

Experimental evidence of complex interactions between biotic and abiotic factors in the dynamics of an intertidal population of the bivalve *Cerastoderma edule*

Intraspecific competition
Tidal elevation
Hydrodynamics
Recruitment
Cerastoderma edule

Compétition intraspécifique
Niveau de marée
Hydrodynamisme
Recrutement
Cerastoderma edule

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ABSTRACT

Densities of the suspension-feeding bivalve *Cerastoderma edule* (L.) were manipulated inside field enclosures at two tidal elevations (low water level, LWL, and mid-tide level, MTL) on an intertidal sand flat in Arcachon Bay to test the influence of both adult densities and emersion time on (1) individual growth rate, (2) settlement rate, and (3) survival rate of cockles. These experiments were conducted during two consecutive years, in plots with ambient (1 \times) and modified (1/3 \times , 3 \times , or 10 \times) densities of adult cockles.

Growth rate and condition index of both adults and juveniles were significantly higher at the lowest tidal elevation (LWL), which is in accordance with the feeding mode of the species. The highest juvenile growth rate was recorded in the low-density treatments (160-200 adults m⁻²), which suggests a competitive interaction with adults; for the latter, growth rate was depressed only at the highest density (2000 m⁻²). Survival of adults was affected neither by immersion time nor by densities. Contrasted results were found for the settlement rate and the survival of recruits. During the first year of experiment, density-treatments had no effect on settlement at MTL, whereas high adult densities negatively influenced settlement at LWL, but only during the period of high settlement; during the second year, a significant effect of adult densities on settlement was found on a single occasion at MTL. However, at the end of both experiments (195 and 252 d, respectively), recruit densities did not significantly differ between density-treatments. Although the difference in tidal elevation between the two experimental sites was only 1.0 m, settlement peaks were clearly distinct: they occurred in April (\approx 4000 m⁻²) at LWL but not earlier than July (\approx 12000 m⁻²) at MTL; however, the final recruitment was higher at LWL than at MTL.

Preliminary results of a laboratory flume study show that, in conditions of smooth turbulent flow ($u_* = 0.51$ cm s⁻¹, $Re_* = 1.8$), juvenile cockles are able to leave the substratum, to migrate by byssus drifting into the water column over several metres and to avoid resettlement in areas with high densities of conspecific adults. Although competition with adults may occur during larval settlement, subsequent migration of juveniles between different tidal levels is likely to affect significantly the growth and recruitment of intertidal cockle populations.

RÉSUMÉ

Mise en évidence expérimentale d'interactions complexes entre facteurs biotiques et abiotiques dans la dynamique d'une population intertidale du bivalve *Cerastoderma edule*.

L'impact de la densité et de la durée d'immersion sur la croissance, le recrutement et le taux de survie du bivalve suspensivore *Cerastoderma edule* (L.) a été recherché au moyen d'expériences réalisées *in situ* à deux niveaux de marée (niveau de basse mer, LWL, et niveau de mi-marée, MTL) sur un estran sableux du Bassin d'Arcachon. Ces expériences, réalisées lors de deux années consécutives, ont été conduites en maintenant dans des enclos des densités normales (1×) ou modifiées (1/3×, 3× ou 10×) de coques adultes.

Le taux de croissance et l'indice de condition des adultes et des juvéniles ont été significativement supérieurs au niveau de basse mer, conformément au mode de nutrition de l'espèce. Chez les juvéniles, les taux de croissance les plus élevés ont été mesurés dans les traitements à plus faible densité (160-200 adultes m⁻²), suggérant une interaction compétitive avec les adultes ; pour ces derniers, le taux de croissance n'a été affecté que pour de très fortes densités (2000 m⁻²). La survie des adultes n'a été affectée ni par la durée d'immersion, ni par les densités. Le recrutement et la survie des recrues ont présenté des résultats variables. Lors de la première année, les densités n'ont pas eu d'effet sur le recrutement à MTL, alors que les fortes densités d'adultes ont eu un impact négatif sur le recrutement à LWL, mais seulement pendant la période maximale de sédentarisation ; durant la seconde année, un effet significatif des densités d'adultes sur le recrutement n'a été enregistré qu'en une seule occasion à MTL. Cependant, à la fin des expériences (soit après, respectivement, 196 et 252 jours), les densités de recrues ne différaient pas significativement entre les différents traitements. Bien que la différence de niveau de marée entre les deux sites expérimentaux ne fut que de 1,0 m, le pic de recrutement s'est produit en avril avec une faible intensité (≈ 4000 m⁻²) à LWL et seulement en juillet mais de façon très marquée (≈ 12000 m⁻²) à MTL ; le recrutement final a néanmoins été plus élevé à LWL qu'à MTL.

Des résultats préliminaires obtenus en canal hydrodynamique ont montré que, dans des conditions de flot non turbulent ($u_* = 0.51$ cm s⁻¹, $Re_* = 1.8$), les juvéniles de coque pouvaient quitter le substrat, migrer dans la colonne d'eau sur une distance de plusieurs mètres en dérivant grâce à des filaments muqueux, et se sédentariser à nouveau en évitant les zones à forte densité de coques adultes. Bien qu'une compétition avec les adultes puisse intervenir pendant la phase de sédentarisation larvaire, il est suggéré qu'une migration secondaire de juvéniles entre différents niveaux de marée, sous l'action des courants, peut affecter significativement la croissance et le succès du recrutement des populations intertidales de coques.

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INTRODUCTION

In the past two decades, correlational field data as well as field and laboratory experiments have provided evidence that biological interactions, especially predation and competition, play an important role in regulating densities of soft-bottom marine invertebrates. Competitive interactions in infaunal communities may operate through a wide variety of mechanisms, including (1) direct interference, (2) exploitative competition for food, and (3) indirect interference through alteration of the physical environment [see reviews by Peterson (1980), Woodin (1983), Wilson (1991)]. In benthic suspension feeders the occurrence of either direct interference competition for space (Peterson and Andre, 1980) or sediment-mediated interactions (Jensen, 1985) has been rarely demonstrated. Most experiments

have shown that food depletion is the main mechanism of competition acting in established populations of suspension feeders (Peterson, 1982; Peterson and Black, 1987; Peterson and Beal, 1989; Kamermans, 1993); this is in accordance with studies which showed that suspension-feeding bivalves filter tremendous volumes of water (*e.g.* Bayne *et al.*, 1976) and thus may significantly deplete suspended food in the benthic boundary layer (*e.g.* Fréchette *et al.*, 1989 and 1993). Consequently, the outcome of competition for food among infaunal suspension feeders is generally a reduction in individual growth rates (Peterson and Andre, 1980; Peterson, 1982; Weinberg, 1985; 'Olafsson, 1986 and 1989; Peterson and Black, 1987 and 1993; Peterson and Beal, 1989; Jensen, 1992 and 1993; Kamermans, 1993), although some experiments did not demonstrate any density-dependent effect on growth (Brock, 1980;

Peterson and Andre, 1980; Peterson, 1982; Peterson and Black, 1987 and 1993; Kamermans *et al.*, 1992). Other documented effects of inter- or intraspecific competition in infaunal suspension feeders include an increase of emigration or a reduction of reproductive effort (Peterson and Andre, 1980; Peterson, 1982; Jensen, 1985), whereas mortality rate is generally unchanged with increasing density (Peterson, 1992).

Interactions between established adults and settling larvae or early juveniles, which result partly from competition and partly from predation (Woodin, 1983; Wilson, 1991), have also long been considered important in structuring marine soft-bottom communities (Thorson, 1966). Several investigators have shown that adult suspension feeders can depress settlement directly by ingesting larvae from the water column (Mileikovsky, 1974; Woodin, 1976; Young and Chia, 1987; André *et al.*, 1993) and that many benthic invertebrates can cause mortality indirectly by burying juveniles with sediment displaced by feeding and burrowing (Woodin, 1976). Field data and experimental tests of the effects of suspension-feeding bivalves on settlement and juvenile survival through intra- or interspecific interactions have yielded variable results. As predicted by Woodin (1976), several studies have demonstrated a negative effect of adults on settlement (Williams, 1980; Möller, 1986; Hines *et al.*, 1989; André and Rosenberg, 1991; Bachelet *et al.*, 1992 *a* and *b*; André *et al.*, 1993) or recruitment (Hancock, 1973; Brock, 1980; Jensen, 1985 and 1992; Flach, 1992 and 1993) of conspecifics or other infauna. However, some studies have failed to demonstrate an inhibition of settlement (Hunt *et al.*, 1987; 'Olafsson, 1989; Bachelet *et al.*, 1992 *a* and *b*) or recruitment (Young and Young, 1978; Peterson, 1982; Maurer, 1983; Commito, 1987; Black and Peterson, 1988; Commito and Boncavage, 1989; Hines *et al.*, 1989; Peterson and Black, 1993). In these cases, explanations for non-significant effects of adult suspension feeders on settlement include differential predation rates due to species-specific larval defence mechanisms (Cowden *et al.*, 1984), differences in spatial scales between experimental plot size and areas where predation effects occur (Ertman and Jumars, 1988; Young, 1989 and 1990), and low statistical power due to small effect sizes (Young, 1990).

Although numerous experimental studies have demonstrated the importance of competitive interactions in assemblages of infaunal suspension feeders, it is clear that abiotic factors may also influence the outcome of these interactions. In the intertidal zone, tidal elevation is of prime importance for filter feeders because it sets the submersion time and hence determines their feeding period and supply of food. However, to our knowledge, only two field studies on suspension-feeding bivalves have assessed experimentally the role of competition and tidal elevation acting at the same time. Peterson and Black (1987) designed factorial field experiments to test the effect of site, adult density, and their interaction on growth of three species of bivalves; they showed that growth rate was density-dependent in two species out of three, but that tidal level effects on individual growth were far stronger than density effects. Similar results were found by Dobbins *et al.* (1989) who transplanted a venerid bivalve at different den-

sities between different shore levels: growth rate and survival decreased as tidal height increased, whereas density treatments had no significant effect on growth.

The edible cockle, *Cerastoderma edule* (L.), is an infaunal suspension-feeding bivalve living in sandy, shallow sediments along the European Atlantic coast. It burrows just below the sand surface and may reach adult densities of up to several thousands m^{-2} , mainly in the intertidal zone. Its planktotrophic larvae develop in the plankton for three to five weeks and settle onto the bottom at a size of approximately 280 μm in shell length. Previous experiments in Arcachon Bay have shown that cockle settlement was significantly lower at increased adult densities in one site, whereas it did not depend on adult densities in another site; it has been hypothesized that the lack of adult-juvenile interactions at the latter site was related to a weak larval input due to the high tidal level of this station (Bachelet *et al.*, 1992 *a* and *b*). The purpose of the present study was to manipulate the abundance of *C. edule* at two tidal elevations on the same site and measure the response of cockles in terms of growth, mortality, and settlement, as a test of whether immersion time modulates intraspecific competition. Additionally, we found that the seasonal variation of spat distribution could be explained by post-larval dispersal, whether active or passive, as it has been recently shown for several invertebrate species (Günther, 1992; Armonies, 1994 *b*; Roegner *et al.*, 1995). Therefore, we also performed flume experiments to test whether juvenile cockles were able to migrate and select a substratum for secondary settlement.

MATERIALS AND METHODS

Study area

The study site was a moderately protected intertidal sand flat at the Banc d'Arguin in Arcachon Bay (44°40' N; 01°10' W), a large (156 km^2) embayment on the south-western Atlantic coast of France. The tidal amplitude ranges from 4.35 m at spring tide to 0.95 m at neap tide. The sand flat is relatively narrow (approx. 50 m between low water and mid-tide levels), with a beach slope of about 3%. Tide is locally asymmetric with flooding speed 1.5 to 2.3 times faster than ebbing speed. Salinities remain high year-round (32-35) because of the location of the Banc d'Arguin at the entrance of the bay. Mean surface water temperature fluctuates between 9.5 °C in winter and 21.1 °C in summer (Bouchet, 1968). The sediment is dominated by medium sand (mean grain size: 350 μm ; silt-clay content: 1-5%; organic matter content: 0.4-1.5%). The macrofauna has been described elsewhere (Bachelet and Dauvin, 1993).

Field experiments

To test for intraspecific interactions, the abundance of *Cerastoderma edule* was manipulated within 0.25 m^2 topless enclosures constructed to maintain varying density treatments by preventing emigration and immigration of adult bivalves. Each enclosure consisted of a 50 × 50 ×

25 cm metal frame meshed with 10-mm plastic net, buried 15 cm and projecting 5 cm above the sediment, and anchored with iron bars.

First-year experiment

In 1992, nine enclosures were installed in a single file parallel to the shoreline at each of two tidal elevations: 0.9 m above chart datum, *i.e.* at mean low water level, and 1.9 m above chart datum, *i.e.* at mid-tide level; these levels (hereafter referred to as LWL and MTL, respectively) corresponded to mean emersion times of 21 and 41 %, respectively. The enclosures were regularly spaced with 2 m access paths between them. They were first cleared of all adult bivalves (*Cerastoderma edule*, plus some sparse individuals of *Ruditapes decussatus* and *R. philippinarum*) by ploughing the surface sediment with fingers to a depth of *ca.* 5 cm. Then, the enclosures were assigned to three treatments: (1) low cockle density ($1/3\times = 160 \text{ ind. m}^{-2}$), (2) normal cockle density ($1\times = 480 \text{ ind. m}^{-2}$), and (3) high cockle density ($3\times = 1440 \text{ ind. m}^{-2}$). All the cockles used in the manipulation experiments were sampled at MTL and their size-frequency distributions [mean shell length, $25.4 \pm 2.4 \text{ mm}$ ($n = 140$); extremes, 19–32 mm] were made similar across the enclosures. Three replicates of each treatment were established in a random design at each tidal elevation.

Second-year experiment

A similar experiment was conducted in 1993, but only at MTL and with two density treatments: (1) normal cockle density ($1\times = 200 \text{ ind. m}^{-2}$), and (2) high cockle density ($10\times = 2000 \text{ ind. m}^{-2}$). During this second year, adult cockles were smaller [mean shell length, $21.6 \pm 2.2 \text{ mm}$ ($n = 260$); extremes, 17–28 mm] and less abundant than in 1992. Consequently, the '93-1 \times -treatment was similar to the '92-1/3 \times -treatment, and the '93-10 \times -treatment received only 39 % more adult cockles than the '92-3 \times -treatment.

The experiments ran for 195 days in 1992 (18 March–29 September) and 252 days in 1993 (24 February–3 November). During the experimental periods the enclosures were regularly cleaned of any drifting macroalgae and empty shells. Every two weeks, two cores (6.9 cm diameter \times 1 cm deep) were randomly taken from within the 40 \times 40-cm central square of each enclosure to avoid any boundary effect. Core contents were preserved in 70 % alcohol and stained with Rose Bengal, then gently sieved through nested 2.0- and 0.125-mm meshes. Only juvenile cockles and mussels (*Mytilus* sp.) present between these sieves were counted as recently (≤ 2 weeks) settled spat.

At the end of the experiments, each enclosure sediment was sieved through a 1-mm mesh; all living cockles were counted and their shell length measured to the nearest 0.1 mm. A random sample of 15 cockles per enclosure and per age group was taken, in which sediment and symbiotic crabs were removed. Flesh (FW_i) and shell dry weights (SW_i) were measured separately for each individual after drying at 60 °C for 48 hours. A condition index was calculated as: $CI = \sum FW_i / \sum SW_i \times 10^3$ (Walne and Mann, 1975). To test for possible sediment modifications among treat-

ments, sediment samples were taken within each enclosure and adjacent to the experimental area, and analysed for organic matter and silt-clay contents.

Flume experiments

Experiments on the behaviour of juvenile cockles in flowing water were conducted in a recirculating, racetrack-design flume constructed of transparent, non-toxic plexiglas [Canal Hycobenthos, Laboratoire Maritime du Muséum, Dinard; see Lambert (1991) and de Montaudouin (1995) for a more detailed description]. The flume has a developed length of 13 m and the channel is 50 cm wide by 30 cm deep. Water is recirculated by friction by means of an 80 cm-diameter wheel made of 14 vertical discs located in the middle of one of the two straight lines of the flume. The working section is in the 3.5-m long straight line opposite the wheel and consists of five 0.08 \times 1.0-m sediment boxes. These boxes were filled with medium sand (median grain diameter: 350 μm) collected in the natural habitat of cockles and previously defaunated for two days in fresh water. In all flume experiments water depth was 15 cm, salinity was 28 and temperature ranged between 15.7 and 17.0 °C. Velocity profiles were obtained with an ultrasonic current meter (Minilab model SD-12, Sensor Data, Bergen, Norway) and determined for a flow speed of 10 cm s^{-1} measured in the centre of the sediment array and 15 cm above the bottom. Shear velocity, u_* , was calculated from the logarithmic section of the velocity profile by fitting the velocity measurements to the function described by the 'law of the wall' (Jumars and Nowell, 1984),

$$u(z) = u_* / \kappa \ln(z/z_0)$$

where $u(z)$ is the mean velocity at height z above the bottom, z_0 is the boundary roughness and κ the von Karman's constant (0.41). From u_* the roughness Reynolds number, Re_* , was calculated,

$$Re_* = u_* k_S / \nu$$

where k_S is the sand roughness scale (350 μm) and ν is the kinematic viscosity of seawater (0.01 $\text{cm}^2 \text{s}^{-1}$). In our experiments u_* was 0.51 cm s^{-1} and Re_* was 1.8; the boundary layer was thus characterized as hydraulically smooth turbulent (Nowell and Jumars, 1984).

Experiment A

This first experiment was designed to test for the occurrence of an active dispersal of juvenile cockles in conditions of smooth-turbulent flow by comparing the behaviour of living and dead individuals. After filling the flume, 250 live juveniles [shell length: 1.9 ± 0.7 (SD) mm] and 250 dead juveniles (same size) previously stained with Rose Bengal were gently mixed and placed together on the flume bottom, in a row 1.2 m upstream from the leading edge of the sediment array (Fig. 1a). Water was then set in motion for 4 h in order to mimic half a tide cycle. At the end of the experiment, the flume was slowly drained. Each of the five sediment boxes was divided into four 8 \times 25 cm rectangles which were sampled by skimming the top 5 mm of sand with a spoon. Samples were sieved on 200 μm

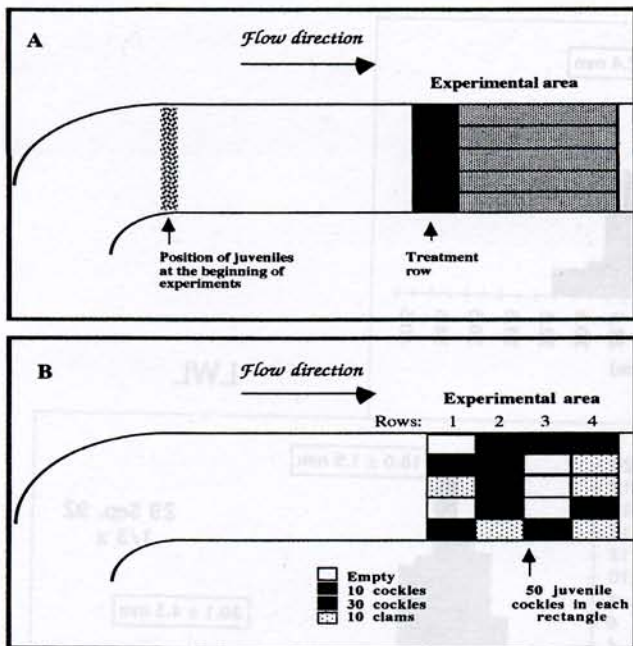


Figure 1

Experimental designs in the Hycobenthos flume. A) In experiments A, B, and C, the juvenile cockles were placed 1.2 m upstream from the sediment area; the 25-cm long upstream part of this area contained the treatments in experiments B and C ("treatment row"). B) In experiment D, the experimental area was divided into 20 rectangles assigned to 4 treatments; juveniles were added in each rectangle.

Protocole expérimental dans le Canal Hycobenthos. A) Dans les expériences A, B et C, les coques juvéniles étaient placées 1,2 m en amont de la zone sédimentaire ; la partie amont, longue de 25 cm, de cette zone contenait les traitements des expériences B et C (« treatment row »). B) Dans l'expérience D, la zone expérimentale a été divisée en 20 rectangles auxquels ont été attribués 4 traitements ; 50 coques juvéniles ont été introduites dans chaque rectangle de sédiment.

mesh, and live and dead juveniles were counted in each rectangle of sediment. To avoid artefacts due to diversion of currents, numbers were cumulated for each of the four rows of rectangles.

Experiment B

To investigate the possible negative effect of adults on the distribution of drifting juveniles, 30 adult cockles (20–28 mm in shell length) were placed in each 25 cm upstream part of the five sediment boxes. The "treatment row" (Fig. 1 a) thus included an adult density (1500 m^{-2}) similar to that of the high density treatments in the field experiments. When the adult cockles had buried, 150 live juvenile cockles [shell length: 1.6 ± 0.6 (SD) mm] were added as in experiment A. Duration and sampling were as in experiment A.

Experiment C

Compared to the latter experiment, adult cockles were replaced by 60 plastic sticks (1 cm wide \times 1 mm thick) projecting 1 cm above the sediment, in order to create turbulences without pre-emption of space.

Experiment D

This experiment was designed to test for a selection by drifting live juveniles for areas occupied by different densities of adult bivalves. The sediment area was divided into twenty 8×25 cm rectangles by burying small strips of 2 mm plastic net in the sand. These rectangles were assigned to four treatments: (1) 10 adult cockles (mean shell length: 25.7 mm) per rectangle (i.e. $500 \text{ m}^{-2} \approx$ density in the '92-1 \times -treatment), (2) 30 adult cockles per rectangle (i.e. $1500 \text{ m}^{-2} \approx$ density in the '92-3 \times -treatment), (3) 10 adult clams *Ruditapes decussatus* (mean shell length: 33.2 mm) per rectangle, and (4) no adult bivalve. Five replicates of each treatment were established in a random design (Fig. 1 b). Fifty live juvenile cockles [shell length: 1.3 ± 0.5 (SD) mm] were added in each rectangle at the beginning of the flow conditions. Duration and sampling were as in experiment A.

Statistical analyses

Length-frequency distributions of cockles in the field experiments were separated into gaussian components using the method of Bhattacharya (1967) and the parameters of each component were calculated according to the Hasselblad (1966)'s method with χ^2 test (NORMSEP program). Modal lengths were then compared with Student's *t*-test after control of homogeneity of variances with *F*-test. Analyses of variance were employed for all other comparisons, following the procedures outlined by Sokal and Rohlf (1981) and Underwood (1981). In order to test the null hypothesis that adult density had no effect on recruitment, juvenile abundances were compared for each tidal level and for each sampling date, using a two-level mixed-hierarchical ANOVA with enclosures (random factor) nested within treatments (fixed factor). For the other parameters compared in field experiments, a fixed-cross ANOVA was performed with tidal level and abundance as fixed factors. For the flume experiments, we used a randomized blocks design ANOVA with experimental treatment as fixed factor and appropriate sediment rectangle as random factor. Prior to performing any ANOVA, Cochran's test for homogeneity of variances was employed (Winer, 1971) with $\alpha = 0.05$. If the data failed this test, logarithmic transformations were applied, which was sufficient in our study to achieve homogeneity. Whenever an ANOVA was significant, the treatments were separated by *a posteriori* tests: SNK-test when the number of treatments was ≤ 3 , or Tukey's HSD-procedure when the number of treatments was > 3 (Day and Quinn, 1989).

RESULTS

Field experiments

Survival, individual growth and condition of cockles

The size distribution of adult cockles was clearly unimodal at the beginning of the 1992 experiment (Fig. 2) and slightly bimodal in early 1993 (Fig. 3); nevertheless, for more clarity, these cockles will be assigned to a single year class

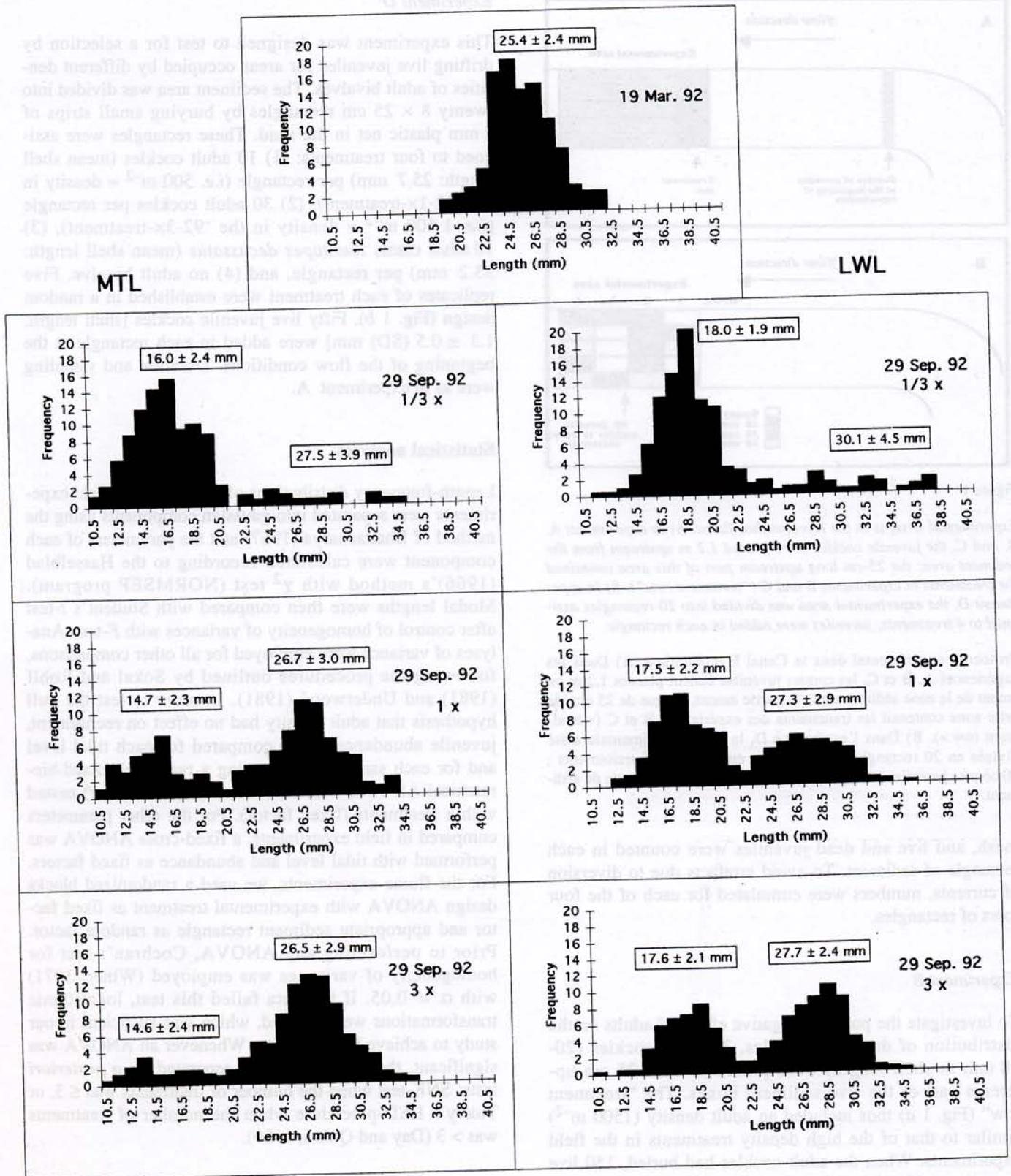


Figure 2

Size (shell length) frequency distributions of *Cerastoderma edule* in enclosures at the start (19 March; top histogram) and at the end (29 September; bottom histograms) of the 1992 experiment. The initial size distribution was similar in all enclosures. The final size distributions are shown for enclosures installed at mid-tide level (MTL, left) and at low-tide level (LWL, right). Density treatments and mean shell lengths (\pm SD) of each year class are given for each size distribution.

Distribution des fréquences de taille (longueur de la coquille) de *Cerastoderma edule* dans les enclos au début (19 mars ; histogramme du haut) et à la fin (29 septembre ; histogrammes du bas) de l'expérience de 1992. La distribution initiale des tailles était semblable dans tous les enclos. Les distributions de tailles finales sont données pour les enclos installés au niveau de mi-marée (MTL, à gauche) et au niveau de basse mer (LWL, à droite). Les traitements densitaires et les tailles moyennes (\pm DS) de chaque classe d'âge sont indiqués dans chaque cas.

(1 +). At the end of both experiments, the new recruits (0 +) were distinctly separated from the adults in the size-frequency histograms (Fig. 2, 3).

Survival rates in the 1+ year class did not differ significantly between tidal levels at the end of the 1992 experiment (Tab. 1, 2). On the other hand, adult cockles exhibited lower average survival rates as density increased in both years of the experiment (Tab. 1). Compared to the 1/3 \times -treatment, average mortalities at MTL in 1992 were 2.0 and 3.0 times higher in the 1 \times - and 3 \times -treatments, respectively; a similar increase of mortality figures was recorded at LWL (1.4 and 2.2 times, respectively). In 1993 also, mortality was 1.5 higher in the 10 \times -treatment than in the 1 \times -treatment at MTL. Accordingly, the final patterns of density treatments were 0.5 \times -1 \times -1.8 \times at MTL and 0.4 \times -1 \times -1.5 \times at LWL instead of 1/3 \times -1 \times -3 \times at the beginning of the 1992 experiment, and 1 \times -5.9 \times instead of 1 \times -10 \times at the beginning of the 1993-experiment. However, there was a high variation of survival rate within treatments in both experiments and the null hypothesis that cockle densities had no effect on adult survival could not be rejected by a two-level mixed ANOVA (Tab. 2).

Whatever the density treatments were, individual growth rate was significantly higher at LWL than at MTL for both year classes (Tab. 3; Fig. 2, 3). At the end of the 1992 experiment shell length at MTL was depressed by a factor of 12-17 % for the 0 + year class and by a factor of 2-9 % for the 1+ year class, compared with size at LWL.

Individual growth varied significantly with density treatment in six out of ten comparisons (Tab. 3; Fig. 2, 3). In the 1992 experiment, growth of both year classes at both tidal levels was significantly higher in the 1/3 \times -treatment than in the 1 \times -treatment: individual growth rate declined by a factor of 38.1 % (MTL) or 59.6 % (LWL) for the 1 + year class and by a factor of 8.1 % (MTL) or 2.8 % (LWL) for the 0 + year class, between the 1/3 \times - and 1 \times -treatments. During this first-year experiment, comparison of average sizes between the 1 \times - and 3 \times -treatments did not show any significant difference in either age group. In the 1993 experiment, cockle growth responded to density by showing significantly lower growth rate by a factor of 18.8 % (1 + year class) to 3.6 % (0 + year class) in the 10 \times - than in the 1 \times -treatment.

In both year classes, condition index at the end of the 1992 experiment was significantly higher at LWL than at MTL, but similar between density treatments (Tab. 1, 2).

Settlement and recruitment of cockles

During the 1992 experiment, settlement of cockles exhibited highly different patterns at the two tidal levels (Fig. 4). At LWL, settlement reached its maximum on 16 April, then regularly diminished until the end of July. The two-way nested ANOVA revealed significant treatment effects on juvenile numbers on 16 April, 5 and 19 May, when SNK-tests showed a higher settlement in the two lowest density treatments than in the 3 \times -treatment; no treatment effect was detected at other dates. At MTL, settlement in consistent numbers started only in May and the peak of settlement occurred considerably later (on 15 July, *i.e.* with a time lag of three months) than at LWL. Moreover, the maximum cockle settlement was far higher at MTL (about 12 000 m⁻²)

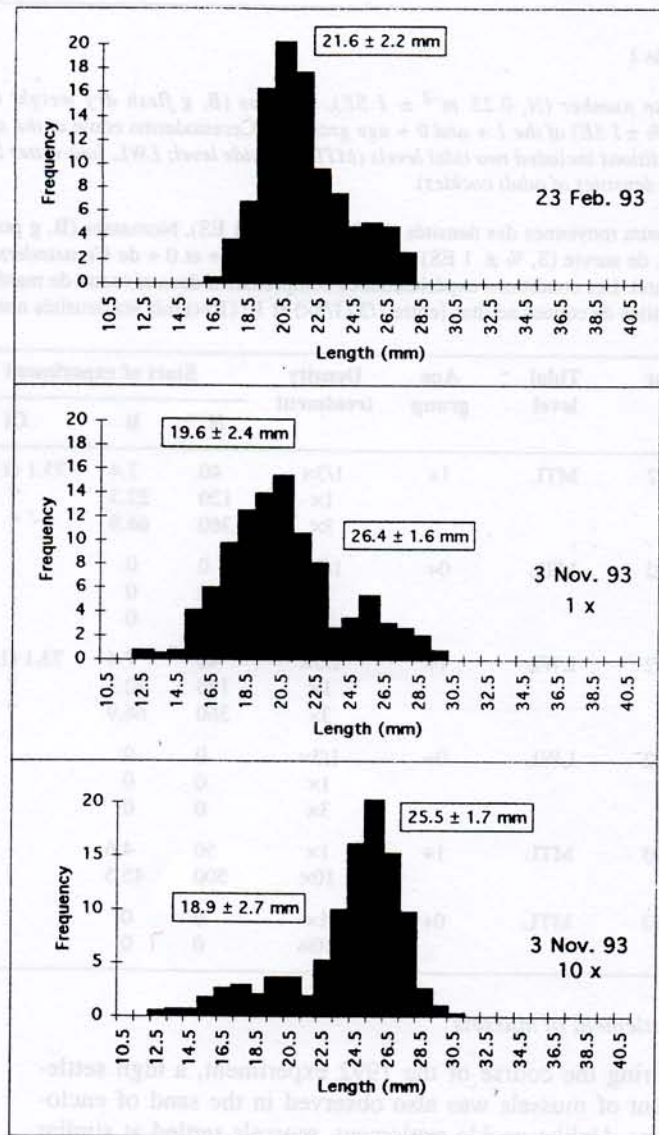


Figure 3

Size (shell length) frequency distributions of *Cerastoderma edule* in enclosures at the start (23 February; top histogram) and at the end (3 November; bottom histograms) of the 1993 experiment conducted at mid-tide level. Density treatments and mean shell-lengths (\pm SD) of each year class are given for each size distribution.

Distribution des fréquences de taille (longueur de la coquille) de *Cerastoderma edule* dans les enclos au début (23 février; histogramme du haut) et à la fin (3 novembre; histogrammes du bas) de l'expérience de 1993 conduite au niveau de mi-marée. Les traitements densitaires et les tailles moyennes (\pm DS) de chaque classe d'âge sont indiqués dans chaque cas.

than at LWL (about 3800 m⁻²). Density treatment had no significant effect on settlement at MTL (except on 16 April, this effect having little meaning because of the very low density of juveniles on this date). At the end of the 1992 experiment, the final abundance of the 0 + year class was not affected by the density treatments but, paradoxically, was significantly lower at MTL than at LWL (Tab. 1, 2).

In the 1993 experiment conducted solely at MTL, settlement was lower in the 10 \times - than in the 1 \times -treatment on each occasion, although this difference was statistically significant on a single occasion (Fig. 5). The final recruitment was also the lowest in the 10 \times -treatment (Tab. 1).

Table 1

Mean number (*N*, 0.25 m⁻² ± 1 SE), biomass (*B*, g flesh dry weight 0.25 m⁻² ± 1 SE), condition index (*CI* ± 1 SD), and survival rate (*S*, % ± 1 SE) of the 1+ and 0+ age groups of *Cerastoderma edule* at the start and at the end of field experiments in 1992 and 1993. Experimental conditions included two tidal levels (MTL, mid-tide level; LWL, low-water level) and varying density treatments (between 1/3 and 10 times the normal densities of adult cockles).

Valeurs moyennes des densités (*N*, 0,25 m⁻² ± 1 ES), biomasses (*B*, g poids sec de chair, 0,25 m⁻² ± 1 ES), indice de condition (*CI* ± 1 DS) et taux de survie (*S*, % ± 1 ES) des groupes d'âge 1+ et 0+ de *Cerastoderma edule* au début et à la fin des expériences de 1992 et 1993 en milieu naturel. Les conditions expérimentales comprenaient deux niveaux de marée (MTL, niveau de mi-marée; LWL, niveau de basse mer) et différentes densités de coques adultes [entre 1/3 (1/3×) et 10 (10×) fois les densités normales].

Year	Tidal level	Age group	Density treatment	Start of experiment			End of experiment			
				N	B	CI	N	B	CI	S
1992	MTL	1+	1/3×	40	7.4	73.1 (11.1)	31 (10)	4.5 (1.5)	62.0 (15.4)	77.7 (25.7)
			1×	120	22.3	"	66 (25)	10.5 (3.9)	61.9 (16.2)	55.7 (20.4)
			3×	360	66.9	"	118 (41)	18.5 (6.5)	61.5 (14.3)	33.7 (11.4)
1992	MTL	0+	1/3×	0	0		47 (10)	1.0 (0.2)	44.1 (15.1)	-
			1×	0	0		35 (4)	0.5 (0.1)	43.3 (18.2)	-
			3×	0	0		23 (3)	0.3 (0.0)	43.6 (22.0)	-
1992	LWL	1+	1/3×	40	7.4	73.1 (11.1)	27 (12)	4.4 (1.9)	73.5 (18.3)	66.0 (28.5)
			1×	120	22.3	"	64 (7)	12.5 (1.4)	72.1 (17.4)	52.7 (6.8)
			3×	360	66.9	"	93 (45)	19.2 (9.4)	71.7 (19.7)	26.0 (12.5)
1992	LWL	0+	1/3×	0	0		67 (37)	3.3 (1.8)	62.2 (15.9)	-
			1×	0	0		84 (10)	3.4 (0.4)	62.3 (14.6)	-
			3×	0	0		65 (3)	2.4 (0.4)	59.0 (16.8)	-
1993	MTL	1+	1×	50	4.6	-	27 (10)	5.6 (2.2)	-	54.5 (20.5)
			10×	500	45.5	-	158 (18)	29.0 (3.3)	-	31.5 (3.6)
1993	MTL	0+	1×	0	0		136 (35)	9.2 (2.3)	-	-
			10×	0	0		29 (5)	1.7 (0.3)	-	-

Settlement of mussels

During the course of the 1992 experiment, a high settlement of mussels was also observed in the sand of enclosures. Unlike cockle settlement, mussels settled at similar densities and synchronously at both tidal levels (Fig. 6). Two-way nested ANOVAs did not detect any significant effect of cockle densities on mussel settlement.

Effects of enclosures on sediment

Density treatments had no effect on silt-clay and organic matter content of sediment within enclosures (Tab. 2). Tidal level significantly affected these sediment parameters (Tab. 2): within enclosures, both silt-clay content and organic content were slightly higher at LWL than at MTL (1.8-4.8 % vs. 1.2-4.3 % for silt-clay and 0.5-1.5 % vs. 0.4-

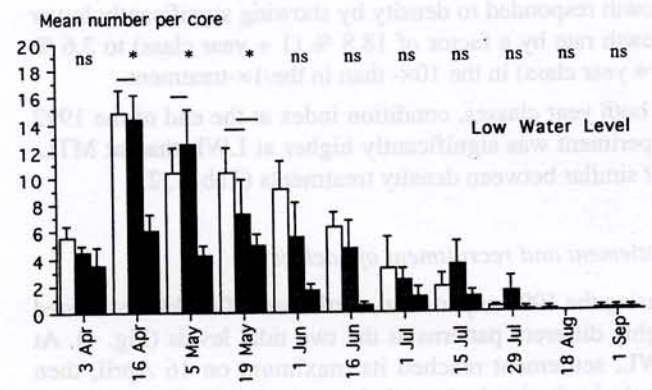
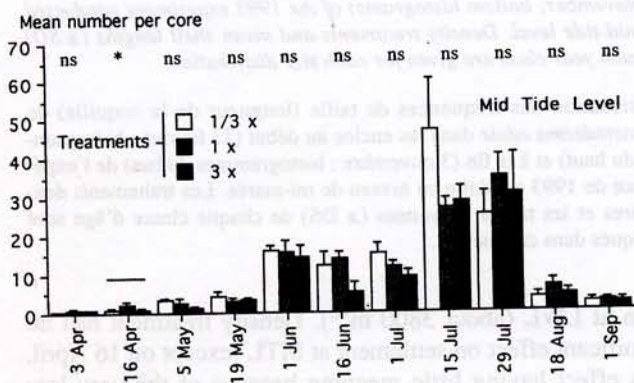


Figure 4

Effects of varying densities of adult *Cerastoderma edule* on mean abundance (± 1 SE) of conspecific juveniles per 37-cm² core during the 1992 experiment conducted at mid-tide level (top) and low-water level (bottom). 1/3×, 1×, and 3× represent treatments with 1/3, 1, and 3 times the ambient initial density of adults, respectively. Significance levels are given for effects of treatment using a two-way nested ANOVA (ns = not significant; * = *p* < 0.05). Lines above bars connect means which are not significantly different (*p* > 0.05) in SNK-tests.

Effets de différentes densités de *Cerastoderma edule* sur l'abondance moyenne (± 1 ES) de coques juvéniles par carotte de 37 cm² au cours de l'expérience de 1992 menée au niveau de mi-marée (en haut) et au niveau de basse mer (en bas). 1/3×, 1× et 3× représentent les traitements contenant, respectivement, 1/3, 1 et 3 fois la densité normale initiale d'adultes. La significativité de chaque traitement a été déterminée par une ANOVA à deux facteurs imbriqués (ns = non significatif ; * = *p* < 0,05). Les lignes horizontales au-dessus des barres relient des moyennes qui ne sont pas significativement différentes (tests SNK ; *p* > 0,05).

Table 2

Results of two-way crossed ANOVAs comparing the effect of tidal level and adult cockle density on sedimentary and biological variables measured at the end of the 1992 field experiment. *df* = degrees of freedom; ns = not significant; * = $p < 0.05$; *** = $p < 0.001$.

Résultats des ANOVAs à deux facteurs orthogonaux comparant l'effet du niveau de marée et de la densité de coques adultes sur les variables sédimentaires et biologiques mesurées à la fin de l'expérience en milieu naturel en 1992. *df* = degrés de liberté; ns = non significatif; * = $p < 0,05$; *** = $p < 0,001$.

Variables	Sources of variation	df	F
Sediment organic matter content	Tidal level (a)	1	11.15*
	Adult density (b)	2	2.89 ns
	Interaction (axb)	2	2.07 ns
	Error	12	
Sediment silt and clay content	Tidal level (a)	1	10.02*
	Adult density (b)	2	0.31 ns
	Interaction (axb)	2	1.20 ns
	Error	12	
Condition index of the 0+ year class	Tidal level (a)	1	68.61***
	Adult density (b)	2	0.29 ns
	Interaction (axb)	2	0.27 ns
	Error	12	
Condition index of the 1+ year class	Tidal level (a)	1	22.75***
	Adult density (b)	2	0.03 ns
	Interaction (axb)	2	0.01 ns
	Error	12	
Survival rate of the 1+ year class	Tidal level (a)	1	0.22 ns
	Adult density (b)	2	2.40 ns
	Interaction (axb)	2	0.02 ns
	Error	12	
Density of the 0+ year class	Tidal level (a)	1	6.96*
	Adult density (b)	2	0.68 ns
	Interaction (axb)	2	1.53 ns
	Error	12	

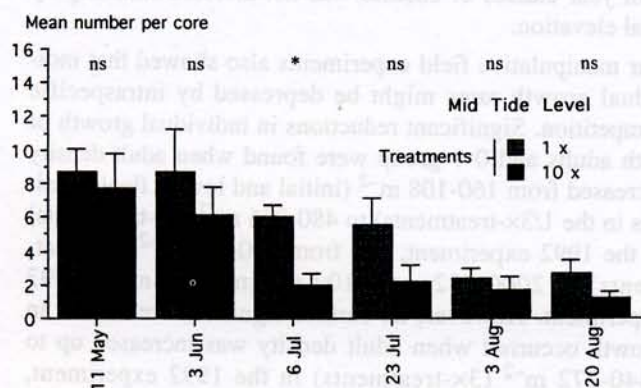


Figure 5

Effects of varying densities of adult *Cerastoderma edule* on mean abundance (± 1 SE) of conspecific juveniles per 37-cm² core during the 1993 experiment conducted at mid-tide level. 1x and 10x represent treatments with 1 and 10 times the ambient initial density of adults, respectively. Significance codes as in Figure 4.

Effets de différentes densités de *Cerastoderma edule* sur l'abondance moyenne (± 1 ES) de coques juvéniles par carotte de 37 cm² au cours de l'expérience de 1993 menée au niveau de mi-marée. 1x et 10x représentent les traitements contenant, respectivement, 1 et 10 fois la densité normale initiale d'adultes. Voir Figure 4 pour les codes de significativité.

Table 3

Results of Student's *t*-tests comparing mean shell lengths of the 0+ and 1+ year classes of *Cerastoderma edule* according to tidal level (MTL, mid-tide level; LWL, low-water level) and density treatments (1/3x, 1x, 3x, 10x) at the end of the 1992 and 1993 field experiments. For each comparison the tidal level or the density treatment which are underlined are those where the largest size has been recorded. *df* = degrees of freedom.

Résultats des tests *t* de Student comparant les longueurs moyennes des classes d'âge 0+ et 1+ de *Cerastoderma edule* selon le niveau de marée (MTL, niveau de mi-marée; LWL, niveau de basse mer) ou le traitement densitaire (1/3x, 1x, 3x, 10x), à la fin des expériences en milieu naturel en 1992 et 1993. Pour chaque comparaison, le niveau de marée ou le traitement densitaire soulignés correspondent à ceux où a été notée la plus grande taille. *df* = degrés de liberté.

Comparisons	<i>t</i> -test
Between tidal levels	
0+, 1/3x, 1992	MTL vs. <u>LWL</u> $t = 8.65$, <i>df</i> = 328, $p < 0.01$
0+, 1x, 1992	MTL vs. <u>LWL</u> $t = 10.71$, <i>df</i> = 353, $p < 0.01$
0+, 3x, 1992	MTL vs. <u>LWL</u> $t = 9.30$, <i>df</i> = 253, $p < 0.01$
1+, 1/3x, 1992	MTL vs. <u>LWL</u> $t = 2.03$, <i>df</i> = 52, $p < 0.05$
1+, 1x, 1992	MTL vs. <u>LWL</u> $t = 2.03$, <i>df</i> = 397, $p < 0.05$
1+, 3x, 1992	MTL vs. <u>LWL</u> $t = 5.57$, <i>df</i> = 638, $p < 0.01$
Between density treatments	
0+, MTL, 1992	<u>1/3x</u> vs. 1x $t = 4.23$, <i>df</i> = 240, $p < 0.01$
0+, LWL, 1992	<u>1/3x</u> vs. 1x $t = 2.95$, <i>df</i> = 441, $p < 0.01$
0+, MTL, 1992	1x vs. 3x $t = 0.26$, <i>df</i> = 159, $p > 0.05$
0+, LWL, 1992	1x vs. <u>3x</u> $t = 0.49$, <i>df</i> = 445, $p > 0.05$
0+, MTL, 1993	1x vs. 10x $t = 2.93$, <i>df</i> = 527, $p < 0.01$
1+, MTL, 1992	<u>1/3x</u> vs. 1x $t = 2.88$, <i>df</i> = 218, $p < 0.01$
1+, LWL, 1992	<u>1/3x</u> vs. 1x $t = 8.64$, <i>df</i> = 231, $p < 0.001$
1+, MTL, 1992	1x vs. 3x $t = 0.78$, <i>df</i> = 566, $p > 0.05$
1+, LWL, 1992	1x vs. <u>3x</u> $t = 1.63$, <i>df</i> = 469, $p > 0.05$
1+, MTL, 1993	<u>1x</u> vs. 10x $t = 4.39$, <i>df</i> = 517, $p < 0.001$

0.8 % for organics, respectively). This pattern of increasing organic content at LWL was also found outside the enclosures (comparison between enclosures and controls taken outside the enclosures by a one-way ANOVA; $p > 0.05$) and thus could not be ascribed to enclosing.

Flume experiments

Experiment A showed that living juvenile cockles were able to resuspend and migrate in a relatively slow water current. During the four-hour experiment, living juveniles up to 4 mm in shell length were often observed drifting at several centimetres above the bottom, with the valves gaping and their ventral margins upwards. After migrating over several metres, juveniles suddenly fell on the bottom, sometimes remaining there, sometimes leaving the substratum again. At the end of this experiment, 57.2 % of live juveniles were retrieved in the sediment area, with 26.4 % in the first row and about 10 % in each of the other three rows (Fig. 7 a). Missing live juveniles were distributed on the other parts of the flume bottom. The behaviour of dead juveniles was totally different: they moved slowly, rolling on the bottom, and never resuspended. Almost all dead juveniles stayed on the PVC bottom upstream the sediment area; only 14.8 % reached this area, most in the first row (Fig. 7 a).

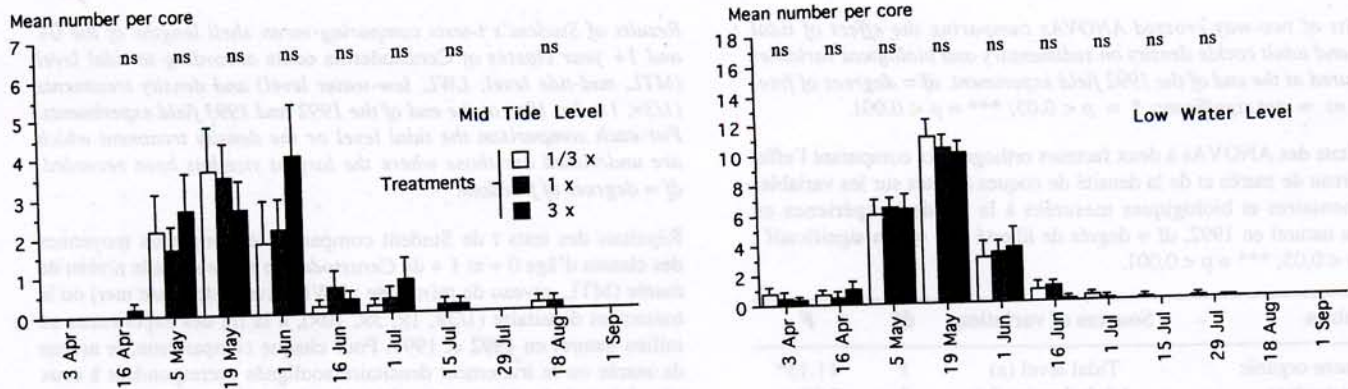


Figure 6

Effects of varying densities of adult *Cerastoderma edule* on mean abundance (± 1 SE) of juvenile mussels per 37-cm² core during the 1992 experiment conducted at mid-tide level (top) and low-water level (bottom). Significance codes as in Figure 4.

Effets de différentes densités de *Cerastoderma edule* sur l'abondance moyenne (± 1 ES) de moules juvéniles par carotte de 37 cm² au cours de l'expérience de 1992 menée au niveau de mi-marée (en haut) et au niveau de basse mer (en bas). Voir figure 4 pour les codes de significativité.

During Experiment B, juveniles were also observed to migrate into the water column; when adults inhaled juveniles, their siphons contracted in most cases, thus preventing predation upon juveniles. At the end of the experiment, 56.0 % of the juveniles were retrieved in the sand area, with 21.6 % in the first row containing adult cockles (Fig. 7 b).

In Experiment C, with plastic sticks in the first row, 58.4 % of juveniles were retrieved in the experimental area (36.4 % in the first row; Fig. 7 c).

A randomized block ANOVA comparing the percentages of live juveniles in each row of Experiments A, B, and C showed that treatments did not affect the distribution of juveniles ($F_{2,8} = 2.14$; $p > 0.05$).

In Experiment D, juvenile abundances differed according to treatments (ANOVA; $p < 0.05$); significantly lower numbers of juveniles were found in the treatment with 30 adult cockles than in the other treatments (Tukey's test, $p < 0.05$; Fig. 8).

DISCUSSION

Growth and survival of cockles

Our field experiments demonstrated that individual growth rate and condition in all age groups of cockles, *Cerastoderma edule*, declined with increasing tidal elevation. Previous observations and experiments in the intertidal zone have shown a similar trend in this species (Thamdrup, 1935; Kreger, 1940; Cole, 1956; Kristensen, 1957; Richardson *et al.*, 1980; Reise, 1985; Sanchez-Salazar *et al.*, 1987; Jensen, 1992 and 1993; Kamermans, 1993) as well as in other infaunal filter-feeding bivalves (Goulletquer *et al.*, 1987; Peterson and Black, 1987 and 1988; Dobbinson *et al.*, 1989; Wanink and Zwarts, 1993). To explain the higher growth rate of intertidal suspension feeders towards the low tidal levels, a trophic interpretation has been widely accepted by most authors (*e.g.* Peterson and Black, 1987; Dobbinson *et al.*, 1989): duration of submersion determines the time available for feeding and hence

the supply of phytoplanktonic food; additionally, high-shore organisms might receive water masses already depleted of suspended food by low-shore dense assemblages of suspension feeders (Peterson and Black, 1991). However, Peterson and Black (1988) found that tidal elevation alone was insufficient to explain completely growth responses in the populations of suspension-feeding bivalves they studied: for example, they calculated that the magnitude of the percentage reduction in growth with increased elevation was 2-3 times the percentage reduction in average daily submergence. In the present study, during the 1992 experiment, the percent decline in average growth from LWL to MTL (*i.e.* for a 25 % reduction in the average daily duration of water coverage) was 12-17 % (depending on the density-treatment) for the 0 + year class and 32-55 % for the 1 + year class. This suggests that growth of both year classes of cockles was not affected similarly by tidal elevation.

Our manipulative field experiments also showed that individual growth rates might be depressed by intraspecific competition. Significant reductions in individual growth of both adults and 0 + group were found when adult density increased from 160-108 m⁻² (initial and lowest final densities in the 1/3 \times -treatments) to 480-256 m⁻² (1 \times -treatments) in the 1992 experiment, and from 200-108 m⁻² (1 \times -treatments) to 2000-632 m⁻² (10 \times -treatments) in the 1993 experiment. However, no further significant reduction in growth occurred when adult density was increased up to 1440-372 m⁻² (3 \times -treatments) in the 1992 experiment, suggesting that a certain threshold may have been already reached. Because densities alone are not sufficient to characterize bivalve populations with large individual size, the percentage of available surface area covered by cockles in each density treatment has been calculated according to equations given by Jensen (1985). These calculations show that significant reductions in growth occurred when the 'area fraction' covered by cockles increased from ≈ 6 % (average value between initial and final area fractions calculated at both tidal levels in the 1/3 \times -treatments) to ≈ 13 % (1 \times -treatments) in the 1992 experiment, and from ≈ 9 % (1 \times -treatments) to ≈ 33 % (10 \times -treatments) in the 1993 experiment. This suggests that, in our experimental

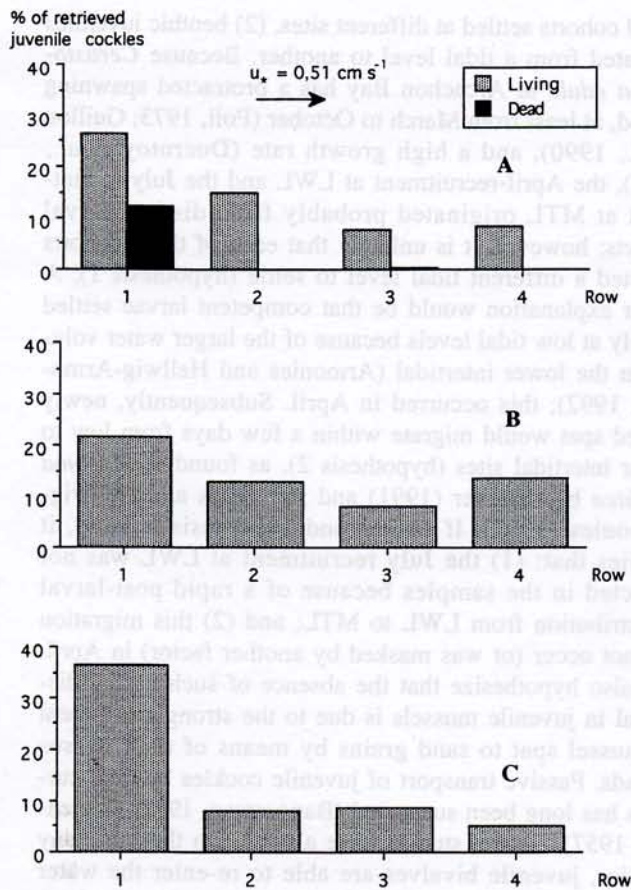


Figure 7

Percentage of juvenile cockles retrieved in each 25x50-cm row of the experimental area of the flume at the end of experiments A (top), B (middle), and C (bottom). Row 1 was upstream, row 4 was downstream.

Pourcentage de coques juvéniles retrouvées dans chaque rangée de 25x50 cm de la zone expérimentale du canal à la fin des expériences A (en haut), B (au milieu) et C (en bas). La rangée 1 était en amont, la rangée 4 en aval.

conditions, an area fraction covered by cockles of approximately 10 % was a threshold above which growth rates were significantly reduced. In another population of *Cerastoderma edule*, reduced growth has been observed for area fractions as high as 29-39 % (Jensen, 1992); similarly, Kamermans *et al.* (1992) found that even densities of 2000 cockles m^{-2} had no effect on growth of laboratory-reared bivalves. The probable cause of reduced growth in a population covering an area as small as ca. 10 % is competition for food (Peterson and Black, 1987; Peterson, 1992). Consequently, the magnitude of competitive effects will depend on the local amount of available food. In addition, the burrowing and ploughing habit of cockles may increase the contacts between individuals, thereby disturbing filtration activity and reducing growth (Peterson and Andre, 1980; Jensen, 1992). At high abundances, Richardson *et al.* (1993) observed an increased frequency of collisions between cockles which induced emergence of bivalves.

Despite significant effects of shortened submersion time and increasing density on growth and condition of cockles, survival rate of the 1 + year class was not depressed significantly by either factor. This result is in agreement with

Peterson (1992)'s conclusion that competition for food in infaunal suspension-feeding bivalves results in a reduction of growth rates but not in competitive exclusion.

Settlement and recruitment of cockles

According to Woodin (1976)'s hypotheses on adult-larval interactions in dense infaunal assemblages, larval settlement should be lower at increasing densities of suspension feeders. While most field data have confirmed that recruitment of suspension-feeding bivalves is generally negatively correlated with adult densities, field experiments have generated conflicting results (*see* Introduction). In a previous study on adult-juvenile interactions in cockle populations in Arcachon Bay (Bachelet *et al.*, 1992 *a* and *b*), recruitment was depressed at high adult density in one of two stations, and only at the time of maximum settlement. Results have also been variable in the present study, both between tidal levels and between years. During the 1992 experiment, the numbers of juveniles were never affected by adult density at MTL, while they were significantly reduced by high densities of adults at LWL; moreover, competitive effect at the latter tidal level was observed only during the peak of settlement. During the second experiment, juvenile numbers at MTL were constantly lower (although the difference was significant in only one of six samples) at high adult densities. Therefore, in our experiments, negative effects of adult cockles on their own recruitment occurred at very high densities of adults or during the massive arrival of young stages. Although we used extremely high experimental densities of adult cockles (2000 m^{-2}) in the 10x-treatment in 1993, these figures are not unrealistic for the species and are found in natural populations, such as the Bay of Somme (Bachelet *et al.*, 1992 *a*) or the Wadden Sea (Jensen, 1992).

Of the two conditions necessary to observe settlement patterns in benthic invertebrates – namely a sieve size small enough to sample settlement-sized individuals and a short time interval between settlement and sampling (Luckenbach, 1984) – only the first one was totally fulfilled in our field experiments. The two-week interval separating two consecutive samplings probably did not permit the sampling of juveniles just after settlement. Therefore, it is difficult to ascribe the negative effects of adult cockles on differential settlement of larvae or on differential survival of early juveniles (Keough and Downes, 1982). Larval cannibalism in suspension feeders has been commonly observed in the laboratory (Young and Chia, 1987). However, the extent to which this mechanism can be effective in regulating larval settlement in the field is still a matter of debate (Ertman and Jumars, 1988; Young, 1989, 1990; André *et al.*, 1993). In the present study, comparison of juvenile abundance patterns at LWL in the 1992 experiment shows that both cockles and mussels settled simultaneously and that adult density had a significant effect only on juvenile cockles; unless mussel larvae possess some defence mechanisms against predators, it is unlikely that adult cockles may discriminate between larvae of closely related species and prey solely on their own larvae. After settlement in a dense assemblage of suspension feeders, the most likely causes of benthic juveniles mortality are bio-

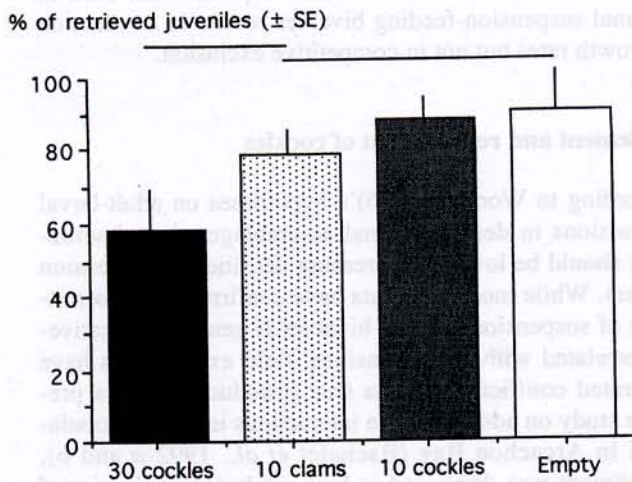


Figure 8

Mean percentage (± 1 SE) of juvenile cockles retrieved in each of the four treatments of experiment D. Significant difference among treatments was detected by a randomized-block ANOVA ($p < 0.05$). Lines above bars connect means which are not significantly different ($p > 0.05$) in Tukey's test.

Pourcentage moyen (± 1 ES) de coques juvéniles retrouvées dans chacun des quatre traitements de l'expérience D. Une différence significative entre traitements a été détectée par une ANOVA mixte en bloc aléatoire complet ($p < 0,05$). Les lignes horizontales au-dessus des barres relient des moyennes qui ne sont pas significativement différentes (test de Tukey ; $p > 0,05$).

turbation and ingestion by adults. Kristensen (1957) observed small resuspended cockles (0.6–0.9 mm length) being inhaled by adult cockles, then released through the inhalant siphon and dying within a few hours. However, according to Kristensen (1957) this phenomenon occurred rarely; in most cases the adults closed their shell at the first touch of the inhalant siphon by juveniles 0.5–3 mm in shell length, thereby preventing the juveniles from being preyed upon. A similar behaviour of adults was observed in our flume experiments; therefore, if juvenile ingestion by adult cockles does occur, its effect should be insignificant at the population scale. Bioturbation by adult cockles through burrowing or suffocation by pseudofaeces may be the most important mechanism regulating recruit abundances. Surface sediment in the high density treatments was often strongly disturbed by the migration activities of cockles. Jensen (1985) showed that bioturbation by cockles may significantly affect the survival rate of the amphipod *Corophium volutator*.

One of the most striking results of our field experiments is the seasonal pattern of cockle settlement at the two tidal levels: a first moderate settlement peak occurred in April at LWL, then a peak of much higher amplitude was recorded in July at MTL. The highest numbers of cockle recruits are usually found in the lower part of the intertidal zone (Kreger, 1940; Reise, 1987; Bachelet *et al.*, 1992 a; Jensen, 1992). However, the abundance pattern of recruits may be reversed some months later (Kreger, 1940); this also occurred in our experiments where recruits were finally more abundant at LWL. The occurrence of non-simultaneous peaks in juvenile numbers at two different tidal levels might be explained by two hypotheses: (1) distinct

larval cohorts settled at different sites, (2) benthic juveniles migrated from a tidal level to another. Because *Cerastoderma edule* in Arcachon Bay has a protracted spawning period, at least from March to October (Poli, 1973; Guillou *et al.*, 1990), and a high growth rate (Ducrottoy *et al.*, 1991), the April-recruitment at LWL and the July-recruitment at MTL originated probably from distinct larval cohorts; however, it is unlikely that each of these cohorts selected a different tidal level to settle (hypothesis 1). A better explanation would be that competent larvae settled mainly at low tidal levels because of the larger water volume in the lower intertidal (Armonies and Hellwig-Armonies, 1992); this occurred in April. Subsequently, newly settled spat would migrate within a few days from low to upper intertidal sites (hypothesis 2), as found in *Macoma balthica* by Günther (1991) and Armonies and Hellwig-Armonies (1992). If our second hypothesis is valid, it implies that: (1) the July recruitment at LWL was not detected in the samples because of a rapid post-larval redistribution from LWL to MTL; and (2) this migration did not occur (or was masked by another factor) in April. We also hypothesize that the absence of such a tidal dispersal in juvenile mussels is due to the strong attachment of mussel spat to sand grains by means of their byssus threads. Passive transport of juvenile cockles by tidal currents has long been suspected (Baggerman, 1953; Kristensen, 1957). Recent studies have also shown that, in many species, juvenile bivalves are able to re-enter the water column, to be transported by currents and to achieve secondary settlement by byssus-drifting [Sigurdsson *et al.*, 1976; review by Armonies (1994 b)].

Flume experiments have demonstrated that juvenile cockles were able to resuspend and migrate in the water column in conditions of relatively slow, smooth-turbulent flow. The size range of these juveniles (0.5–4 mm in shell length) was identical to that found by Armonies (1994 b) in byssus-drifting cockles. In at least one instance we were able to follow a juvenile drifting over a complete flume lap, *i.e.* 13 m. Similarly, Günther (1992) observed post-larvae of *Macoma balthica* migrating 16 m per tide. This phenomenon should be increased in the field, especially in the intertidal zone, where tidal currents are sometimes fast and often generate strong turbulences. Therefore, juvenile bivalves are able to drift over considerable distances. Although we did not observe the mucous byssus threads found in *Cerastoderma edule* by Yankson (1986), the different behaviour observed in our flume experiments between live and dead juveniles suggests that byssus drifting plays an important role in the tidal migrations of young cockles. According to Armonies (1994 a and b), juvenile cockles reside for only a few days at the same site, and this may result in a totally reverse pattern of abundance between intertidal levels within three months.

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Palaeontology, cladistics and the evolutionary importance of larval versus adult traits

The fossil record shows that the evolution of the marine biota has been affected by a series of major extinction events (climate and oceanographic changes, bolide impacts, etc.). However, debate continues as to whether extinctions initiated by these events were primarily selective or non-selective. Problems of sampling and preservation prevent palaeontological data from having any role to play in determining species-level patterns, but there are two ways of exploring the relative influence of biotic and abiotic factors on larval and adult traits in the evolution of higher taxa. The first approach is to compare clade survivorship data across geologically important taxonomic levels and apply a statistical approach to discover whether specific biological traits (e.g. leontophyly versus planktonophyly) correlate significantly with survivorship. Such work has been pioneered in molluscs and has begun to be applied to echinoids. The second approach is to construct phylogenies of extant data based on molecular (molecular and morphological) data which are then transformed into trees by calibrating against the fossil record. This permits analysis of the relative levels of homoplasy associated with larval versus adult traits and recognition of periods in the geological past when rates of change have altered markedly.

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