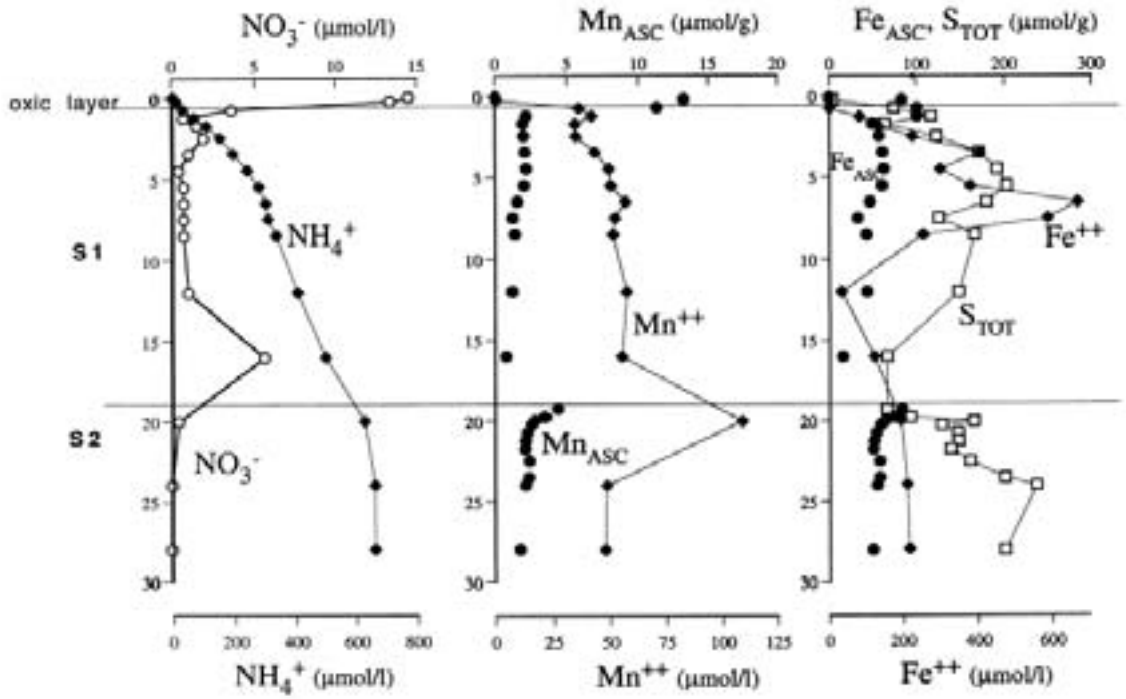

Figure 5. Vertical profiles of redox sensitive species in sediments of the Station K. The pore water compounds are given in µmol/l (NO_3^-, NH_4^+, Mn^{2+}, Fe^{2+}). The value indicated at depth 0 cm represents the value measured in the bottom water. The reactive particulate phases are given in micromole per gram of dry sediment (µmol/g) and correspond to ascorbate extractable manganese (Mn_{ASC}) and iron (Fe_{ASC}), and total sulfur (S_{tot}).

values in the top centimeter of the core for Mn and in the top 1.5 cm for Fe. The concentrations decrease abruptly to intermediate values in the unlaminated and high porosity facies between 1.5 and 6 cm. The lowest concentrations are measured in the silty and sandy facies in the bottom part of S1. A second maximum of Fe_{ASC} and Mn_{ASC} is detected in the top cm of the unit S2.

Solid sulfur represents less than 20 µmol/g in the oxic part of the core. The concentrations increase below the oxic layer. The shape of the S_{TOT} profile in the S1 unit is very similar in shape to the Fe_{ASC} profile.

4. Discussion

a. Rose Bengal staining

Rose Bengal stain is commonly used for the recognition of live benthic foraminifera. This non-vital stain, which attached to proteins, ideally provokes a bright pink color. Unfortunately, rose Bengal will stain both healthy and necrotic protoplasm, as well as bacterial films at the test interior (Bernhard, 1988; 2000). Because of interspecific differences in staining intensity, criteria have to be selected for each taxon. But even within a taxon, important variability of staining intensity may be found, increasing the subjectivity

of the method. Nevertheless, the rose Bengal technique is still the only methods, which allows us to recognize the living foraminifera in large assemblages of mixed (alive and dead) foraminiferal tests.

Because of the appearance of fairly rich stained faunas in anoxic sediments, several authors (e.g. Douglas *et al.,* 1978; Corliss and Emerson, 1990; Jorissen *et al.,* 1995) have questioned whether these stained tests really correspond to live individuals, or, rather, to dead specimens which were preserved in anoxic conditions, where protoplasm decay may be a relatively slow process. Douglas *et al.* (1980) estimated that about 30% of stained foraminifera found in anoxic sediments in Santa Monica Basin, showed signs of protoplasm decay, and were probably dead at the time of collection. Bernhard (1988) showed that foraminifera still stained four weeks after their death in oxic conditions. Corliss and Emerson (1990) estimate maximum values for the protoplasm decay period of 0.07–2 years at the oxic sediment-water interface, and 2–80 years in deeper sediment layers. Unfortunately, none of these authors mention how exactly the protoplasm of dead foraminifera is stained. In our experience (which is based on the analysis of the faunas of more than 50 stations down to 5 to 10 cm depth in the sediment), most specimens found at the sediment surface, have all chambers clearly stained (often with the exception of the last chamber). But also for these presumable living specimens, the brightness of the staining is very variable between species. In specimens sampled in well oxygenated sediments, the difference between stained and unstained specimens is obvious, protoplasm degradation is apparently rapid, and the subjectivity involved in the quantification of the living fauna is minimal. In the deeper, dysoxic or anoxic sediment layers, a wide range of staining intensities can be found. Some specimens are still brightly stained, in others, perhaps recently dead specimens with necrotic protoplasm, staining is duller, and in still other specimens, perhaps with a more advanced state of protoplasm decay, only a few chambers are weakly stained. It is evident that the quantification of the live faunas is more subjective here. The risk of identifying important amounts of dead foraminifera as living one can be minimized by the application of very strict staining criteria, based on observations on the staining of the same species in the surface sediment layer.

Unfortunately, the faunas from sequence S2 were only stained about 4 weeks after core retrieval. Therefore, the weakly stained specimens found in the top of this sequence, all of which are rejected as living by our usual staining criteria, cannot be interpreted unambiguously. The faunas may have still been alive at the time of sampling, and in that case the weak aspect of the staining could be due to partial protoplasma degradation in the four weeks following sampling. A second, in our opinion more probable, possibility is that dead specimens still stained weakly several months after the deposition of the turbidite, and the ensuing death of the foraminifera. This prolonged period of time can be explained by the fact that the sediment at the top of sequence S2 rapidly became anoxic after the deposition of sequence S1. In both cases, the presence of these weakly stained foraminifera confirms that the deposition of sequence S1 took place in the recent past. Unfortunately, this

information does not allow us to precise the period elapsed since the death of the foraminiferal fauna.

b. Benthic foraminiferal recolonization

The recent fauna is strongly dominated by *Technitella melo*. This rather poorly known agglutinated taxon has been described from low oxygen environments (Bernhard, 1992). In the Bay of Biscay, the taxon has never been encountered in any of the other ten sampling stations (e.g. Fontanier *et al.,* 2002). The accompanying three taxa are more common, and are typical of the Capbreton canyon area. *Bolivina subaenariensis, H. balthica* and, to a lesser degree, *Bulimina marginata* strongly dominate the extremely rich live faunas (up to 8600 specimens under a 72 cm^2 surface) sampled at station G, positioned in the Capbreton Canyon at 450 m depth (unpublished data). *B. subaenariensis* has been described as a major species in an assemblage influenced by periodic upwelling off Florida (Sen Gupta *et al.,* 1981). *S. fusiformis* is considered as an opportunistic early colonizer (Alve, 1994; 1999). Many other references show the success of these taxa in high productivity (and sometimes low oxygen) environments, confirming the opportunistic behavior of these taxa.

We think that both the surface fauna and the fauna at the top of turbiditic sequence S2 correspond to an early stage of ecosystem colonization. The very low species diversity, the sediment surface microhabitats and the opportunistic behavior of the dominant taxa strengthen our opinion. These early stages of colonization would mean that the periods of time between the successive turbiditic sequences is in most cases too short to reach more mature faunas. A similar phenomenon was observed in Wilmington Canyon (Western Atlantic), where low foraminiferal densities and a total absence of foraminifera below the first cm were explained by the physical instability of the canyon environment, keeping the faunas in an early stage of colonization (Jorissen *et al.,* 1994).

In the case of Capbreton canyon station K, *Technitella melo,* which we never observed in our other ten stations from the Bay of Biscay, was probably one the first species colonizing the abiotic environment after the deposition of the turbiditic sequence S1. In more advanced stages of ecosystem colonization, represented by the slightly more diverse fauna on top of sequence S2, this taxon is probably absent because of its lower competitive abilities in comparison with other taxa. We speculate that *T. melo,* which is otherwise a very rare species, strongly dominates the recolonizing assemblage, because it may be adapted to the rather specific conditions following turbidite deposition. The turbiditic sediment is composed of silts with about 1.8% of organic matter. Although this concentration of organic matter is very high for deep sea sediments, visual inspection suggests that it concerns mainly plant debris. Since cellulose is not metabolisable without the intervention of fermenting anaerobic microbial communities (Fenchel and Finlay, 1995), it is possible that despite the elevated percentage of organic matter, the environment was very oligotrophic in the first days after turbidite deposition. We speculate that *T. melo* could be a species specialized in colonizing such an oligotrophic environment. The eventual absence of

suitable food particles in an initial colonization stage of colonization could also explain the relatively long recovery time.

The absence of *T. melo* in the living as well as dead assemblages of sequence 2 is intriguing. It seems highly improbable that the species was living here in December 1999, just before turbidite deposition, and that all tests subsequently disintegrated (a common phenomenon for certain agglutinated taxa) in the few months following turbidite deposition. Another possibility would be that the completely population of this surface-living taxon was swept away during turbidite deposition, together with the topmost millimeters of the sediment. However, also this possibility is very unlikely in view of the presence of living *T. melo* down to 1 centimeter, and the absence of a clear vertical species succession in the recent fauna. Therefore, we conclude that for an unknown reason, *Technitella melo* did not make part of the foraminiferal fauna recolonizing turbiditic sequence S2.

c. Depth of bioturbation

The planktonic foraminiferal record shows a clear two-stepped density-profile. The maximum densities (about 150 specimens/50 cc) in the topmost 0.5 cm of sequence S1, are interpreted as the result of a direct input by hemi-pelagic sedimentation after the deposition of turbiditic sequence S1. The intermediate densities (about 50 specimens/50 cc) found between 0.5 and 1 cm, on the contrary, are probably the result of downward mixing by the benthic fauna. This is confirmed by the presence of scarce live benthic foraminifera in this depth interval. The same interpretation is probably valid for sequence S2. The relatively low density, of planktonic as well as benthic foraminifera, in the topmost cm suggests the top of sequence S2 comprises only the lower part of the former hemipelagic sediment. The upper part (a few mm) of sequence S2 has probably been eroded during the deposition of turbiditic sequence S1. The slightly lower numbers (about 50 specimens/50 cc) in the 1–2 cm level of sequence S2, suggests that these tests have been introduced there by bioturbation. Below the second cm of sequence S2, only trace quantities of planktonic foraminifera are found.

d. The distribution of redox species

i. The establishment of the anoxic condition. The arrival of a turbidity current provokes a mixing of allochthonous particles, pore waters, and oxic bottom waters. The composition of the interstitial waters and sedimentary particles of core K is the result of the geochemical reactions and diffusive transport of dissolved compounds since the deposition of the turbidite. The disappearance of oxygen in almost the entire core, and particularly at the previous interface at the top of unit S2, indicates that enough time has elapsed to allow the consumption of all free oxygen by oxidation of reduced species, like Fe-sulfide, or organic carbon through oxic respiration. The high organic carbon concentrations (around 2%) suggest that the O_2 consumption was probably fast. We have conducted an experiment in which anoxic sediments, collected from a neighboring station with a very similar concentration of organic carbon, were vigorously mixed with O_2-saturated seawater with a

fresh sediment:seawater volume ratio of 1:1. After 24 hours, O_2 was totally consumed. This experiment confirms that O_2 will be rapidly consumed after isolation of the sediments from oxygenated bottom waters, and explains the absence of free oxygen below the several month old turbidite.

The presence of reduced dissolved species in unit S1 could result from diffusion of these species from below. However, dissolved Fe does not show a diffusion profile. It shows a layer where dissolved Fe is produced, probably due to the reduction of particulate Fe(III) phases, located in the first decimeter below the oxic layer. Therefore, anaerobic processes occur in the newly deposited unit S1, where oxic particles are reduced. We have observed concentrations of Fe_{ASC} above 50 μmol/g in unit S1, which indicates that reactive Fe(III) phases are available to sustain the reaction of Fe(III) reduction. The particulate sulfur profile follows the Fe_{ASC} profile. Therefore, reactive Fe(III) phases may have resulted from the partial oxidation of iron sulfide after the mixing of reduced and oxic sediments during the turbidite event. Both dissolved oxygen or particulate Mn-oxides are potential oxidants for iron sulfides.

ii. The new oxic layer. The high concentrations of Mn_{ASC} and Fe_{ASC} at the top of the core results first from an accumulation of Mn- and Fe-oxides linked to the oxidation of dissolved Mn(II) and Fe(II) diffusing upwards from the anoxic sediment, and second, from the deposition of oxides with detrital particles of background sedimentation after turbidite deposition. The first process occurs, since we have observed a concentration gradient of dissolved Fe and Mn. The establishment of such an oxic layer by the diffusion process needs time. The time required for this accumulation of oxides can be estimated using a diffusion model, assuming that the detrital input was zero, and the gradient of dissolved Fe and Mn remained constant during time. This assumption is probably erroneous, but it allows us to calculate a rough maximum age for the turbidite.

First we have calculated from the porosity and concentration data the excess of Mn_{ASC} and Fe_{ASC} present in the oxic layer of the sediment in comparison with the underlying sediment. In a surface section of 1 cm^2, the excess of Mn is 4.4 μmol and the excess of Fe is 20 μmol. The comparison of these values with a diffusive flux expressed in μmol per cm^2 per unit time allows us the estimation of the time required to develop the observed metal-oxide enrichment.

The fluxes of species dissolved in pore waters can be calculated, assuming transport by molecular diffusion, from the concentration gradients according to Fick's first law: $J = -\phi D_s dC/dX$, where J is the flux, ϕ is the porosity, dC/dX is the concentration gradient, and D_s is the bulk sediment diffusion coefficient corrected for tortuosity, i.e. $D_s = D_o/\theta^2$ where θ is the tortuosity and D_o is the diffusion coefficient in water (Berner, 1980). D_o values were obtained from Li and Gregory (1974) and the value of θ^2 is assumed to equal to $1 - \ln(\phi^2)$ (Boudreau, 1996).

The concentration gradient of dissolved Mn occurs at about 1 cm depth. At this depth the calculated D_s of Mn is 3.48 10^{-6} cm^2/s. The concentration gradient is difficult to estimate

accurately, because it occurs within two successive 0.5 cm-thick samples. The concentration of dissolved Mn is 36 μmol/l in the 1–1.5 cm sediment slice and close to zero μmol/l in the 0.5–1 cm slice. Therefore the decrease of 36 μmol/l occurs within 0.5 cm at the most, and probably less. Then, the calculated gradient is at least 72 nmol/cm^4. The diffusive flux calculated with this minimum value is 0.213 pmol/cm^2/s. This flux can supply the Mn in excess in the oxic layer within 8 months. If we consider a concentration gradient, which is twice higher than the estimated minimum value, then, the excess Mn is supplied in 4 months, which corresponds approximately to the time elapsed between the core sampling and the estimated date of turbidite formation in December 1999. Therefore, this constant diffusion model accurately explains the peak of particulate Mn in the oxic layer.

The concentration gradient of dissolved Fe is linear between 3.5 and 1 cm depth. The diffusion flux calculated from this gradient is 0.443 pmol/cm^2/s. This flux supplies the excess of Fe present in the oxic layer in 1.4 years. This value is higher than the time estimated for Mn. This suggests that the processes that control the enrichment of metal oxide at the top of newly deposited sediments are not quantitatively the same for Mn and Fe. An important part of the Fe in excess probably originates from a downward flux of sedimenting Fe(III) particles rather than exclusively from an upward flux of dissolved Fe. It is also possible that the profile of dissolved Fe is not at steady state.

iii. The previous sediment-water interface. The top of S2 unit is also enriched in Mn_{ASC} and Fe_{ASC}. This suggests that the sediment-water interface formed prior to the deposition of unit S1 has only been eroded very weakly, or even not at all. However, both sedimentological (erosive contact) and foraminiferal evidence argue for erosion of the top millimeters. The presence of metal oxides indicates that they have not been totally reduced within the few months after being buried in an anoxic environment. The profile of dissolved Mn shows however a maximum concentration in the sample located at the top of S2. This peak clearly indicates that Mn-oxides were being reduced at the time of core sampling. Except this peak, the background concentration of dissolved Mn in the core is relatively constant, and close to 50 μmol/l. Therefore, the concentration of Mn is probably controlled by an equilibrium with a solid phase. The removal of dissolved Mn could be related to the precipitation of secondary Mn-containing carbonates. The precipitation of authigenic carbonates is favored by the production of alkalinity linked to anaerobic mineralization of organic carbon (Mucci *et al.,* 1999). Dissolved manganese is most likely precipitated as a mixed calcium-manganese carbonate (Middelburg *et al.,* 1987) as the pore waters become supersaturated with respect to both calcite and rhodochrosite following the production of carbonate alkalinity via sulfate reduction. At the top of S2, the higher concentration of dissolved Mn, but also the higher pH, indicates that interstitial waters are supersaturated here with the Mn-bearing-carbonate phase. The peak of dissolved Mn is limited to the sample located near the top of S2. One can expect that shoulders of this peak should be present above and below this level due to the diffusive transport of the

concentration anomaly. In a purely diffusive transport, the vertical distance z of the concentration anomaly growing ahead of the reductive dissolution zone depends on time t and the coefficient of diffusion D_s according to the Einstein relation (Boudreau, 1997), where $z = (2D_s t)^{0.5}$. Considering an age of the turbidite S1 of four months, the concentration anomaly should be detectable about 7 cm above and below the top of S2. The peak of dissolved Mn is much thinner. Therefore, Mn^{2+} is probably trapped as an authigenic phase close to the S1–S2 interface. This suggests that the current reductive dissolution of Mn-oxide at the paleo-interface produces an environment, which is temporarily supersaturated with a Mn-carbonate phase, probably due to kinetic effect of carbonates precipitation, but the Mn-carbonate becomes the definitive sink of Mn.

The profile of dissolved iron shows no peak at the top of S2. This suggests that, unlike Mn, Fe-oxides are not, or only very weakly, reduced at the paleo-interface. They appear to be more refractory and are not transformed to another authigenic phase within four months. Manganese oxides and oxyhydroxides are oxidants for Fe^{2+} (Myers and Nealson, 1988; Postma, 1985; Hyacinthe *et al.,* 2001), which can explain the removal of Fe^{2+} and a part of the reductive dissolution of particulate Mn.

iv. Nitrate and ammonia. The new oxic interface at the top of the sediment core presents a distribution of dissolved nitrogen species, which is common in hemipelagic sediments. We observe that nitrate is present in the oxygen-containing layer and then decreases downwards, whereas ammonia concentration is close to zero at the top of the core and increases downwards in the anoxic sediment. The presence of nitrate in the oxic layer is attributed to the succession of reactions that lead to the bacterial nitrification of organic N or ammonia that diffuses from below. The consumption of nitrate below the oxic layer is due to the bacterial denitrification. The presence of a peak of nitrate at 2.5 cm depth, below the oxic layer suggests that nitrate is produced anaerobically, probably from the oxidation of ammonia with manganese oxides as suggested in several recent studies (e.g. Hulth *et al.,* 1999; Anschutz *et al.,* 2000).

The ammonia profile shows a smooth gradient from the bottom to the oxic layer. The classical explanation for this is that ammonia is produced from the anaerobic mineralization of organic N at depth. In the oxic layer, nitrifying bacteria oxidize ammonia with oxygen to nitrite and nitrate, and nitrate is subsequently reduced anaerobically to dinitrogen by denitrifying bacteria.

The top of unit S2, which corresponds to the paleo-oxic interface, presented probably similar profiles of dissolved nitrogen species prior to the deposition of unit S1, with high nitrate and low ammonia concentration. After four months, ammonia and nitrate profiles are smooth. They show no indication of the previous oxic condition. This indicates that nitrate has been rapidly consumed by denitrification, probably shortly after the consumption of all free oxygen. In the absence of O_2, ammonia produced by organic-N mineralization was allowed to accumulate in the interstitial waters. Recent publications show that ammonia may also be directly oxidized by manganese oxide, either to dinitrogen (Luther *et*

al., 1997; Hyacinthe *et al.,* 2001), or to nitrate in anaerobic sediments (Aller *et al.,* 1998; Hulth *et al.,* 1999; Anschutz *et al.,* 2000). Our profiles do not show these reactions, which should be marked by a minimum in the ammonia profile and a peak in the nitrate profile. However, the reduction of manganese oxide by ammonia cannot be excluded, first because it is thermodynamically feasible, second, because it has been observed in experiments (Hulth *et al.,* 1999) and in the field (Deflandre *et al.,* 2002). In the present case the effects of this reaction are not shown in the profile of nitrogen species, because the high concentration of labile organic matter buried at this depth probably promotes competitive reactions such as rapid denitrification and efficient organic-N mineralization to ammonia. A peak of dissolved nitrate is observed above unit S2, in the sandy and organic-C depleted part of the unit S1. This layer also contains dissolved reduced species, which probably exclude the infiltration of oxic water to this depth to explain the presence of nitrate. Here, nitrate can be anaerobically produced from ammonia oxidation with Mn-oxides. The low concentration of organic-C at this depth prevents the following utilization of the nitrate for denitrification. This hypothesis may explain the peak of nitrate, but cannot be confirmed nor ruled out. Pore water sampling with a higher vertical resolution is needed to better constrain the interactions between nitrogen and the metals after the sudden burial of an oxic sediment-water interface.

5. Conclusions

We have studied a sediment core collected in the axis of Capbreton canyon at 640 m depth. The sediment consists of a succession of three turbidite layers. Most available data suggest that the 18-cm-thick turbidite layer identified at the top was deposited only four months before core collection. The composition of the benthic foraminiferal fauna suggests that the benthic environment is still in a very early state of colonization four months after the turbidite deposition. *Technitella melo,* which has not been previously observed in the faunas of Capreton canyon, appears to be the first colonizing species. We speculate that this taxon is adapted to food-impoverished conditions dominating the benthic ecosystem in the days after turbidite deposition. The slightly more diverse fauna found in the top of unit 2 is more comparable to faunas found in other stations from the Capbreton canyon. We think that, as a consequence of repeated turbidite deposition, and the prolonged period of time needed for full ecosystem recovery, the canyon environments remain systematically in early stages of recolonization. Apparently the periods of time between the successive turbidites are too short to allow complete ecosystem recovery.

The top of the newly deposited turbidite forms an oxic layer, which is rapidly enriched in Mn- and Fe-oxides. The enrichment of manganese oxides is mostly due to the oxidation of dissolved Mn^{2+}, which diffuses from below. The enrichment of iron oxides is partly explained by the oxidation of the upward flux of dissolved Fe^{2+}, but the input of detrital iron oxide after the turbidite deposition appears to be important as well.

The distribution of redox-sensitive species clearly shows that anaerobic processes of organic matter mineralization rapidly occur in the turbidite layer and in the previous oxic

sediment-water interface. Manganese oxides, which are buried under the new turbidite layer, are rapidly reduced. However, manganese remains trapped in the sediment as Mn-containing carbonates. Iron-oxides do not undergo significant reductive dissolution in the time frame observed. The behavior of nitrogen species needs further investigation.

Acknowledgments. This research is a contribution of the CNRS UMR 5805 "Environnements et Paléoenvironnements Océaniques", and was funded by the program PROOF of the Institut National des Sciences de l'Univers and the Région Aquitaine. Karine Dedieu contributed to the laboratory analyses. We are grateful to Olivier Weber, Thierry Mulder, Silvia Hess, and Pierre Cirac for several discussions that clarified the ideas developed in this paper. We thank the crew of the "Côtes de la Manche" and all the participants of the Oxybent missions.

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Received: *11 October, 2001;* revised: *19 November, 2002.*

Annexe 3

Les sapropèles de Mer Méditerranée: Utilisation des foraminifères benthiques en paléo-océanographie

L'étude des archives sédimentaires du Quaternaire, en Mer Méditerranée orientale, ne peut se faire sans tenir compte de ces dépôts récurrents que sont les sapropèles. Initialement identifiés lors de la *Swedish Deep Sea Expedition* (1947) (Küllengerg, 1952 ; Olausson, 1961), les sapropèles se définissent de prime abord comme des sédiments riches en matière organique. D'abord décrits qualitativement, ces dépôts furent l'objet d'une définition plus quantitative, et d'une nomenclature encore utilisée (Kidd et al., 1978) : « Le sapropèle est un niveau discret, épais de plus de 1 cm, développé dans les sédiments pélagiques de mer ouverte et dont la teneur pondérale en carbone organique est supérieure à 2% ». Les sapropèles Plio-Pléistocène de la Mer Méditerranée s'apparentent le plus souvent à des accumulations pluri-centimétriques bien laminées, représentant des dépôts pluri-millénaires de matière organique essentiellement marine (Nesteroff, 1973).

L'origine de la formation de ces dépôts de matière organique demeure une énigme (voir révision de Rohling, 1994). Pour certains spécialistes en chimie organique, une augmentation des exportations de matière organique jusqu'au sédiment en relation direct avec un accroissement de la production primaire des eaux de surface peut justifier une préservation accrue des détritus organiques dans les archives sédimentaires (Pedersen et Calvert, 1990 ; Calvert et al., 1992 ; Calvert et al., 1993). Pour d'autres chercheurs, la matière organique détritique, pour être préservée plus efficacement dans un sédiment, doit préférentiellement s'accumuler sous des conditions anoxiques (Demaison et Moore, 1980; De Lange, 1992). Aussi, deux phénomènes indépendants ou complémentaires pourraient justifier une sous-oxygénation des eaux de fond expliquant les accumulations sapropéliques en Mer Méditerranée orientale:

- *Une stratification des eaux de surface minimisant ou annihilant à long terme la ventilation des fonds par diminution de la création d'eau profonde et intermédiaire*

méditerranéenne (e.g. Thunell et al., 1983; Thunell et Williams, 1989 ; Rossignol-Strick, 1985, Perissoratis et Piper, 1992)

- *Une augmentation considérable de la production des eaux de surface induisant une une hyper-eutrophisation des paléo-environnements benthiques et corrélativement une consommation totale de l'oxygène dans le sédiment (Schrader et Matherne, 1981; Thunell et Williams, 1982; Ganssen et Troelstra, 1987; Parisi, 1987).*

Cette deuxième hypothèse revient à considérer comme valable l'idée soutenue par Pedersen et Calvert (1990).

L'étude des faunes fossiles des faunes de foraminifères benthiques le long d'enregistrement sédimentaire, tant d'un point de vue des assemblages fossiles que du signal isotopique ($\delta^{13}C$ et $\delta^{18}O$) d'espèces stratégiquement choisies permet d'élaborer des interprétations quant aux changements des conditions paléo-environnementales des biotopes benthiques durant les épisodes sapropéliques. Dans la mesure où le flux exporté de matière organique et les degrés d'oxygénation à et sous l'interface eau-sédiment sont potentiellement des paramètres majeurs structurant les communautés actuelles des foraminifères benthiques des écosystèmes marins profonds, une connaissance précise et juste des exigences écologiques actuelles des espèces, des populations et des communautés de foraminifères benthiques est fondamentalement nécessaire pour parfaire leur application dans des études paléo-océanographiques aussi passionnantes que celles des sapropèles de Méditerranée. L'étude des faunes de foramaminifères benthiques dans les sapropèles peut également appporter restrospectivement des renseignements essentiels sur le devenir des peuplements des foraminifères dans des conditions d'écosystèmes extrèmes rarement échantillonnés aujourd'hui.

L'application de l'étude des foraminifères benthiques et planctoniques

Les deux articles qui suivent présentent des interprétations paléoenvironnementales possibles quant aux processus de mise en place et de pérennisation des évênements sapropèliques en Mer Méditerranée orientale. Ces deux travaux sont basés sur des études exhaustives des successions de faunes de foraminifères planctoniques et benthiques le long de diverses carottes prélevées en Mer Egée et dans le Bassin Levantin, ainsi qu'une batterie exceptionnelle d'analyses isotopiques ($\delta^{13}C$ et $\delta^{18}O$) réalisées sur des espèces-clés.

Le premier article traite des successions des foraminifères planctoniques et leur signal isotopique ($\delta^{13}C$ et $\delta^{18}O$). Il suggère que la mise en place du dernier sapropèle en Mer Egée, durant l'Holocène (S1), est conditionnée préalablement par un lent enrichissement des eaux profondes et intermédiaires du bassin en nutriments en réponse à une stratification marquée des eaux du surface et à une coupure pérenne de la ventilation des eaux de fond (Casford et al., 2002). L'épisode sapropèlique résulterait d'une augmentation de la production primaire favorisée par des conditions hyper-eutrophes prévalant dans la partie superficielle de la colonne d'eau. La seconde note suggère que les évênements sapropèliques peuvent être interrompus par des épisodes plus ou moins long de ré-oxygénation dont l'enregistrement est clairement explicité par la présence d'assemblages faunistiques de foraminifères benthiques riches en espèce oxyphiles (Casford et al., 2003). C'est notamment le cas de la Mer Egée qui a vraisemblablement continué à jouer un rôle moindre mais effectif de zone préférentielle de formation d'eau profonde durant les épisodes sapropèliques. Ces deux articles utilisent des données faunistiques et isotopiques de la carotte SLA-9 dont l'étude a été réalisée lors d'un stage de DEA sous la supervision de F. Jorissen, E.J. Rohling et C. Pujol (Fontanier, 2000).

PALEOCEANOGRAPHY, VOL. 17, NO. 2, 10.1029/2000PA000601, 2002

Circulation changes and nutrient concentrations in the late Quaternary Aegean Sea: A nonsteady state concept for sapropel formation

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Received 20 October 2000; revised 17 February 2002; accepted 17 February 2002; published 1 June 2002.

[1] The modern Aegean Sea is an important source of deep water for the eastern Mediterranean. Its contribution to deep water ventilation is known to fluctuate in response to climatic variation on a decadal timescale. This study uses marine micropalaeontological and stable isotope data to investigate longer-term variability during the late glacial and Holocene, in particular that associated with the deposition of the early Holocene dysoxic/anoxic sapropel S1. Concentrating on the onset of sapropel-forming conditions, we identify the start of "seasonal" stratification and highlight a lag in $\delta^{18}O$ response of the planktonic foraminifer *N. pachyderma* to termination T1b as identified in the $\delta^{18}O$ record of *G. ruber*. By use of a simple model we determine that this offset cannot be a function of bioturbation effects. The lag is of the order of 1 kyr and suggests that isolation of intermediate/deep water preceded the start of sapropel formation by up to 1.5 kyr. Using this discovery, we propose an explanation for the major unresolved problem in sapropel studies, namely, the source of nutrient supply required for export productivity to reach levels needed for sustained sapropel deposition. We suggest that nutrients had been accumulating in a stagnant basin for 1–1.5 kyr and that these accumulated resources were utilized during the deposition of S1. In addition, we provide a first quantitative estimate of the diffusive (1/*e*) mixing timescale for the eastern Mediterranean in its "stratified" sapropel mode, which is of the order of 450 years. *INDEX TERMS:* 1050 Geochemistry: Marine geochemistry (4835, 4850); 3030 Marine Geology and Geophysics: Micropaleontology; 3339 Meteorology and Atmospheric Dynamics: Ocean/atmosphere interactions (0312, 4504); 4267 Oceanography: General: Paleoceanography; 4870 Oceanography: Biological and Chemical: Stable isotopes; *KEYWORDS:* sapropel, Mediterranean, Holocene, foraminifera, climate variability

1. Introduction

[2] The present-day Aegean Sea (Figure 1) is an important source of deep water for the eastern Mediterranean [*Lacombe et al.*, 1958; *Miller*, 1963; *Roether et al.*, 1996; *Lascaratos et al.*, 1999]. Aegean Intermediate Water (AEIW) is derived from Levantine Intermediate Water (LIW), with its source in the Rhodes Gyre. As this travels north along the Turkish Coast, prevailing offshore winds allow upwelling of the intermediate water to the surface [*Lascaratos*, 1989; *Yüce*, 1995]. In these shallow eastern shelf areas the AEIW consequently forms a single uniform water mass from the surface to the seafloor. As the upwelled AEIW progresses northward, its salinity continues to increase due to evaporation. Winter winds across the Athos Basin (Figure 1) in the far north further enhance the salinity of AEIW, and this together with winter cooling increases its density. This buoyancy loss drives the formation of Aegean Deep Water (AEDW) [*Bruce and Charnock*, 1965; *Burman and Oren*, 1970; *Theocharis*, 1989; *Yüce*, 1995]. Today, AEDW settles in the deeper parts of the Aegean Basin, below 300 m. Traditionally, AEDW formation was considered of minor importance to the deep water ventilation of the open eastern Mediterranean [*Wüst*, 1961]. However, recent studies show that specific (cold) climatic forcing over the Aegean has throughout the 1990s caused AEDW to replace Adriatic Deep Water (ADW) as the main deep water in the open eastern Mediterranean [*Roether et al.*, 1996; *Samuel et al.*, 1999]. The Aegean's rapid response to atmospheric forcing makes it an ideal case study for the analysis of deep water formation and its relationship with climatic change.

[3] Dramatic deep water ventilation changes on longer timescales are also witnessed in the sedimentary record of the Mediterranean by the presence of sapropels. These dark organic-rich layers are found throughout the eastern Mediterranean. Sapropel formation is related to slowing down of deep water ventilation in response to climate related reductions in buoyancy loss [*Rossignol-Strick et al.*, 1982; *Jenkins and Williams*, 1983; *Rossignol-Strick*, 1983, 1985, 1987; *Parisi*, 1987; *Cramp and Collins*, 1988; *Cramp et al.*, 1988; *Perissoratis and Piper*, 1992; *Rohling*, 1994]. These reductions are thought to be caused by changes to much wetter climatic conditions at times of increased Northern Hemisphere insolation (precession cycle minima) [*Rossignol-Strick et al.*, 1982; *Rossignol-Strick*, 1983, 1985; *Rohling and Hilgen*, 1991; *Hilgen*, 1991; *Lourens et al.*, 1996]. In addition to suppression of deep water production, sapropel formation has also been associated with increases in export productivity [*Rohling and Gieskes*, 1989; *De Lange et al.*, 1990; *Rohling*, 1994; *Rohling and Hilgen*, 1991; *Thomson et al.*, 1995; *Cramp and O'Sullivan*, 1999].

[4] Modeling of circulation during deposition of the most recent, Holocene, sapropel (S1) has suggested that relatively small increases in surface buoyancy can lead to suppression of deep water circulation in the eastern Mediterranean. An increase of 20–30% in the freshwater budget is thought to be enough to allow interruption of deep water production [*Myers et al.*, 1998; *Rohling and De Rijk*, 1999; *Rohling*, 1999b]. Using the Myers [*Myers et al.*, 1998] circulation model, the biogeochemical implications of

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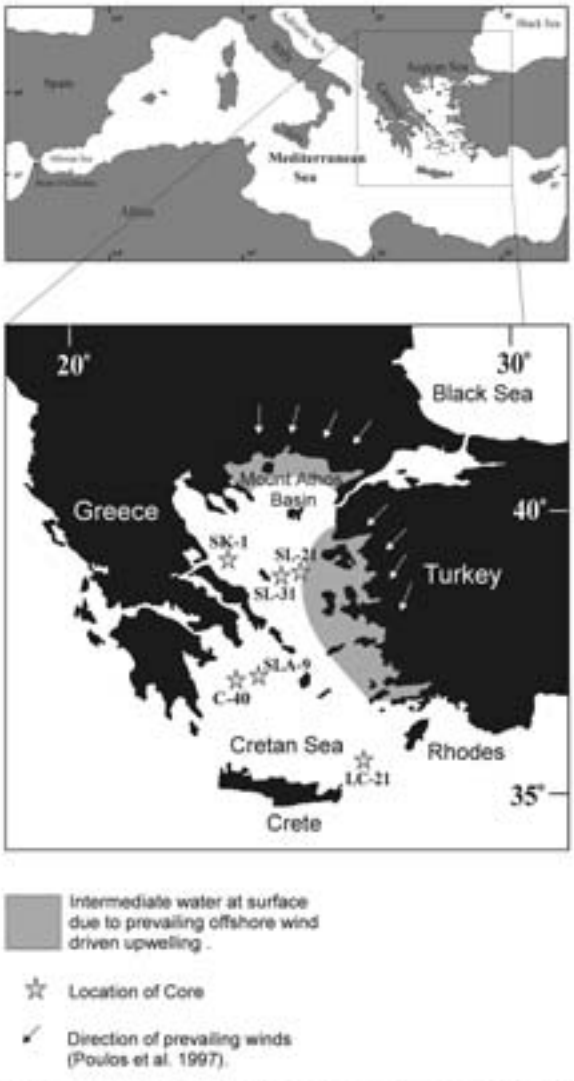

Figure 1. Location map illustrating the core positions for SL-31 (water depth 430 m), SL-21 (317 m), SLA-9 (250 m), and LC-21 (1520 m). The shaded area represents the approximate area of AEIW upwelling to the surface. This water mass extends from the surface to ~200 m depth in the shallow shelf areas off the Turkish coast [*Theocharis*, 1989; *Ilice*, 1995; *Poulos et al.*, 1997].

sapropel formation have been assessed [*Stratford et al.*, 2000]. Preserving the antiestuarine circulation of the eastern Mediterranean and using a threefold increase in river inputs [after *Kallel et al.*, 1997], organic fluxes in coastal regions and marginal basins were found to approach the required levels for sapropel deposition [*Stratford et al.*, 2000].

[5] The model of *Stratford et al.* [2000] highlights a common problem recognized in all current models for sapropel formation, with emphasis on the much studied and well-dated S1: "Where did the nutrients come from to sustain organic matter burial over the ~3 kyr of S1 deposition in the eastern Mediterranean?" It appears that steady state models cannot import sufficient nutrients into the basin, outside of the coastal regions and marginal seas, to sustain this accumulation. The steady state models assume that nutrients lost via C_{org} burial are continuously balanced by fluvial/aeolian influxes. We here present evidence to suggest that the steady state approach is seriously flawed in that a significant period of potential nutrient accumulation in a stagnant basin may have preceded the actual sapropel deposition.

[6] We use abundance variations of planktonic foraminifera together with species-specific oxygen and carbon stable isotope ratios in these forams to derive a picture of the oceanographic processes leading up to, during, and after the most recent sapropel deposition in the Aegean. We observe a conspicuous change in hydrography, starting ~6 kyr prior to S1. We validate our observations with a simple bioturbation model and use the validated records to suggest that long-term (1.5 kyr) storage of nutrients may have occurred in the Aegean Basin. When this reservoir became available for production, the formation of S1 commenced.

2. Methods and Materials

[7] We present results for two gravity cores from the Northern Aegean Basin (SL-21 and SL-31) and an additional gravity core (SLA-9) together with one piston core (LC-21) from the southern Aegean (Figure 1). All four cores are comprised of microfossil-rich hemipelagic ooze, with a clearly defined darker band of sapropelic material.

[8] Each core was sampled in a continuous sequence: SL-21, SL-31, and SLA-9 were sampled at 0.5 cm intervals, and LC-21 was sampled at 1 cm intervals. The samples were freeze-dried and weighed, and selected (weighed) subsamples were disaggregated and wet sieved using demineralized water. The sieved fractions were collected on 600, 150, 125, and 63 μm mesh sizes. The >150 μm fractions were subdivided using a random splitter to provide an aliquot of ~200 individual planktonic foraminifera. These were then determined and sorted on Chapman slides and counted. Results were obtained as numbers g^{-1} and as percentages (Figure 2).

[9] Several AMS radiocarbon dates were obtained for cores LC-21, SLA-9, and SL-31 using only hand-picked clean planktonic foraminiferal tests with no evidence of pyritization or overgrowth. The samples were too small for monospecific dating, but no systematic differences would be expected for such dates relative to our results (see *Jorissen et al.*'s [1993] comparison of planktonic versus benthic dating). The picked material was submitted for analysis at the Natural Environment Research Council (NERC) radiocarbon laboratory at SURRC (LC-21) and at the Leibniz AMS Laboratory at Kiel (Germany) (SLA-9 and SL-31). Radiocarbon convention ages obtained were calibrated using the marine mode of the program Calib 4.2 [*Stuiver and Reimer*, 1993]. A reservoir age correction of 149 ± 30 years for the Aegean was used [*Facorellis et al.*, 1998]. The results are listed in Table 1. All ages in this paper are reported in calibrated kyr B.P. unless otherwise stated.

[10] Detailed stable oxygen and carbon isotope records have been constructed for individual planktonic foraminiferal species in cores LC-21, SLA-9, SL-21, and SL-31, with resolutions on the order of 1 cm (Figure 3). The species chosen were the very shallow, surface-dwelling *Globigerinoides ruber*; the deeper-dwelling *Globorotalia inflata* associated with deep (winter) mixing, and the deep-living species *Neogloboquadrina pachyderma*, which has been associated with the deep chlorophyll maximum at the base of the euphotic layer. This selection follows global and specific Mediterranean habitat descriptions by *Hemleben et al.* [1989], *Pujol and Vergnaud-Grazzini* [1995], *Rohling et al.* [1993a, 1995, 1997], *De Rijk et al.* [1999], and *Hayes et al.* [1999]. The analyses were performed at two separate intercalibrated facilities: the Europa Geo 20–20, with individual acid bath preparation, at the Southampton Oceanography Centre (SOC), and the VG-Optima with a common acid bath preparation at NERC Isotope Geoscience Laboratory (NIGL), Keyworth.

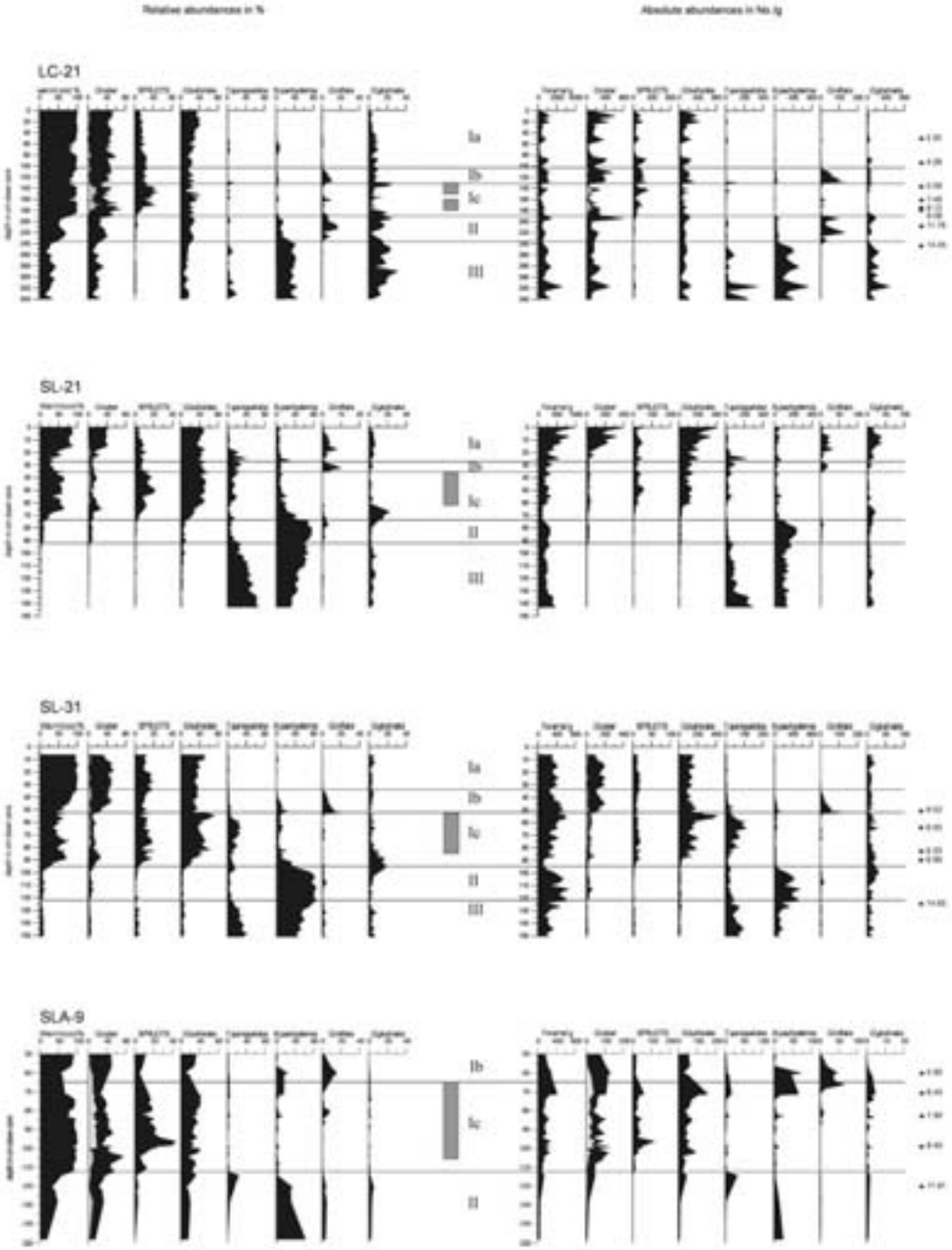

Figure 2. Relative and absolute abundances of planktonic foraminifera in cores SLA-9, SL-21, SL-31, and LC-21. The vertical shaded box indicates the extent of the benthic sapropel, identified from the presence of low-oxygen-tolerant benthic foraminifera and/or total absence of benthic fauna that is equated with truly anoxic bottom waters [*Fontanier*, 2000]. Warm/cold plots are percent warm species/(percent warm + percent cold), following the method of *Rohling et al.* [1997]. The previously defined biozonal boundaries I/II and II/III are also shown [*Jorissen et al.*, 1993]. All dates in Figure 2 are expressed as uncalibrated radiocarbon convention ages, uncorrected for reservoir effect, discussed further in Table 1.

Table 1. Dating Calibration[a]

Sample Code	Median Depth	Conventional Age	± Errors	Calibrated Years B.C.	Calibrated Years B.P.	±1 Sigma
			LC-21			
CAM-41314	50	3370	60	1070	3020	100
CAM-41313	95.5	4290	60	2260	4210	100
CAM-41311	137.5	5590	60	3890	5840	90
CAM-41315	161.5	7480	60	5830	7780	70
CAM-41312	174.25	8120	60	6450	8400	60
AA-30364	179.5	9085	65	7590	9540	320
AA-30365	209	11765	80	11190	13140	370
CAM-41316	242.5	14450	60	14610	16560	240
			SL-31			
KIA9467	51.75	6515	45	4870	6820	70
KIA9468	65.75	7950	60	6330	8280	80
KIA9469	84.25	9330	60	7870	9820	150
KIA9470	91	9990	55	8650	10600	380
KIA9471	126.25	14650	80	14840	16790	250
			SLA-9			
KIA9472	60.5	5950	45	4260	6210	50
KIA9473	71.5	6445	55	4790	6740	70
KIA9474	83.25	7900	45	6240	8190	70
KIA9475	99.5	8400	50	6820	8770	120
KIA9476	120.5	11910	70	11220	13170	350

[a]Dates are show as radiocarbon convention ages (conventional age), calibrated radiocarbon years B.C. (calibrated years B.C.) and as calibrated radiocarbon years B.P. (calibrated years B.P.). Analytical errors are given as years (± errors), and calibration fitting errors for a 1 sigma spread are shown in years (±1 sigma). Dating on LC-21 is after *Mercone et al.* [2000]. Samples with codes starting CAM were prepared as graphite targets at the NERC radiocarbon laboratory and analyzed at the Lawrence Livermore National Laboratory AMS facility. Sample codes AA were prepared at Scottish Universities Reactor Research Centre at East Kilbride and analyzed at the Arizona Radiocarbon Facility. KIA sample codes indicate the Leibniz AMS Laboratory at Kiel. Radiocarbon dating was calibrated using CALIB 4.2 after *Stuiver and Reimer* [1993] and using the marine data set [*Stuiver et al.*, 1998]. A reservoir age correction (ΔR) of 149 ± 30 years was used [*Facorellis et al.*, 1998].

Isotope results are reported as per mil standardized to Vienna Peedee belemnite. Machine error are is of the order of <06‰ (standard deviation).

3. Results

3.1. Planktonic Foraminifera

[11] Five distinct assemblages were identified in this study (Figure 2). The main boundaries equate well with the previously identified biozonal boundary II/III, and biozonal boundary I/II [*Jorissen et al.*, 1993] and this nomenclature is used. The three remaining assemblages consist of subdivisions of biozone I of *Jorissen et al.* [1993]. Relevant Mediterranean habitat characteristics have been summarized by *Rohling et al.* [1993a, 1993b, 1995], *Pujol and Vergnaud-Grazzini* [1995], *De Rijk et al.* [1999], and *Hayes et al.* [1999]. From old to young we identify the following five assemblages. (1) Assemblage III is an assemblage dominated by *N. pachyderma* and *Turborotalita quinqueloba*, with lower densities of *Globorotalia scitula* and *Globigerinita glutinata*, and a generally low to very low abundance of *G. ruber*. This fauna dominates the cool "glacial" intervals. (2) Assemblage II is an intermediate assemblage characterized by presence of *T. quinqueloba*, somewhat enhanced numbers of *N. pachyderma* and *G. glutinata*, especially in the central Aegean cores, and the presence of *G. ruber* and *G. inflata*. (3) Assemblage I is an assemblage dominated by the warm subtropical species *G. ruber* and the SPRUDTS group (including but not requiring *Globigerinella siphonifera, Hastigerina pelagica* (absent in the Aegean), *Globo turborotalita rubescens, Orbulina universa, Globigerinella digitata, Globoturborotalita tenella*, and *Globigerinoides sacculifer* [see *Rohling et al.*, 1993a, 1993b]. In addition it includes abundant *Globigerina bulloides* and somewhat increased *T. quinqueloba* compared with the preceding assemblage II. (4) Assemblage Ic is characterized by elevated absolute and relative abundances of the pink morphotype, *G. ruber* rosa. A peak in *G. inflata* is also present at the base of this assemblage, followed by a marked absence in this species in the remainder of Ic. Core LC-21 shows an interruption in assemblage Ic with a return to a fauna resembling assemblage II, which corresponds to an "interruption" of the darker-colored sapropel [*Hayes et al.*, 1999; *De Rijk et al.*, 1999; *Mercone et al.*, 2000]. (5) Assemblages Ib and Ia are diverse assemblages dominated by *G. ruber* and *G. bulloides*, with SPRUDTS, *G. inflata*, and *G. glutinata*. Ib is characterized by elevated numbers of *G. inflata* and appears to be of short duration. Ia shows a fauna similar to that seen in the present-day Mediterranean (core top data of *Thunell* [1978]). Assemblage Ia shows slightly lower abundances of "warm" preferring species than assemblage Ic.

3.2. Stable Isotopes

[12] Combination plots of the monospecific isotopic profiles of $\delta^{18}O_{ruber}$, $\delta^{18}O_{inflata}$, and $\delta^{18}O_{pachyderma}$ (Figure 3) show several distinct, previously unreported features: Oxygen isotopes initially show a high degree of synchronicity, being similar in value and variation. This is followed by a depletion in $\delta^{18}O_{ruber}$ that separates it from of the unaffected signal of *N. pachyderma*. This first separation between $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$ coincides with the biozonal boundary III/II and corresponds in age with glacial termination T1a. After a short interval of little change, $\delta^{18}O_{ruber}$ shows a second rapid depletion to its typical Holocene values, while $\delta^{18}O_{pachyderma}$ remains at pre-Holocene values or even shows an enrichment. This enrichment, while generally small, is well within the sensitivity of our equipment and must be regarded as real. It is most obvious in cores SLA-9 (0.8‰ over five samples), SL-21 (0.5‰ over 10 samples), and SL-31 (0.4‰ over four samples), while the available resolution leaves the signal in LC-21 inconclusive in this respect. The $\delta^{18}O$ signal of *G. inflata* shows an inflection to lighter values at the same time as this second depletion in $\delta^{18}O_{ruber}$, while the absolute $\delta^{18}O_{inflata}$ values remain

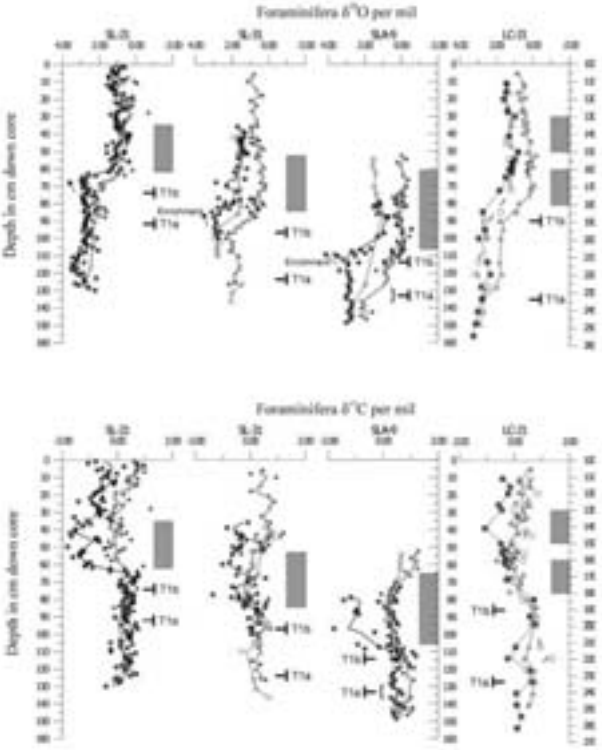

Figure 3. Stable isotope data, showing $\delta^{18}O$ and $\delta^{13}C$ versus depth, for *G. ruber* (thick shaded line with triangles), *N. pachyderma* (thin solid line with squares) and *G. inflata* (dashed line with circles) in cores SLA-9, SL-21, SL-31, and LC-21. The superimposed lines represent a 10 cm running Gaussian smoothing of the data. The shaded boxes represent the extent of the sapropel as defined by the switch from oxygen-requiring benthic foraminifera to the presence of low-oxygen fauna only in the case of LC-21, the total absence of benthic forams. Glacial terminations T1a and T1b are also shown. Arrows on $\delta^{18}O$ plots of SL-21, SL-31, and SLA-9 indicate enrichment trends in $\delta^{18}O_{pachyderma}$. All values are in per mil versus Vienna Peedee belemnite (‰ VPDB) and calibrated with standards NBS18 and 19.

intermediate between those of $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$. This second sharp depletion in $\delta^{18}O_{ruber}$ equates with termination T1b. Finally, after a period on the order of ~1 kyr, the values of $\delta^{18}O_{pachyderma}$ also start depleting to this species' Holocene values.

[11] Shortly after the start of the depletion in $\delta^{18}O_{pachyderma}$ to Holocene values, we observe a general depletion in $\delta^{13}C$. The $\delta^{13}C$ records show an initial synchronous drop in both $\delta^{13}C_{ruber}$ and $\delta^{13}C_{pachyderma}$, which is followed in SL-21, SL-31, and SLA-9 by a separation of values as $\delta^{13}C_{pachyderma}$ continues to deplete after $\delta^{13}C_{ruber}$ has leveled out. This separation in the $\delta^{13}C$ records coincides with the onset of sapropel deposition.

3.3. Bioturbation Model

[14] The offset in the isotopic responses for $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$ around T1b is conspicuous, and we need to assess whether this is a genuine feature or the result of bioturbation. Owing to the rapid fall in numbers of *N. pachyderma* before the depletion, bioturbation might mix a relatively large proportion of undepleted foraminifera with the comparatively few depleted forams. This could potentially shift the resultant isotopic composition to less depleted values. To test whether such processes could explain the observed trends, we developed a simple model, which assumes a hypothetical step change in the isotopic compositions of both *G. ruber* and *N. pachyderma* at the same point in time. The model then simulates a progressive homogenization (bioturbation) of each successive 0.5 cm of deposited sediment with the previous 5 or 10 cm (separate model runs). Two versions of this simulation were run. An extreme version based on a large step change in numbers of both *G. ruber* and *N. pachyderma* at the same point as the isotopic shift and a run based on the actual numbers observed for these species. The results of the bioturbation model are shown in Figure 4.

[15] All simulations smoothed the imposed step-like $\delta^{18}O$ change into more gradual depletions similar to those seen in the sedimentary record, with differences in the profiles for the two species. However, in all cases the inflection point for the $\delta^{18}O$ values of both species is the same, with both values start to deplete at the same point. This differs markedly from the observed data with a separation in the inflection points of these species by up to >15 cm. Only in our most extreme scenario do we approach the real data, with a lag on the order of 5–10 cm, although even here the infection points are synchronous on closer observation. The models also totally failed to reproduce the enrichment trend in *N. pachyderma* (5–10 data points) that is seen in the actual data during the major depletion in *G. ruber* (this is most clearly seen in cores SL-21, SL-31, and SLA-9).

[16] The bioturbation model leads us to suggest that the actual $\delta^{18}O$ depletion may have been more step-like than is preserved in the sedimentary record. We also deduce that the offset in inflection points seen in our cores reflects a real change in isotopic gradients within the water column during this period.

[17] Interestingly, the signal from *G. inflata* does appear to parallel the *N. pachyderma* signal shape seen in our model. It too sees a marked decline in numbers over the period of isotopic depletion. This signal may therefore provide an indication of the strength of bioturbation below the sapropel, suggesting that homogenization of foraminiferal sized particles due to bioturbation was <5 cm. This would agree with observations in the faunal counts where species *N. pachyderma*, *G. inflata*, and *G. glutinata* fall abruptly to zero in between consecutive samples at 2.5 cm spacing.

4. Discussion

[18] Changes in stable isotope composition have led to considerable speculation on the variability of Mediterranean freshwater budgets [*Huang and Stanley*, 1972; *Cita et al.*, 1977; *Ryan and Cita*, 1977; *Williams et al.*, 1978; *Rossignol-Strick et al.*, 1982; *Thunell and Williams*, 1989; *Kallel et al.*, 1997; *Rohling and De Rijk*, 1999]. Recent work points out that oxygen isotopic ratios from planktonic foraminifera cannot be used to determine absolute salinities in any straightforward way on geological timescales. Rather, they show responses to hydrographic changes that may be several times greater than the corresponding changes in conservative properties, i.e., salinity [*Rohling and De Rijk*, 1999; *Rohling*, 1999a, 1999b]. Such problems associated with temporal gradients are avoided in comparisons of isotopic compositions of different species within an individual sample since foraminifera are then analyzed from an area in a single hydrological regime. Thus differences in the signal between species will reflect real, contemporaneous differences between their preferred habitats.

[19] We propose that our multiproxy records are best interpreted in combination with the foraminiferal abundance records, as a series of successive changing, climatically driven, dynamic regimes. These are illustrated as a series of transitory states together with a schematic summary of the main isotopic and faunal changes recognized in our Aegean records (Figures 5 and 6). Each state represents a single point in time, which may be considered

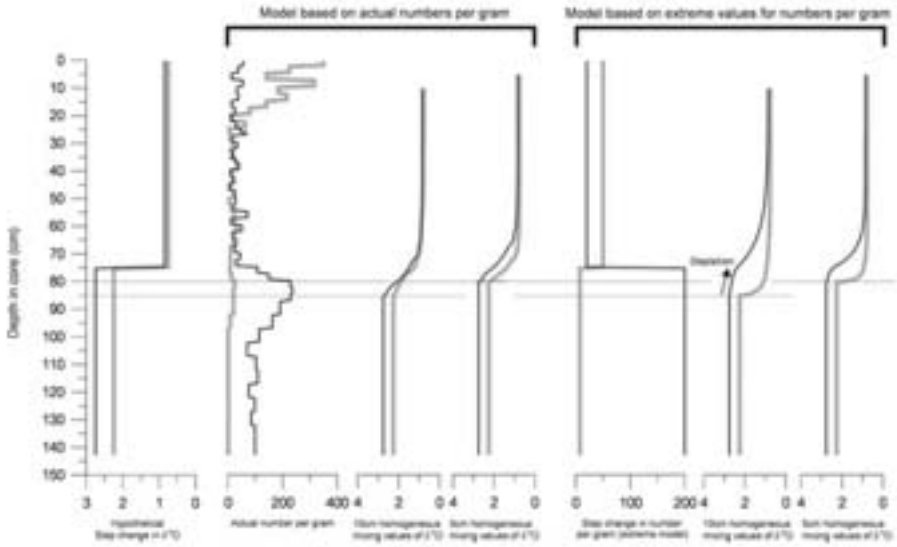

Figure 4. Bioturbation model, which illustrates the smoothing of a hypothetical stepped change in isotopic values (left panel) with a progressive homogenization to simulate bioturbation effects. This includes two runs of the model: one based on the actual numbers per gram of *G. ruber* (thick shaded line) and *N. pachyderma* (thin solid line) found in core SL-21 and another based on a hypothetical extreme step change in numbers per gram, with this change taking place at the same point as the step change in isotopic value. Each version was run with a 5 and a 10 cm homogenization, and these are plotted adjacent to each other for comparison. The horizontal tie lines (dotted lines) highlight the timing of the inflections in the derived $\delta^{18}O$ records.

typical of the particular climatic/circulation regime. These transitory states are described in detail below.

4.1. State A

[20] State A is interpreted as typical of the glacial Aegean Sea. This state is characterized by the absence of warm mixed layer species. We observe coinciding values of $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$ as well as $\delta^{13}C_{ruber}$ and $\delta^{13}C_{pachyderma}$, suggesting that there were no isotopic gradients between these shallow- and subsurface-living species. Thus it is deduced that the water column during state A comprised of a single homogenized water mass, with intermediate water undistinguished from surface water. The presence of *G. inflata* is regarded as indicative of deep seasonal mixing and is hence shown in association with winter mixing [*Hemleben et al.*, 1989; *Rohling et al.*, 1995; *Pujol and Vergnaud-Grazzini*, 1995] (summarized by *Rohling et al.* [1993a] and *Reiss et al.* [2000]). The faunal assemblage comprised of predominantly cool-water species, with only very rare occurrences of the warm dweller *G. ruber*. *T. quinqueloba* is shown as the principal surface dweller [cf. *Rohling et al.*, 1993a]. *G. scitula* and *N. pachyderma* are shown living at depth. *N. pachyderma* is known to thrive at or just above the base of the euphotic zone and generally prefers stable stratified environments [*Hemleben et al.*, 1989; *Rohling and Gieskes*, 1989; *Rohling et al.*, 1993a, 1995; *Reiss et al.*, 2000]. *G. scitula* in particular is tolerant of low temperatures [*Hemleben et al.*, 1989], and we therefore shown it as present exclusively in winter, although we cannot exclude its possible presence from other seasons on the basis of the data available.

4.2. State B

[21] This state is typical of the regime we believe marks the appearance of distinct seasonal stratification in the post-glacial Aegean. The earliest depletion in $\delta^{18}O_{ruber}$ represents termination 1a. The onset of a separation between the $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$ records suggests that *G. ruber* lived in an isotopically different water mass than *N. pachyderma*. Where available, the $\delta^{18}O_{inflata}$ values clearly follow the $\delta^{18}O_{pachyderma}$ record. Therefore we show these two species in state B as inhabiting the same water mass: *G. inflata* in the deep winter mixed season and *N. pachyderma* below the seasonal thermocline in the previous winter's water. The increased abundance of *G. ruber* over termination 1a itself also indicates the development of seasonal stratification with a warm mixed layer since *G. ruber* has a minimum temperature requirement of ~14°C [*Hemleben et al.*, 1989; *Bijma et al.*, 1990a, 1990b; *Reiss et al.*, 2000]. Hence we infer that termination 1a was associated with significant development/strengthening of the summer thermocline. This is further corroborated by the increase in *N. pachyderma* abundances since this species is known to prevail in stable stratified settings with a well-developed deep chlorophyll maximum [*Hemleben et al.*, 1989; *Rohling and Gieskes*, 1989; *Rohling et al.*, 1993a, 1993b; *Reiss et al.*, 2000]. Plankton tows from the modern NW Mediterranean clearly illustrate *N. pachyderma*'s preference for such hydrographic conditions [*Rohling et al.*, 1995]. The continued presence of the *G. inflata* and its peak in abundance toward the end of biozone II strongly suggests the persistence of seasonal mixing to considerable depth. The shallower-living (~75 m) species *G. glutinata* [*Reiss et al.*, 2000] also occurs in state B. This species is a specialist diatom feeder [*Hemleben et al.*, 1989] and is normally associated with the spring bloom, triggered by the newly available nutrients at the end of winter mixing and increased solar irradiation. Thus we interpret the overall evidence for state B as indicative of seasonal, thermal stratification, alternating with vigorous seasonal overturn of the water column in the colder months.

4.3. State C

[22] State C in particular represents a transitory phase, marking a "snapshot" within the changing conditions from the start of termination 1b to the onset of sapropel production. This regime sees the first occurrence of *O. universa* and other members of the

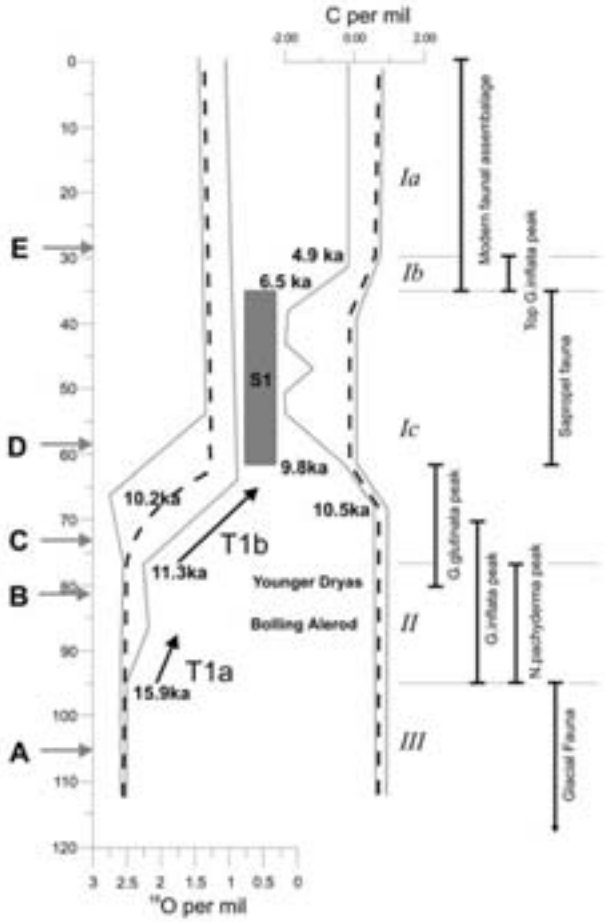

Figure 5. Summary of major changes in isotopic signals $\delta^{18}O$ and $\delta^{13}C$. The thick shaded line indicates $\delta^{18}O_{ruber}$, thin solid line indicates $\delta^{18}O_{pachyderma}$, and the dashed line indicates $\delta^{18}O_{inflata}$. Depth scale is based on core SL-21, and the vertical shaded box indicates the extent of the benthic foraminiferal defined sapropel. Bold letters refer to state summaries in Figure 5. All dates are expressed as calibrated radiocarbon convention ages, corrected for reservoir effect (kyr B.P.) and derived from average ages for the event from cores in this study (Table 2). The hatched area of dysoxic water may be truly anoxic at greater depths (e.g., LC-21, 1500 m). The positions of the Younger Dryas and the Bölling-Alerød are also indicated.

SPRUDTS group. These taxa prefer warm conditions and are shown in Figure 5 above the thermocline. *O. universa* lives in a temperature range of 12°–31°C, and although its photosynthetic symbionts show a dominant habitat in shallower waters, with sufficient light penetration, it can be found down to 250 m, [*Hemleben et al.*, 1989]. We interpret the increase in SPRUDTS and of *G. ruber* as indicative of an increase in depth and extent of the thermocline. The regime in state C is also characterized by the distinct decoupling of the $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$ signals at the biozone I/II boundary, marking an increasing (isotopic) isolation of intermediate/bottom waters from the surface system. There is a synchronous onset of depletions in $\delta^{18}O_{ruber}$ and $\delta^{18}O_{inflata}$, but $\delta^{18}O_{pachyderma}$, on the contrary, responds initially with a small enrichment. As $\delta^{18}O_{inflata}$ inflects with $\delta^{18}O_{ruber}$ we deduce that the winter water ($\delta^{18}O_{inflata}$) responded to the same climatic trend as the summer water ($\delta^{18}O_{ruber}$). This is what would be expected for a substantial perturbation: the effect is seen first and strongest in the shallow summer mixed layer and subsequently passed on to the more voluminous winter mixed layer. Any species living below the summer mixed layer effectively lives in the previous year's winter water, and hence even subsurface summer species should reflect the main isotopic change. However, as $\delta^{18}O_{pachyderma}$ shows a completely independent and opposite response, we infer that *N. pachyderma* lived in a water mass "isolated" from the surface water system. For this reason, we indicate *N. pachyderma* in an intermediate water mass (IW) that was strongly differentiated from the surface system, with the mixing indicators restricted to levels above the IW boundary. Such a condition could have resulted from an invasion of intermediate water from a remote source. Despite the presence of a physically stable environment for *N. pachyderma* we see a rapid reduction in this species' abundance, suggesting that its habitat underwent rapid deterioration. This would fit with our proposal of remotely derived intermediate water since an increase in the pathway from its source relative to the previous locally produced AEIW would result in poorer oxygenation for intermediate water masses in the Aegean. State C also shows a marked reduction in numbers of *G. inflata*, implying that seasonal water column homogenization became inhibited. Shortly following state C, *G. inflata* numbers dwindle into insignificance. The only species showing a real increase is *G. glutinata*. *G. glutinata* may require less dramatic vertical mixing and may hence have replaced *G. inflata*. However, as *G. glutinata* has a short reproductive cycle [*Hemleben et al.*, 1989] it's occurrence may also be an opportunistic response to any increase in nutrient availability. We also identify an increase in numbers of the eutrophic species *G. bulloides*. On the basis of its year-round occurrence in the area today [*Pujol and Vergnaud-Grazzini*, 1995] we have represented it with a year-round occurrence. State C therefore represents a progressive warming of climate and a resulting reduction in local intermediate and deep water production. This allows the increasing isolation of the intermediate water, which in turn allows the

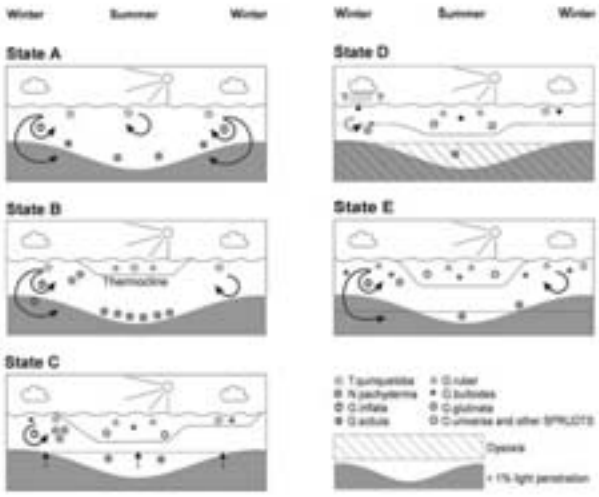

Figure 6. Schematic reconstruction of the history of Aegean circulation. The states illustrated are transitory, and this schematic represents the typical changes in deep water mixing and faunal distribution in the Aegean since the last glaciation. The timing of these transitions and placement of these typical assemblages are summarized in Figure 5.

Table 2. Timing of Events[a]

Event	LC-21, Depth 1520 m	SL-31, Depth 430 m	SK-1	*Geraga et al.* [2000]	SLA-9, Depth 250 m	Mean Age, Calibrated kyr B.P.	Youngest Age, Calibrated kyr B.P.	± (Range/2)
Start of $\delta^{18}O_{ruber}$ depletion T1a	15.7	15.0	–	–	15.9	15.9	15.7	±0.2
III-II	15.8	15.1	15.4	14.8	–	15.5	14.8	±0.6
Start of $\delta^{18}O_{ruber}$ depletion T1b	10.5	11.5	–	–	11.6	11.3	10.9	±0.4
II-Ic	10.5	11.6	11.4	11.1	11.5	11.3	10.9	±0.4
Start $\delta^{13}C$ depletion	10.4	10.3	–	–	10.7	10.5	10.3	±0.2
Start $\delta^{18}O_{pachyderma}$ depletion	10.1	10.2	–	–	10.4	10.2	10.1	±0.2
Age of maximum $\delta^{18}O_{ruber}$ - $\delta^{18}O_{pachyderma}$ difference	10.1	10.2	–	–	10.4	10.2	–	±0.2
Age of level 1/*e* ($\delta^{18}O_{ruber}$ - $\delta^{18}O_{pachyderma}$)	9.85	9.9	–	–	9.55	9.75	–	±0.2
Benthic sapropel	9.5	9.8	–	–	10.1	9.8	9.5	±0.3
End of benthic sapropel	6.1	6.9	–	–	6.4	6.5	6.1	±0.4
Ic-Ib	5.5 (6.1)	6.9	7.1	6.8	6.4	6.6 (6.7)	5.6 (6.1)	±0.8 (±0.5)
Ib-Ia	4.6	5.1	6.1	5.1	–	5.2	4.6	±0.8

[a] This table details the interpolated starting ages of important horizons in cores LC-21, SL-31, and SLA-9. All ages are expressed as calibrated kyr B.P. and are derived by linear interpolation between bracketing dated horizons. The mean age of each event is given in the last column, with the range between cores expressed as an error. Additional dates are given after *Zachariasse et al.* [1997] for core SK1 and *Geraga et al.* [2000] for core C-40. The number in parentheses in the LC-21 column gives the interpolated age of the start of *G. glutinata* increase in LC-21. This also corresponds with the start of benthic reventilation as indicated by an initial reoccurrence of *G. orbiculares*. This point corresponds with an increase of *G. ruber* and a decrease in *T. quinqueloba* and *G. inflata*. We suggest (see text) that the *G. glutinata* increase in the more open setting of LC-21 correlates with the *G. inflata* increase in the more continental settings of the northern Aegean cores.

mineralization products resultant from surface productivity to accumulate in more or less isolated deeper waters.

4.4. State D

[23] This represents the deposition of sapropel S1 and is the culmination of the sequence of changes that started with termination 1b. Roughly 1 kyr after the start of the T1b depletion in $\delta^{18}O_{ruber}$, a similar depletion begins to show up in $\delta^{18}O_{pachyderma}$. The long time lag suggests that diffusive mixing was the major mechanism for transfer of the isotopic depletion from the surface (*G. ruber*) to the deeper environments (*N. pachyderma*) since convective mixing would have caused a virtually instantaneous response between the two species (see, for example, the coincidence between the onsets of depletion in $\delta^{18}O_{ruber}$ and $\delta^{18}O_{inflata}$). The anomalous response of $\delta^{18}O_{pachyderma}$ led us to conclude that it was living subsurface in a water mass unaffected by the local seasonal homogenization (see state C). The $\delta^{13}C_{pachyderma}$ in state D becomes strongly depleted relative to $\delta^{13}C_{inflata}$ and $\delta^{13}C_{ruber}$ suggesting that the strongly reduced *N. pachyderma* population that could survive did so subsurface in an "isolated" poorly ventilated water mass with accumulation of ^{12}C-rich remineralization products. We therefore contend that the eventual depletion in $\delta^{18}O_{pachyderma}$ resulted from a slow diffusive mixing process. Our inference of a halt in convective mixing is supported by the presence of dysoxic indicators in the benthic foraminiferal fauna within S1 since a lack of convective overturn results in poor ventilation and consequently dysoxia in bottom waters. For some intervals, at depth (LC-21, 1500 m), no benthic species survive at all, suggesting that bottom waters became totally anoxic. In the planktonic foraminifera, assemblage Ic dominates, which consists of predominately warm-water species with a notable absence of fall/winter/spring mixing indicators. Hence we infer that there was a strongly developed, possibly year-round, thermocline/halocline. During this regime we see depletion in $\delta^{13}C$ for all species recorded. This may be the effect of influx of terrestrial dissolved organic carbon (DOC) [*Asku et al.*, 1999] since this period is known to coincide with a widespread increase in humidity. This is also evidenced by high North African lake levels, high abundance of humidity markers in the local palynological records, and the isotopic anomalies in speleothem data [*Rossignol-Strick*, 1995; *Edmunds et al.*, 1999; *Bar-Matthews et al.*, 1999; *Tzedakis*, 1999; *deMenocal et al.*, 2000]. The resultant increase in freshwater input is schematically represented by a rainfall symbol in state D, even though much of the fresh water would have arrived in the form of river runoff rather than direct precipitation [*Jenkins and Williams*, 1983; *Shaw and Evans*, 1984; *Thunell and Williams*, 1989; *Rohling and Hilgen*, 1991; *Rohling*, 1994, 1999b]. As mentioned previously, $\delta^{13}C_{pachyderma}$ depletes more than $\delta^{13}C_{ruber}$ and $\delta^{13}C_{inflata}$, which suggests that such any DOC explanation needs to be combined with the concept that *N. pachyderma* survived in an ageing water mass. With the intermediate water isolated and (virtually) stagnating, it would accumulate an excess of ^{12}C from remineralization. In contrast, the shallow $\delta^{13}C_{ruber}$ signal is continually being equilibrated by contact with the atmosphere. Note that the separation in $\delta^{13}C$ signals coincides with the onset of sapropel formation and therefore with the appearance of benthic markers for very poor bottom water oxygenation, suggesting a culmination of subsurface/deep water stagnation.

4.5. State E

[24] Here we recognize the establishment of a modern circulation regime. The $\delta^{18}O_{pachyderma}$ and $\delta^{18}O_{inflata}$ signals have come back together, suggesting that both live in isotopically undifferentiated winter water. The $\delta^{18}O_{ruber}$ is also similar to $\delta^{18}O_{pachyderma}$ and $\delta^{18}O_{inflata}$ in SL-21 but is slightly more depleted in the remaining cores. This suggests that intermediate and surface waters

in this area are once again very similar, which implies direct local communication between these water masses. This may indicate that (1) intermediate waters are upwelling to the surface and/or (2) surface waters directly contribute to intermediate water formation. Slight $\delta^{13}C$ differentiation between *N. pachyderma* and *G. ruber*/*G. inflata* suggests that *N. pachyderma* continued to live subsurface at levels more affected by remineralization than the surface/mixed layer environments preferred by *G. ruber* and *G. inflata*. The return of deep mixing indicator *G. inflata* and the presence of the spring bloom indicator *G. glutinata* suggests that seasonal mixing is again well developed. In addition, we see a dominance of *G. bulloides*, giving an overall faunal aspect that is very similar to that seen in modern records [*Thunell*, 1978; *Pujol and Vergnaud-Grazzini*, 1995].

4.6. Deductions on Mechanism and Timing of Circulation Change

[25] Having identified a general trend of reduced potential for deep overturn in the circulatory system during the 6 kyr leading up to sapropel production, we now consider the mechanism and timing of these changes. The trend starts from a glacial environment characterized by a single well-mixed water mass with strong accordance between isotopic signals in all species analyzed. This suggests little density contrast in the water column, while the presence of deep mixing species like *G. inflata* points to regular homogenization/overturn. We have interpreted this as indicative of year-round mixing. This glacial circulation appears to alter with the start of termination 1a. At that time, a shift in environment is clearly indicated in both the fauna and the isotopic data. Our interpolated dates suggest the onset of this change at ~15.9 ka (Table 2). This change associated with T1a appears to have occurred very rapidly, within a few hundred years.

[26] The subsequent regime is characterized by the start/strengthening of summer stratification. We believe this change in circulation was driven by the combination of climatic warming and rising sea levels at the onset of the Bölling-Allerød. During that interval we see the first substantial occurrence of warm mixed layer species, suggesting a general sea surface warming. Together with the increase in *N. pachyderma*, this leads us to suggest the development/strengthening of a stable summer thermocline in a generally well oxygenated environment. Studies of African lake levels and aeolian dust influxes [*Edmunds et al.*, 1999; *deMenocal et al.*, 2000] suggest that this period also saw the start of a regional humidity increase (African humid phase (AHP)). Any increase in freshwater budget would have increased surface buoyancy, helping to establish (seasonal) stratification. This state persisted until the onset of the Younger Dryas (YD) at ~12.5 ka.

[27] In common with many Mediterranean records, the YD is represented in this study by a plateau in the $\delta^{18}O$ records. The fauna shows increases in the mixing indicator *G. inflata* and a decrease in relative abundance of the warm mixed layer species. This suggests a strengthening of winter convection during this period. The YD has also been identified as an interruption in the AHP [*deMenocal et al.*, 2000], and probably represented a cool arid climatic event [*Rossignol-Strick*, 1993, 1995, 1999]. The YD conditions continue until the start of termination 1b marked at ~11.3 ka in our records.

[28] The start of T1b marks a clear dissociation between $\delta^{18}O_{pachyderma}$ and $\delta^{18}O_{ruber}$/$\delta^{18}O_{inflata}$, from which we deduce that the (intermediate) water mass in which *N. pachyderma* lived was no longer locally connected to the surface system. In addition, we argue that the major source region of intermediate water at this time was somewhere outside of the Aegean. Adriatic intermediate water would be one possible source of our proposed "foreign" intermediate water in the Aegean. This agrees with suggestions of *Myers et al.* [1998] that, the Adriatic Sea was a major source of intermediate water to the eastern Mediterranean during sapropel formation and that this under certain circumstances could enter the Aegean Sea [*Myers and Rohling*, 2000]. This introduction of foreign intermediate water also has implications for the dating of foraminiferal material, a proportion of which will be living in this older water. Correlation between the LC-21 timescale and the GISP II data suggests we see the start of a 350 year offset in LC-21 dates within the anoxic phase. This offset appears to be largely finished by the time of the deposition of the Santorini ash layer [*Rohling et al.*, 2002]. T1b marked the end of the peak in *G. inflata* abundance and a shift toward the dominance of the shallower-living species *G. glutinata* and of warm mixed layer species. This signals the inhibition of deep mixing and the isolation of intermediate waters, corroborating our interpretation of the separation between $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$. From this point on, remineralization products were able to build up in the subsurface to deep waters.

[29] With the ending of the Younger Dryas, the AHP recommenced and persisted until 5.5 ka [*deMenocal et al.*, 2000]. In the Aegean cores we note a depletion in $\delta^{13}C$ for all species analyzed, starting at ~10.5 ka, which we interpret as a possibly the result of increasing humidity in the Aegean Sea. Coinciding with this depletion in $\delta^{13}C$, *G. glutinata* replaces *G. inflata*. This may be tentatively explained in terms of increased freshwater input, which reduced surface buoyancy loss and hence suppressed mixing.

[30] With the suppression of convective mixing in the Aegean, diffusion-type processes become the main driver for property exchange through the water column. At ~10.2 ka, we identify an inflection in $\delta^{18}O_{pachyderma}$, which seems to mark the start of the conveyance of the termination 1b signal to the isolated intermediate water. This allows us to determine a timescale of diffusive mixing. By assessing the time between the maximum $\delta^{18}O_{ruber}$-$\delta^{18}O_{pachyderma}$ gradient and its 1/*e*-fold reduction we can roughly estimate the diffusive timescale for the basin in its stratified sapropel mode. We calculate this to be ~450 years (Table 2).

[31] By ~9.8 ka, deposition of sapropel S1 has commenced (Table 2). This is ~400 years after the total suppression of mixing inferred from the start of the overall $\delta^{13}C$ depletion and the faunal shift to a virtually complete dominance of mixed layer species. The start of sapropel production also occurs ~1500 years after the isolation of the deep/intermediate waters, inferred from the separation of $\delta^{18}O_{ruber}$ and $\delta^{18}O_{pachyderma}$. The isolation of subsurface waters would have allowed subsurface accumulation of remineralization products over a period of up to 1.5 kyr before these products became available for production in the euphotic zone. We suggest that this long-term accumulation provided a major source of excess nutrients that could sustain enhanced productivity during sapropel deposition.

[32] On the basis of benthic foraminiferal indicators, S1 persisted until 6.5 ka (Table 2). At its termination the return of *G. inflata* indicates the restart of seasonal mixing. The warm/cold plots (Figure 2) suggest this may have been a cooling event. In LC-21 the end of the benthic sapropel is marked in the planktonic record by the occurrence of *G. glutinata* first rather than *G. inflata*. This may be related to the proximity of the northern Aegean cores (SL-21 and SL-31) to the area of deep water production in the Athos Basin [*Yüce*, 1995]. While the more remote position of LC-21 from the region of water column overturn, would have resulted in a more gradual increase in seasonal mixing, with a correspondingly different progression in the fauna. The general $\delta^{13}C$ depletion may reflect terrestrial DOC influx due to increased humidity persisted until ~4.9 ka. However, the timing of the $\delta^{13}C$ depletion, some 400 years after suppression of mixing, is of the same order as our *e*-fold diffusive timescale, suggesting that the carbon depletion maybe in part due to the upward advective-diffusive transport of ^{13}C-depleted dissolved inorganic carbon (DIC). This DIC would be supplied from deeper waters, depleted in ^{13}C by remineralization.

Around that time the fauna also settled into its modern abundance distributions (Ib-Ia transition, Table 2).

5. Conclusions

[33] There is a clear link between the Aegean hydrographic regime and the global deglaciation phases. Seasonal stratification is weak to nonexistent before the onset of termination 1a, while intermediate water was virtually indistinguishable from shallow waters. After the onset of termination 1a, we identify a distinct seasonal stratification alternating with vigorous overturning seasons. This resulted in a winter mixed layer of similar characteristics to the intermediate water and a summer mixed layer that was distinguished from this by a marked seasonal thermocline. T1b marks the next distinct hydrographic change when intermediate water became dissociated from the summer/winter mixed layers in the study area. This noncommunication between the surface and intermediate system indicates reduced/curtailed ventilation of intermediate and deeper waters. This implies that property exchanges would have become dominated by slow (diffusive) mixing, and we estimate a $1/e$-fold diffusive mixing timescale of ~450 years. This gives the first ever observation-based quantitative estimate of this timescale in the stratified (sapropel mode) Mediterranean.

[34] Furthermore, the dissociation of surface and intermediate systems allowed remineralization products to accumulate in intermediate and deep waters, over a period of up to ~1.5 kyr prior to sapropel deposition. Meanwhile, the isolated intermediate water would have become progressively more dysoxic, a process augmented by the observed increase in (year-round?) stratification. The sapropel therefore appears to represent the culmination of a dynamic nonsteady state process. This has important consequences for the currently accepted steady state approach to circulation and property budget calculations for the eastern Mediterranean in sapropel mode. The sapropel mode ended with the reoccurrence of winter mixing indicative species at ~6.5 ka, while the return to a modern faunal assemblage was completed by ~4.9 ka.

[35] **Acknowledgments.** We thank Frans Jorissen and John Thomson for their constructive comments and discussion, Hilary Sloane for her help with isotopic analysis of cores SL-21 and SL-31 at the NERC Isotope Geoscience Laboratory at Keyworth, UK, and Connie de Vries for her efforts with the stable isotopes of LC 21 at the SOC isotope facility. LC 21 was recovered within EC-MAST2 programme PALAEOFLUX and is held at the BOSCOR repository in Southampton. Aegean cores were collected with the aid of NCMR in Athens, Greece. Data from this paper have been archived with the NOAA-NGDC.

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PALAEO

Palaeogeography, Palaeoclimatology, Palaeoecology 190 (2003) 103–119

www.elsevier.com/locate/palaeo

A dynamic concept for eastern Mediterranean circulation and oxygenation during sapropel formation

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Received 19 March 2002; received in revised form 26 June 2002; accepted 18 October 2002

Abstract

We propose that intermittent bottom water ventilation occurred throughout periods of sapropel deposition, and that the recently reported sapropel 'interruptions' represent centennial-scale episodes of enhanced frequency/intensity of that process. In essence, the modern high-frequency variability in deep water formation (affected by climatic variability over the northern basins on seasonal to longer time scales) prevailed also at times of sapropel deposition, although the overall ventilation state was much reduced. This concept is supported by: detailed multiple-species isotope records for three Aegean cores; the presence of abundant *Globorotalia truncatulinoides* within especially sapropels S7 and S8 in the western Levantine basin; observations of three rapid benthic repopulations within sapropel S6 in the deep western Levantine basin; a report of continuous benthic presence through sapropel S1 at intermediate-deep locations offshore Libya; and further supporting information from the literature. In the Aegean records, concomitant abundance of low-oxygen tolerant benthic foraminifera and presence of the more oxyphilic benthic foraminifer *Uvigerina mediterranea*, with surface-similar $\delta^{13}C$ values, indicate repeated deep water re-oxygenation events throughout the deposition of S1. The observations of a continuous benthic presence through S1 (offshore from Libya) imply that no persistent anoxia developed at mid-depth levels in that region, which is far removed from direct deep ventilation influences. The abundance of deep mesopelagic *G. truncatulinoides* through several sapropels from the western Levantine basin also suggests the presence of bio-available oxygen at many hundreds of meters of depth. Moreover, the rapid/intermittent benthic repopulations within sapropels from the deep eastern Mediterranean imply that bottom water anoxia was spatially restricted and/or of a highly intermittent nature. The short time scales of these repopulation events are incompatible with titration of an extensively anoxic water column and subsequent re-establishment of water-column anoxia. We suggest that where anoxic/azoic conditions were present, they most likely were restricted to a veneer at the sediment/water interface. The extent of such an anoxic 'blanket' depends on the balance between advective oxygen supply into the deep sea, and biological and chemical oxygen demand. The demand functions imply a decoupling of oxygenation from water mass advection, allowing export production and C_{org} posting

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PII: S0031-0182(02)00601-6

rates to the sea floor to delimit the extent of the anoxic blanket in both space and time. Low-productivity regions would develop no anoxic blanket, allowing for the observed persistence of deep dwelling planktonic and bottom dwelling benthic faunas.

Keywords: eastern Mediterranean; sapropel S1; benthic foraminifera

1. Introduction

The Mediterranean Sea is of particular interest to palaeoceanographers, as it possesses its own thermohaline circulation with deep water being formed in the northern basins (Bethoux et al., 1999). In the eastern Mediterranean, the Adriatic Sea and the Aegean Sea are subject to orographically channelled cold, dry air from high latitudes (Mariolopoulos, 1961; Poulos et al., 1997) similar to the mistral that affects the western Mediterranean (Leaman and Schott, 1991). This drives deep overturn that is known to respond rapidly to climatic variability in both the modern (Theocharis, 1989; Roether et al., 1996) and palaeorecords (Casford et al., 2001; Rohling et al., 2002). We present preliminary observations from RV *Meteor* cruise M51-3 (12 November–11 December 2001) and data from Aegean cores SL-11, SL-21 and SLA-9 (Fig. 1) that suggest that this high-frequency variability may also find expression during times of sapropel formation.

Ever since the first discovery of sapropels in eastern Mediterranean sediments (Kullenberg, 1952) they have been a source of controversy. Although the association between sapropel formation and insolation-driven monsoon maxima is well established (Rossignol-Strick, 1983, 1985), the role of anoxia has become a central issue in the characterisation of processes that underlie sapropel formation. Opinions are divided about the relative importance of two possible processes, either a reduction in ventilation leading to anoxia and hence organic carbon preservation (Olausson, 1961; Cita et al., 1977; Vergnaud-Grazzini et al., 1977; Cita and Grignani, 1982; Vergnaud-Grazzini, 1985), or an increase in primary productivity (DeLange and Ten Haven, 1983; Calvert, 1983; Boyle and Lea, 1989; Pederson and Calvert, 1990; Van Os et al., 1994). Clearly, these scenarios are not mutually exclusive (see Rohling and Gieskes, 1989), as an increase in productivity would enhance export of organic carbon (C_{org}) to the sediment surface and could utilise all the available oxygen, producing anything from dysoxia to anoxia. Increased freshwater influx would enhance nutrient concentrations in the basin that would in turn enhance productivity, especially when there appears to be a potential build-up of nutrients over >1000 years before utilisation (Casford et al., 2002). Observations of high pollen concentrations (Cheddadi and Rossignol-Strick, 1995) provide strong arguments that C_{org} preservation was much improved during sapropel times, compared with the present, and have been used to suggest extensive anoxia. The upper depth limit of sapropel occurrence at ~300 m in the open eastern Mediterranean (Rohling and Gieskes, 1989) and ~125 m in the Aegean Sea (Perissoratis and Piper, 1992), has been used to suggest that anoxia prevailed throughout the water column up to this depth. However, there are no observations to eliminate the possibility that true anoxia only developed as a blanket limited to the sediment/water interface. Indications for this 'Blanket Hypothesis' have been seen in Pliocene sapropel C2 from the Singa section of southern Italy (Rohling et al., 1993). Calvert (1983) implies that low C_{org} sapropels (i.e. those with ≤2% C_{org}) such as the Holocene S1 could be produced, without significant increases in primary productivity, i.e. without the development of a Deep Chlorophyll Maximum (DCM) (Rohling, 1994). Mercone et al. (2001) performed a combined micropalaeontological and geochemical study and infer that the presence of an Oxygen Deficiency Stress (ODS, sensu Rohling et al., 1997) assemblage of benthic foraminifera throughout S1 indicates either intermittent anoxia or continuous dysoxia. They further argue that uncertainties in the mechanism of

Fig. 1. Map of the Mediterranean Sea showing locations of the cores.

Table 1
Core location and type

Core	Type of core	Length (cm)	Depth below sea level (m)	Sedimentation rates (cm kyr^{-1})	Co-ordinates
LC-21[a]	Piston	–	1522	13.7	35°40′N, 26°35′E
SL-11	Gravity	209	258	9.5	39°06′N, 25°48′E
SL-21	Gravity	273	317	6.8	39°01′N, 25°25′E
SLA-9	Gravity	286	260	12.6	37°31′N, 24°33′E
971A	ODP	5880	2026	–	33°42′N, 24°43′E
SL97	Gravity	640	1879	–	33°43′N, 23°30′E
562MC	Multi-core	27	1390	–	32°46′N, 19°11′E

[a] Hayes et al. (1999); De Rijk et al. (1999); Mercone et al. (2000, 2001); Casford et al. (2001); Rohling et al. (2002).
Sedimentation rates are derived from the GISP II tuned time framework of LC-21 and from Casford et al. (2002).

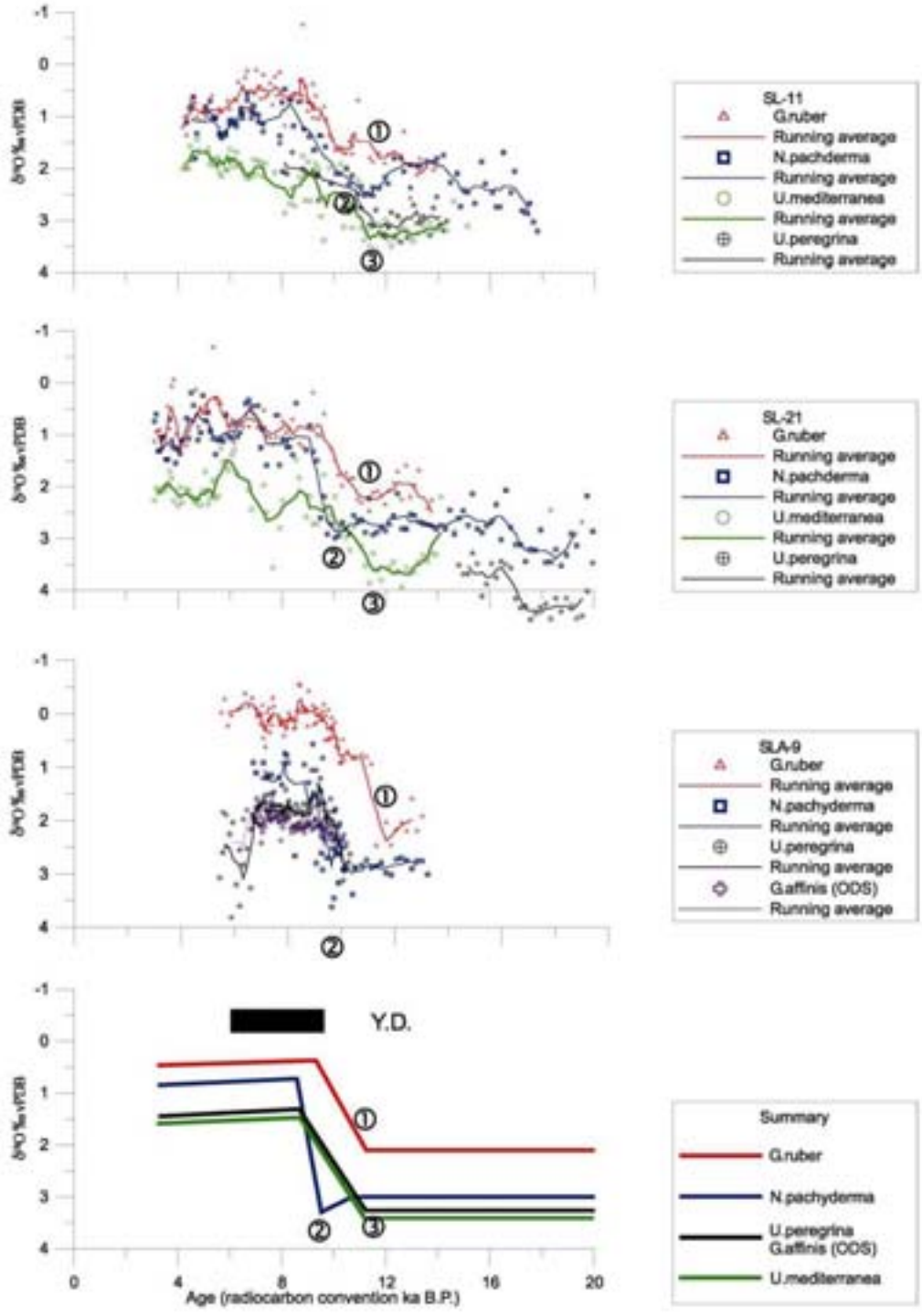
barium uptake in the water column and dissolution processes leave the use of barium as an indicator of palaeoproductivity in S1 open to question. We here offer new observations within the context of previous work to assess whether, at times of sapropel deposition, deep water formation had ceased (or not) and to what extent dysoxic and/or anoxic conditions prevailed. To explain these observations, a new dynamic concept of ventilation and oxygenation is presented.

2. Methods

We present: (1) initial observations from coring on RV *Meteor* cruise M51-3; (2) results from Aegean gravity cores SL-11 and SL-21 (North Aegean) and SLA-9 (South Aegean), which complement previous work on southeast Aegean core LC21 (Mercone et al., 2001; Casford et al., 2001; Rohling et al., 2002); (3) benthic foraminiferal abundance data in sapropel S1 from multicore 562MC off the Gulf of Sirte; and (4) benthic foraminiferal abundance data from sapropel S6 of ODP Hole 971A in the open Mediterranean. These results are placed within the context of observations from the literature. All cores investigated here consist of microfossil-rich hemipelagic ooze, with clearly defined darker bands of sapropel material. Cores SL-11, SL-21, SLA-9, and S6 from ODP Hole 971A were sampled in continuous sequences of 0.5-cm intervals. Given the high sedimentation rates of our cores the 0.5-cm sample interval gives a temporal resolution of between 40 and 75 years (Table 1). Multi-core 562MC was sampled at a 1-cm resolution. These samples were dried, weighed and selected (weighed) subsamples were disaggregated and wet sieved using demineralised water. The sieved fractions were collected on 600-, 150-, 125- and 63-μm mesh sizes. The >150-μm fractions were subdivided using a random splitter to provide an aliquot of about 200 individual planktonic foraminifera (>300 for benthics). For multi-core 562MC benthic fauna was analysed on the >63-μm fraction and between 50 and 100 individuals were counted where present. After sorting and counting, results were expressed as numbers g^{-1} and percentages (see Abu-Zied, 2001; Casford et al., 2002 for the Aegean faunal data). During RV *Meteor* cruise M51-3, core SL97 was sampled to provide an initial biostratigraphy. Several samples were taken from each sapropel and sieved over 150-μm mesh. The faunas were qualitatively assessed on board, using a binocular light microscope.

Detailed monospecific stable oxygen and car-

Fig. 2. Oxygen isotope data from cores SL-11, SL-21 and SLA-9. The main features of these records are summarised in the bottom panel. A solid bar indicates the extent of the sapropel. Explanation: (1) inflection before the depletion into the Holocene from the Younger Dryas (Y.D.) as shown in the record of $\delta^{18}O_{Globigerinoides\ ruber}$; (2) enrichment trend in the *Neogloboquadrina pachyderma* record and the lag in response of $\delta^{18}O_{N.\ pachyderma}$ compared with that of $\delta^{18}O_{G.\ ruber}$; (3) inflection in the benthic $\delta^{18}O$ record, coinciding with the inflection in $\delta^{18}O_{G.\ ruber}$.


SL-11
G.ruber
Running average
N.pachderma
Running average
U.mediterranea
Running average
U.peregrina
Running average
SL-21
G.ruber
Running average
N.pachderma
Running average
U.mediterranea
Running average
U.peregrina
Running average
SLA-9
G.ruber
Running average
N.pachyderma
Running average
U.peregrina
Running average
G.affinis (ODS)
Running average
Y.D.
Summary
G.ruber
N.pachyderma
U.peregrina
G.affinis (ODS)
U.mediterranea
Age (radiocarbon convention ka B.P.)

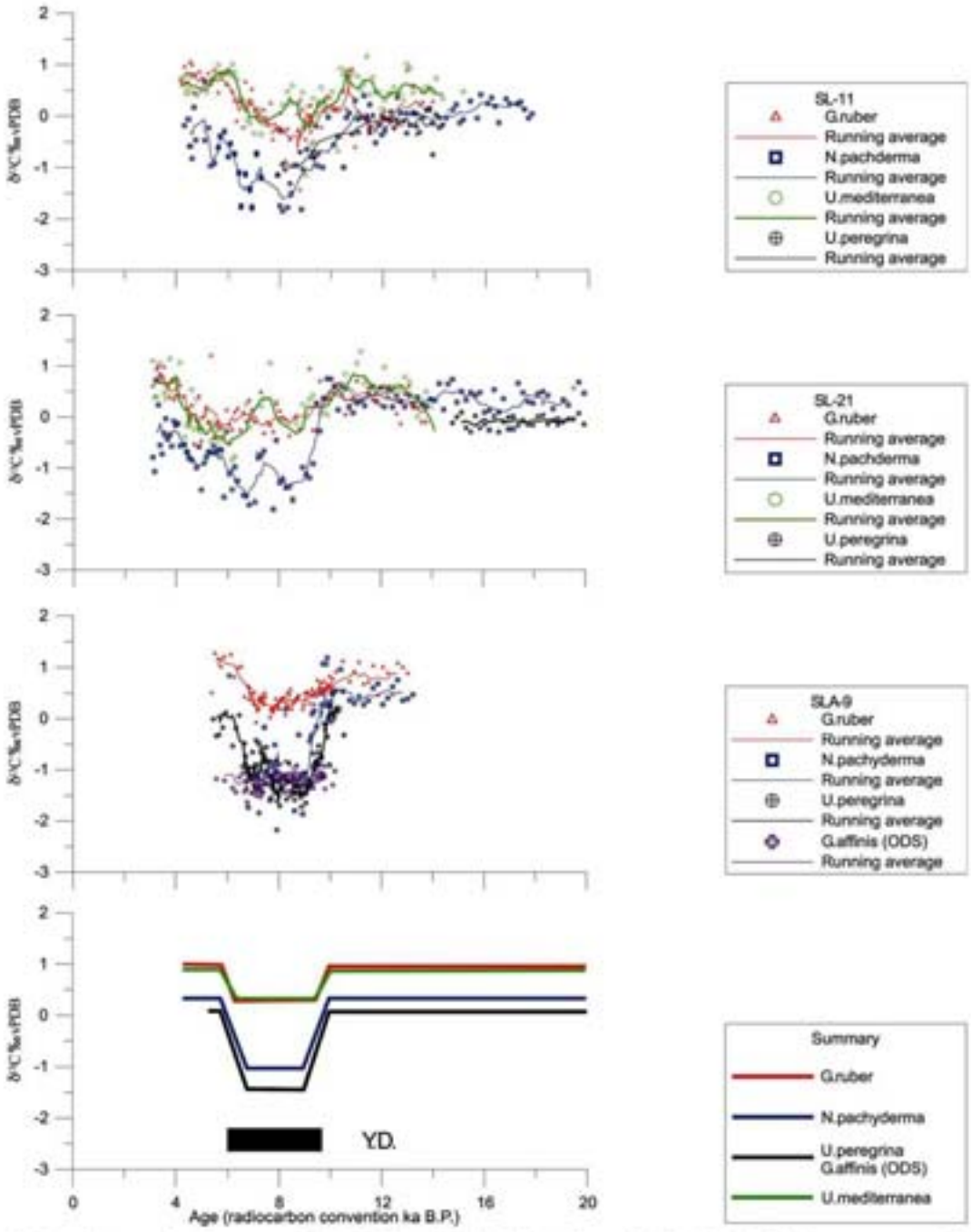


Fig. 3. Carbon isotope data from cores SL-11, SL-21 and SLA-9 showing the marked depletion in $\delta^{13}C$ across sapropel S1. The main features of these records are summarised in the bottom panel with the extent of the sapropel indicated by a solid bar.

bon isotope records were constructed for cores SL-11, SL-21 and SLA-9 with resolutions in the order of 1 cm (Figs. 2 and 3). These were derived from 'alternate' 0.5-cm samples and based on analyses of at least 10 individuals for each chosen species per sample. These chosen species were: the epipelagic (< 50-m) species *Globigerinoides ruber*; the mesopelagic species *Neogloboquadrina pachyderma* (dextral) which thrives in the DCM near the base of the euphotic layer; and the epifaunal/shallow infaunal benthics *Uvigerina mediterranea* (SL-21) and *Uvigerina peregrina* (SLA-9). In core SLA-9 we also analysed the low-oxygen tolerant benthic species *Globobulimina affinis*, which under oxygenated conditions occupies a deep infaunal habitat, at the Redox boundary. The selection of planktonic and benthic species follows global and specific Mediterranean habitat summaries in Hemleben et al. (1989), Rohling and Gieskes (1989), Jorissen et al. (1993), Pujol and Vergnaud-Grazzini (1995), Rohling et al. (1993, 1995, 1997), De Rijk et al. (1999), Hayes et al. (1999), Jorissen (1999), Reiss et al. (2000), and Abu-Zied (2001). The analyses were performed at two separate inter-calibrated facilities: the Europa Geo 20-20, with individual acid bath preparation at the SOC, and the VG-Optima with a common acid bath preparation at the NIGL. Isotope results are reported as ‰, standardised to Vienna Pee Dee Belemnite. External precision is in the order of < 0.06‰ (std).

3. Observations

3.1. High-frequency events in the Aegean Sea

The fact that it is possible to pick mature, clean *Uvigerina mediterranea* in sufficient numbers from all samples of cores SL-11 and SL-21 at a 1-cm resolution indicates that it occurs systematically (if rare) throughout S1 at this locale. This cannot be explained by downslope transport since this species was not found to be systematically associated with other shallow water (sensu De Rijk et al., 1999) faunal elements (Abu-Zied, 2001). In addition, the ridge location of the core sites make downslope transport less likely. Detailed abundance counts of benthic foraminifera in cores SL-31, SLA-9 and LC-21 show that *U. mediterranea* does not correlate with the known low-oxygen tolerant ODS group (Abu-Zied, 2001) and the presence of this group in itself suggests that, in the Aegean at least, deep waters never became persistently anoxic during S1.

The oxygen isotope records (Fig. 2) show obvious depletions into the Holocene, shifting about −2‰ in all species. This reflects a combination of global ice-volume reduction and changing regional climatic conditions as the eastern Mediterranean became warmer and more humid into the Holocene Climatic Optimum following the cooler, drier Younger Dryas (Rohling, 1999b). A clear offset can be seen, however, with the $\delta^{18}O$ of the epipelagic species *Globigerinoides ruber* showing more depleted values than the mesopelagic *N. pachyderma*, both in absolute values and general trends. The $\delta^{18}O$ values of all benthic foraminifera are similar to, or more enriched than, $\delta^{18}O_{Neogloboquadrina\ pachyderma}$. This can be explained in terms of the lower temperatures and higher salinities that characterise subsurface and deep water, relative to the surface mixed layer. Significantly, $\delta^{18}O_{U.\ mediterranea}$ (in cores SL-11 and SL-21) retains the heavy deep water values but inflects to lower values after the Younger Dryas at the same time as the surface-water record of *G. ruber*. This contrasts markedly with the lagged response of $\delta^{18}O_{N.\ pachyderma}$ that suggests an isolation of intermediate waters from surface processes (Casford et al., 2002). The combined data portray a direct link between responses to regional freshwater input in both surface and deepest waters, which is not shared at intermediate levels. We view this as a reflection of the proximity of our cores to an area of active deep water formation, with bottom waters penetrating intermittently below intermediate waters that continuously advect into the Aegean from a remote source area with different $\delta^{18}O$ characteristics (Casford et al., 2002).

The carbon isotope data (Fig. 3) allow further insight into the habitat separations between species. The general $\delta^{13}C$ trend shows relatively constant values before and after periods of sapropel deposition, with depletion in $\delta^{13}C$ values over the

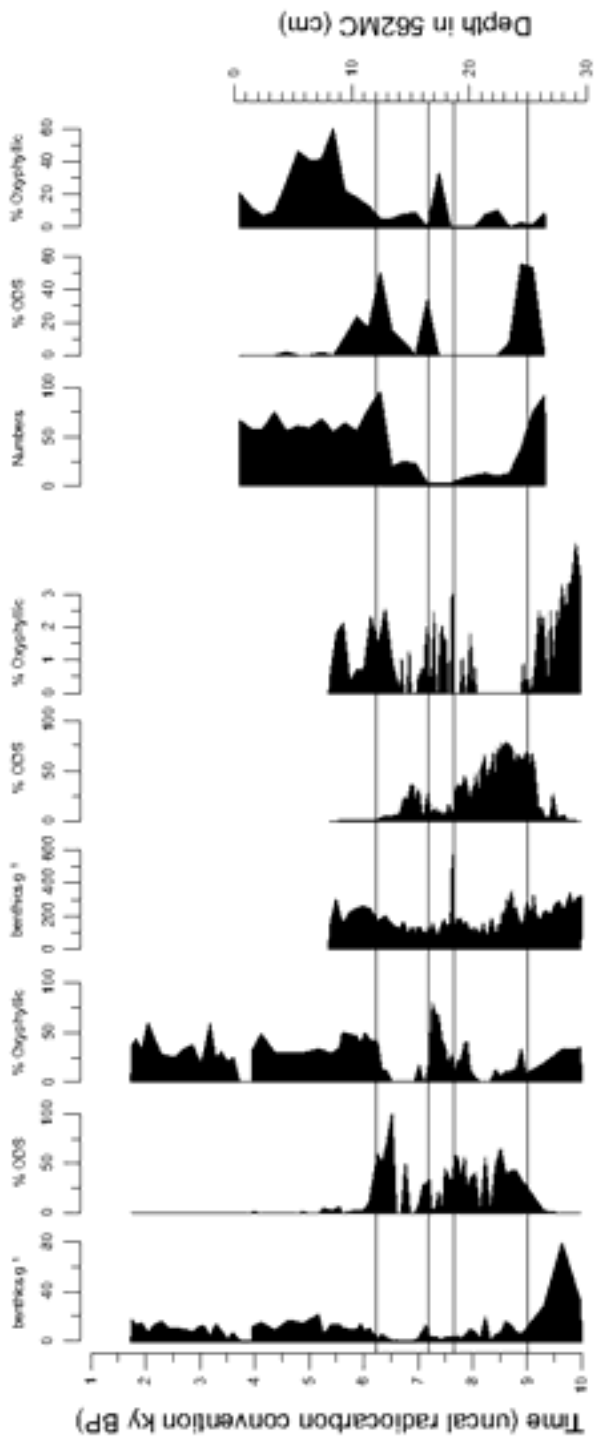


Fig. 4. Summary of (benthic) faunal indicators from cores SLA-9 and LC-21 as well as the preliminary results from multi-core 562MC. Showing numbers of benthic foraminifera per gram in SLA-9 and LC-21, with absolute numbers from 562MC. The % ODS plot indicates the total percentage of the dominant ODS foraminifera *Chilostomella mediterranensis*, *Cassidulinoides bradyi*, *Paramokolus mexicana*, and *Globobulimina affinis*. The oxyphylic plots show the total percentage of milioids, *Cibicides pachyderma* and *Gyroidinoides orbicularis* indicating the presence of oxygen requiring fauna.

sapropel itself. The magnitude of this depletion is greater in the mesopelagic *Neogloboquadrina pachyderma* than in the surface species *Globigerinoides ruber*. The benthic species *Globobulimina affinis* and *Uvigerina peregrina* in SLA-9 (southwest Aegean) show an even stronger depletion than *N. pachyderma*. Since ^{12}C is preferentially taken up during photosynthesis, surface-water Dissolved Inorganic Carbon (DIC) attains relatively high $\delta^{13}C$ values, while remineralisation causes relatively light $\delta^{13}C_{DIC}$ values at depth. Hence, benthic and mesopelagic species would normally be expected to show lighter $\delta^{13}C$ values than epipelagic species. Vital effects might account for constant offsets between the various benthic and deep planktonic species but the general trends in their records should be similar. Paradoxically, the $\delta^{13}C_{\textit{U. mediterranea}}$ signal in the northern Aegean cores SL-11 and SL-21 mimics both the trend and values of the epipelagic species *G. ruber* (Fig. 3). Note that SL-11 and SL-21 are both from locations adjacent to an area of deep water production (the Mount Athos basin) and are sited in relatively shallow water (Table 1). Hence, a likely explanation for the anomalous $\delta^{13}C_{\textit{U. mediterranea}}$ signal is that *Uvigerina mediterranea* lived in newly advected deep water, with a carbon isotope signal that has very recently been 'set' according to air–sea equilibrium, but retaining an oxygen isotope signal that reflects the (cool and saline) deep water signature (Fig. 2). The combination of abundant ODS species (with carbon isotope trends resembling that of *N. pachyderma*) alongside *U. mediterranea*, with an absence of comprehensive repopulation by other species, suggests that advection events were intermittent and short-lived phenomena.

3.2. Centennial-scale sapropel interruptions

'Interruptions' of centennial-scale duration within sapropels have been reported from across the Mediterranean, with examples from the Holocene to the Pliocene (e.g. Van Straaten, 1966, 1972; Thunell et al., 1977; Stanley, 1978; Rossignol-Strick et al., 1982; Cita et al., 1984; Vismara-Schilling, 1984; Perissoratis and Piper, 1992; Rohling et al., 1993, 1997; Mercone et al., 2001). It is important to establish the relationship between the conjectured high-frequency advection events (above) and the longer-term ventilation changes that caused these sapropel interruptions.

First of all, we note that the centennial-scale 'interruption' of S1 in the Aegean core LC-21 shows rapid benthic repopulation, from one sample to the next (i.e. within ~50 years; Fig. 4). SLA-9 also shows these marked shifts, alternating between ODS species and less low-oxygen tolerant opportunists (Abu-Zied, 2001; Mercone et al., 2001); this is also the case in the Adriatic (Jorissen et al., 1993; Rohling et al., 1997; Mercone et al., 2000). Here, we show similar rapid benthic repopulations, bound by azoic intervals, within S6 (Fig. 5). This is a significant observation because the studied S6 comes from ODP Hole 971A, taken at a deep location (~2026 m) in the open eastern Mediterranean, rather than within a deep water source region like the Adriatic or Aegean. Clearly deep ventilation improved sufficiently to allow the presence of bio-available oxygen at the sea floor at this very deep site in the open basin, and it happened both repeatedly and abruptly.

Detailed study of the interruption in S1 has linked it to climatic processes. Its benthic foraminiferal repopulations are indicative of re-oxygenation, related to improved deep water formation and while the entire interval lasted several centuries, its onset was very abrupt, within 50 years (Mercone et al., 2001; Rohling et al., 2002). The reventilations were found to be related to 'cold spells' over northern basins of the Mediterranean (Rohling et al., 1997, 2002; Casford et al., 2001; Mercone et al., 2001), which are considered to be periods of increased frequency or intensity of outbreaks of polar/continental northerly air masses from higher latitudes (Mariolopoulos, 1961; Theocharis, 1989; Roether et al., 1996; Poulos et al., 1997). Individual outbreaks are seasonally dependent, normally lasting 1–5 days, concentrated in the winter months, and interannually variable (Saaroni et al., 1996). Intense periods of concentrated outbreaks can dominate over periods of weeks to months; a recent episode started end November 2001 and lasted into January 2002 (see on-board observations RV *Meteor* cruise M51-3 for the first two weeks of the event; Fig.

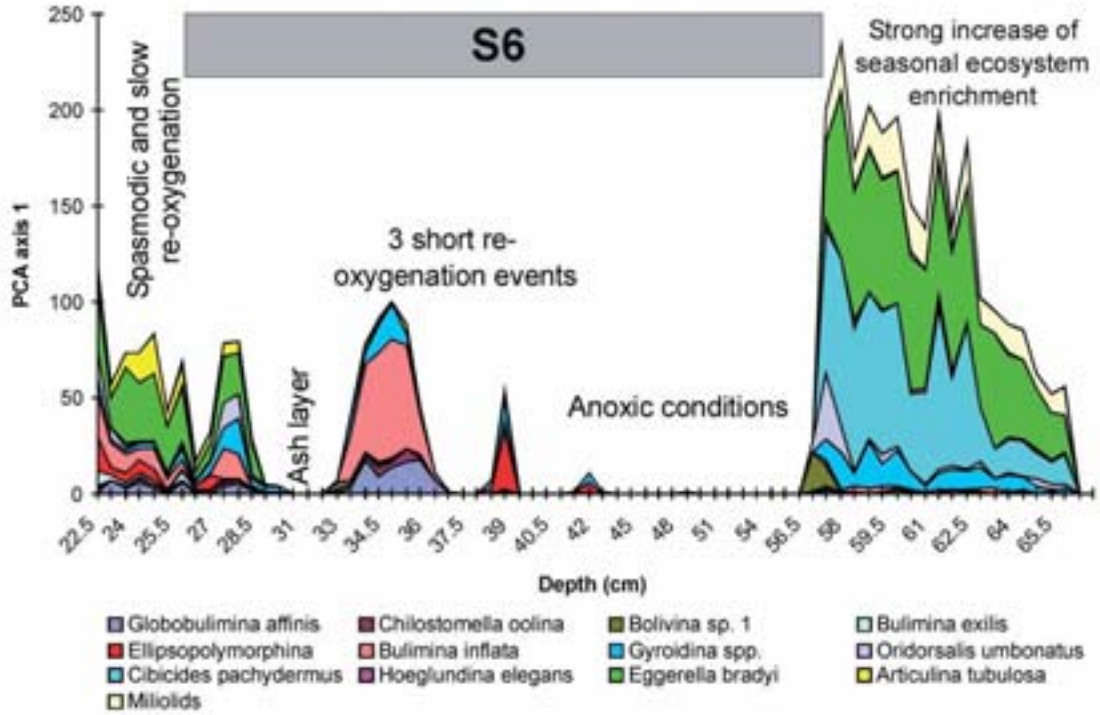


Fig. 5. Core 971 scores on first-principle component for the benthic foraminifera abundance distributions through S6 in ODP Hole 971A, illustrating three abrupt reventilation events in this deep location (2026 m).

6), while a previous episode with particularly intense northerly cooling over the Aegean occurred in the late 1980s–early 1990s (Theocharis, 1989; Roether et al., 1996). Variations in the intensity and frequency of such outbreaks drive variability in the deep water formation rates (Theocharis, 1989; Roether et al., 1996). The Holocene history of centennial-scale cold spells has been linked to the GISP2 ice-core based proxy for intensity of the Siberian High (Rohling et al., 2002). It would appear that the cold spells represent a longer-periodicity 'clustering' of times with particularly abundant and intense northerly outbreaks.

3.3. Other ventilation indicators

A key on-board observation from RV *Meteor* cruise 51-3 relevant to this study concerns the high relative abundances of both right and left coiling morphotypes of the planktonic foraminifer *Globorotalia truncatulinoides*, which we found in several sapropels of core SL97 from the western Levantine basin (especially S7 and S8). This species has been observed in the deepest tows in the Mediterranean at ~300 m (Pujol and Vergnaud-Grazzini, 1995), but is known from oceanic studies to spend significant parts of its life cycle below these levels, down to ~1000 m (Hemleben et al., 1989; Lohmann and Schweitzer, 1990). This unprecedented observation of *G. truncatulinoides* suggests that the upper water column remained regularly ventilated to a depth of many hundreds of meters in this region.

A further important observation concerns the presence of benthic foraminiferal faunas reported here, throughout S1 at mid-depths (1391 m) off Libya in core 562MC (Table 1; Fig. 4), similar to such observations through much of S1 in the southern Aegean (Mercone et al., 2001) and the Adriatic (Jorissen et al., 1993; Rohling et al., 1997). Such continuations imply that either intermittent ventilation or continuous dysoxia pre-

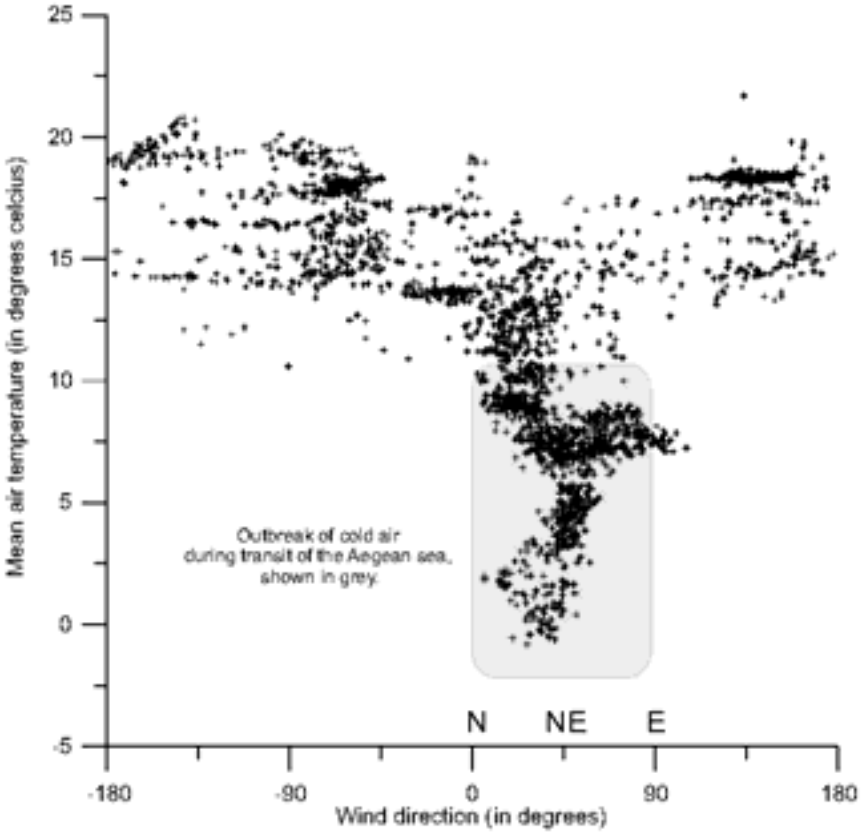


Fig. 6. Plot of wind direction vs. air temperature illustrating the northery flow of the cool/continental air outbreak over the Aegean during RV *Meteor* cruise 51-3 (December 2001).

vailed. The observations off Libya are most surprising because of this area's remote position relative to likely deep ventilation sources.

4. Discussion

Although sample size even in high sedimentation-rate areas limits the temporal resolution of proxy records, some important conclusions can still be drawn from the sedimentary record. The occurrence of *Uvigerina mediterranea* throughout the S1 in the Northern Aegean suggests that it repopulated on a regular basis within our sample resolution. Hence, ventilation must have occurred at least once and possibly several times within the time span of each sample (~50 years). We inferred that the resemblance of the trends in $\delta^{13}C_{U.\ mediterranea}$ to those of the epipelagic species *Globigerinoides ruber* suggests that $\delta^{13}C_{U.\ mediterranea}$ (Fig. 3) reflects DIC values that were recently 'set' at the surface, in agreement with the core's proximity to a sensitive key area of regional deep water production. Hence, intermittent ventilation is suggested throughout S1 within the Aegean (Fig. 7).

The benthic faunas present through S1 off Libya (Fig. 4) also suggest intermittent ventilation, or continuous dysoxia. Similarly, ventilation to a depth of many hundreds of meters is inferred from the abundance of *Globorotalia truncatulinoides* in the open eastern Mediterranean (core SL97) during S7 and S8, while discrete but sustained reventilation events are even observed in

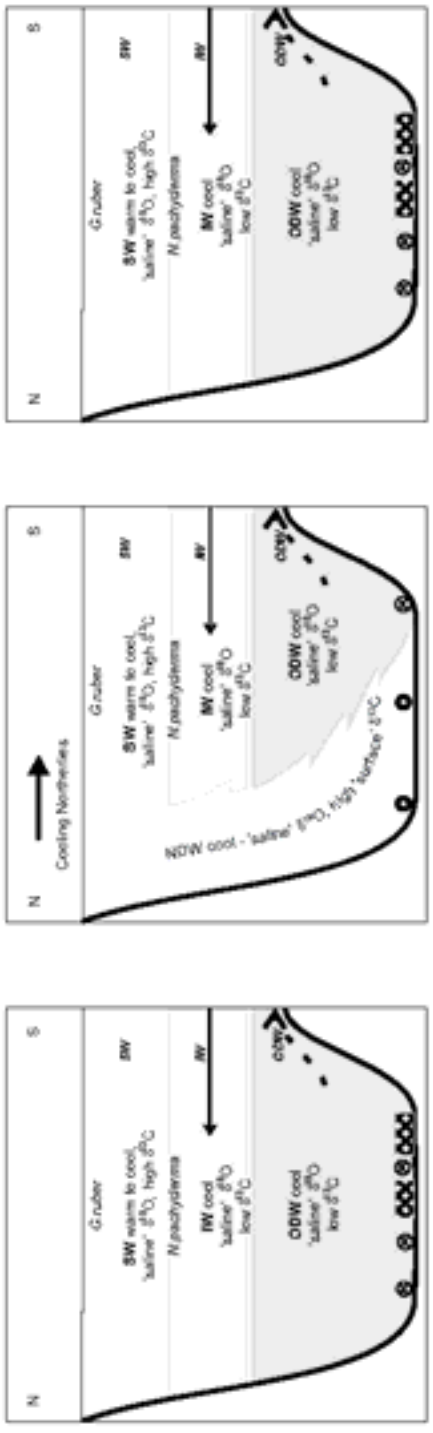


Fig. 7. Three-stage schematic representation of the inferred configuration of water masses before, during and after reventilation in the Aegean Sea. ODW indicates the presence of Old Deep Water; NDW represents the advection of New Deep Water.

the deep water S6 deposit of ODP Hole 971A (Fig. 5).

While persistent ventilation events in small convective regions such as the northern Aegean basin are relatively easy to envision, rapid and sustained repopulations in deep open settings are much more difficult to explain. Such rapid events would require abrupt oxygenation of the bottom waters. This cannot be explained by diffusive oxygen transport, since diffusive mixing operates on time scales >1000 years (~450 years e-folding diffusive time scale (Casford et al., 2002). Consequently, the rapid reventilations must have resulted from direct advection of newly formed bottom waters. This advection must have been strong enough to overcome the titration of any reduced chemical species (e.g. Fe^{2+}, Mn^{2+}) both in the water column and at the sediment/water interface. If the entire water column were anoxic, then a very considerable reservoir of such chemical species would need to be titrated. In addition, any Biological Oxygen Demand (BOD) in the water column would need to be overcome, before a finite amount of bio-available oxygen could be present at the sea floor to sustain viable benthic populations.

Using values summarised in Rohling (1994), modern BOD rates alone would require on the order of 640 years to establish water-column anoxia below 1500 m if advective oxygen supply failed completely. More sophisticated model results (Stratford et al., 2000) suggest that it would take nearer to ~1500 years to establish anoxia. Today advective oxygen supply outstrips this demand by around five times (~2.67 mol O_2 m^{-3} y^{-1}, below 1500 m), so that a re-establishment of today's intensity of advective supply after an anoxic phase would re-oxygenate the water column below 1500 m as rapidly as 1–2 centuries. This is in agreement with Roether and Well (2001) who calculate a figure of 150 years to replace existing deep water. Following the above values for establishment of anoxia and subsequent re-oxygenation, it would require around 740–1700 years which far exceeds the rapid variability observed. Note that this ignores the potential build-up of reduced chemical species in the water column, which would considerably lengthen the calculated recovery period. BOD and chemical titration would remove oxygen from the new deep water resulting in a spatial separation between the oxygenation front and the penetration of the new deep water. Furthermore, these controls will also vary with the strength of export productivity and concentration of reduced species (a function of the degree of anoxia) both of which are likely to show regional and/or spatial variability.

To address the much faster response times observed it would appear much more likely that any anoxia was limited to a thin 'blanket' at the sediment/water interface. Such a 'blanket' would result from remineralisation of organic components that were rapidly posted to the sea floor (e.g. diatom mats; Kemp et al., 1999), and so would reflect the patchy nature of the spatially and temporally variable export productivity distribution.

Observations of deep-living planktonic species (e.g. *Globorotalia truncatulinoides*) and benthics throughout sapropels suggest that they are most common in the more oligotrophic areas of the eastern Mediterranean, e.g. off the Gulf of Sirte. Might this reflect spatial differences in the export productivity levels? Poor ventilation would create dysoxic conditions everywhere, and regions of high export flux developed anoxic 'blankets' whereas oligotrophic regions did not. The patchy nature of such 'blankets' may also allow refugia for certain benthic foraminifera to develop locally, promoting more rapid repopulation.

In addition, there is a clear increase in sedimentary C_{org} concentrations with water depth (Murat and Got, 2000), that appears to conflict with the normal expectations of a mid-depth remineralisation maximum/oxygen minimum. The observed increase with depth may reflect that a remineralisation maximum instead prevailed at the sea floor, presumably due to rapid export/dumping of C_{org}, supporting our proposal that anoxia was constrained to a blanket at the sediment/water interface.

Murat and Got (2000) observations of increasing organic carbon concentrations with depth suggest that deep water isolation also increases with depth. In addition, the probability of significant ventilation in a density-stratified basin decreases with depth. As the indicators, reported here, of

(intermittent) bio-available oxygen within sapropels do not include observations from below 2026 m, we cannot exclude the possibility that abyssal depths developed more widespread and persistent anoxia. This uncertainty calls for high-resolution studies in abyssal sites of sapropels that have known reventilation histories in shallower locales.

5. Summary and conclusions: A dynamic ventilation concept

Integrating the various strands of evidence discussed above, we propose a dynamic concept for the relationship between deep water ventilation and oxygenation at sapropel times. The ventilation state we propose is in fact similar to that of today, in that it remained characterised by intermittent climate-related maxima of new deep water formation that were associated with cooling by interannually variable northerly outbreaks of polar/continental air. However, at sapropel times, the ventilation was weakened overall, due to the additional buoyancy gain imposed by the enhanced freshwater influx into the basin. Our dynamic concept of ventilation decouples water mass advection – driven by new formation and internal mixing – from the oxygen concentrations

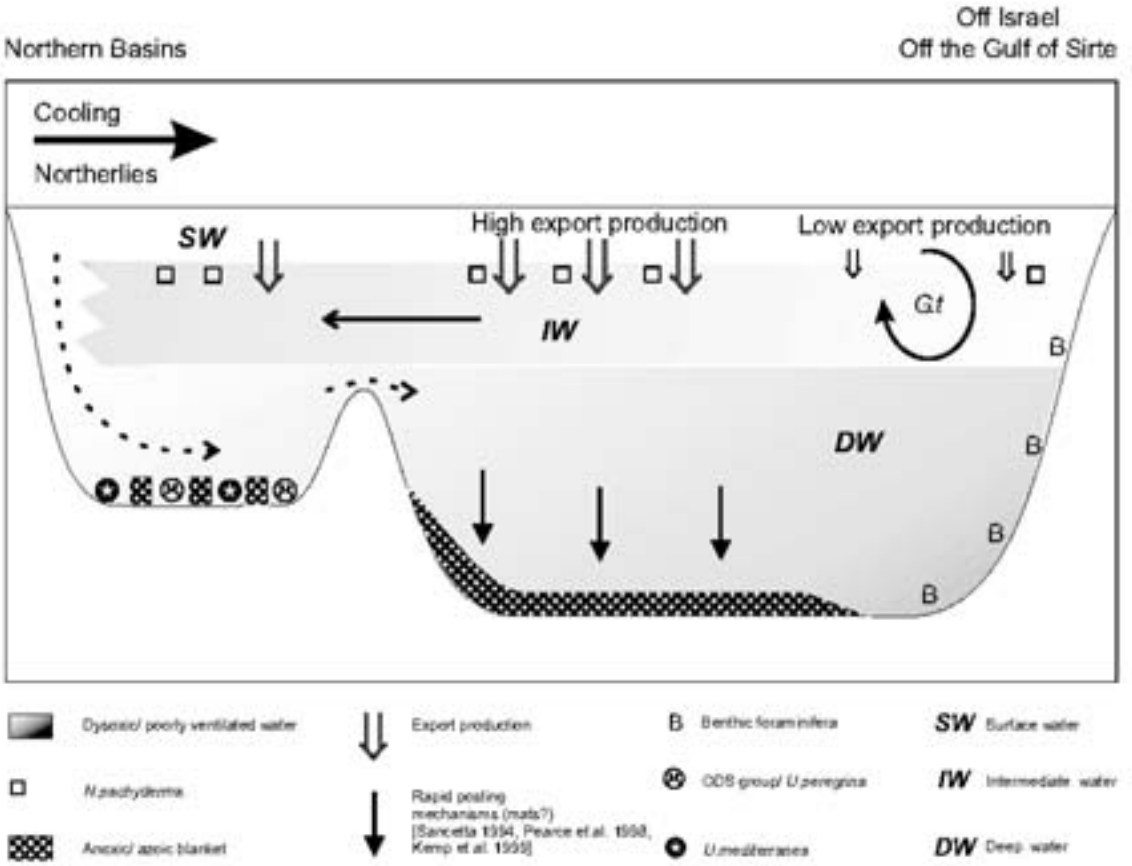


Fig. 8. Schematic 2-D summary of the discussed aspects of deep water advection and oxygenation, based on a compilation of several sapropels. This is intended to represent a hypothetical north-south transect and is therefore not intended to define specific spatial gradients. The letter B in the key represents benthic foraminifera in both the continuous benthic presence off Israel and the rapid repopulation S6. This exemplifies the restricted nature of the anoxic blanket in both space and time.

that are in addition affected by chemical and biological constraints, with their own temporal and spatial variability. This allows for contrasting oxygen concentrations within single water masses, both temporally and spatially.

Fig. 8 aims to summarise these key aspects in a very schematic 2-D representation, which obviously cannot capture all observed 3-D and temporal variability. In addition, this figure does not account for any possible anoxia deeper than 2000 m, as mentioned above. Intermittent ventilation is shown in the north of the profile, as determined throughout S1 in both the Aegean and Adriatic from the presence of benthic faunas and their isotopic composition, in particular contrasting the low-oxygen tolerant species *Globobulimina affinis* and the more oxyphilic *Uvigerina mediterranea*. This deep water ventilation must occur at least once within every sample interval (~50 years), and most probably even more frequently. The graded grey fill illustrates the inferred oxygenation gradient within both deep water and intermediate water masses, and highlights the dissociation of intermediate water from the surface and deep waters in the Aegean Sea (see Casford et al., 2002). A blanket of anoxia develops under areas of higher export production, with the presence of benthic foraminifera in cores from even the deep, southern Mediterranean suggesting the limited extent of these truly anoxic conditions in both space and time. This blanket hypothesis for the development of anoxia removes the requirement to titrate the complete water column upon reventilation, allowing very rapid events of re-oxygenation and return to anoxic conditions seen in the proxy records.

Acknowledgements

We acknowledge the contributions of the scientific team of RV *Meteor* cruise M51-3 (November–December 2001), in particular the chief scientist Professor C. Hemleben. We thank Larry Peterson and Anne Murat for their invaluable comments during review. Additional thanks are also due to S. Cooke and H. Sloane for their technical assistance.

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