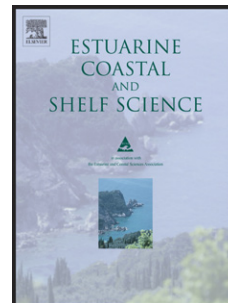


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Seasonal succession of estuarine fish, shrimps, macrozoobenthos and plankton: Physico-chemical and trophic influence. The Gironde estuary as a case study

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1 **Seasonal succession of estuarine fish, shrimps, macrozoobenthos and**
2 **plankton: physico-chemical and trophic influence. The Gironde estuary as a**
3 **case study**

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11 **Abstract**

12 Characterization of the structure and seasonal variability of biotic communities is
13 essential for a better understanding of estuarine ecosystem functioning and in order to manage
14 these highly fluctuating and naturally stressed systems. Numerous studies have investigated the
15 role of environmental factors in controlling temporal variations in biotic communities.
16 However, most have concluded that the explanatory power of physico-chemical variables was
17 significant but not sufficient to explain ecological dynamics. The present study aimed to
18 propose the importance of trophic interactions as an additional structuring factor of species
19 seasonal variability by examining simultaneous dynamics of all estuarine biotic communities,
20 using the oligo-mesohaline area of the Gironde estuary (SW France) as a case study. Data on
21 the main biological groups (fish, shrimps, macrozoobenthos and plankton) sampled during a
22 five-year period (2004-2008) at monthly intervals using a well standardized protocol, as well
23 as data on environmental variables, were compiled here for the first time. According to species
24 composition, the Gironde estuary is used as a nursery, feeding, resident and migratory habitat.
25 For almost all species, strong seasonal fluctuations occurred with a succession of species,
26 indicating an optimization of the use of the available resources over a typical year by estuarine
27 biological communities. Multivariate analyses discriminated four seasonal groups of species
28 with two distinctive ecological seasons. A clear shift in July indicated a biomass transfer from
29 a “planktonic phase” to a “benthic-demersal phase”, corresponding to spring and summer-
30 autumn periods, respectively. With regard to the temporal fluctuations of dominant species of
31 all biological groups, this study highlighted the possible influence of trophic relationships,
32 predation in particular, on seasonal variations in species abundance, in addition to the physico-
33 chemical influence. This study enabled us to collate important seasonal data and to discuss

34 their integration into seasonal models of estuarine functioning and/or specific prey-predator
35 models. In a global change context, prey abundance variations could generate changes in the
36 temporal dynamics of their predators (and conversely), and potentially in the functioning of the
37 whole estuarine system.

38

39 Keywords: fish, shrimps, macrozoobenthos, zooplankton, seasonal dynamics, environmental
40 variables, trophic interactions, Gironde estuary.

41

42 **1. Introduction**

43 Estuarine and coastal areas are widely considered to be among the most productive and
44 valuable aquatic areas in the world (Day et al., 1981; Costanza et al., 1997). They are
45 associated with important ecological functions such as primary and secondary production and
46 nutrient cycling and provide permanent or transitory habitats for reproduction, migration,
47 feeding and nursery for many animal species (Beck et al., 2001; Elliott and Hemingway, 2002;
48 Gili, 2002). Due to these ecological properties, estuaries and coasts are also associated with
49 highly valuable goods and services for human society (Costanza et al., 1997) and are
50 consequently subjected to high human pressures such as fishing, harbour activities, dredging or
51 industrial pumping (Post and Lundin, 1996). Estuaries are transition zones between seas and
52 freshwater and are therefore also characterized by large fluctuations in the physico-chemical
53 conditions of the environment. As a consequence, species that inhabit such ecosystems must be
54 able to tolerate a wide range of environmental conditions. It is now fully recognized that
55 human activities have an increasing effect on the quality of fresh and marine waters
56 (Vanderborcht et al., 2007). In this context, the need to protect these essential habitats is
57 becoming clear to authorities who have implemented directives during these last decades, such
58 as the European Water Framework Directive (WFD; EU, 2000) or the European Marine
59 Strategy (EU, 2008). Implementating these directives implies, first and foremost, a better
60 understanding of the functional aspects of ecosystem dynamics (de Jonge et al., 2006).
61 Knowledge of the simultaneous structure and variability of the dominant biological
62 compartments is essential for comprehending ecosystem functioning but such information is
63 very scarce for European aquatic ecosystems, and for French estuaries in particular.

64

65 In fluctuating habitats such as temperate estuaries, biotic communities are characterized
66 by a strong seasonal, and spatial, heterogeneity and variability (McLusky and Elliott, 2004).
67 Such temporal variations have been attributed to fluctuations in physico-chemical variables

68 (both short- and long-term physico-chemical water conditions: e.g. wind speed and direction,
69 turbidity, wave height, salinity, state of the tide, time of day and temperature) (Baird et al.,
70 1991; Thiel et al., 1995; Beyst et al., 2001; McLusky and Elliott, 2004; Selleslagh and Amara,
71 2007, 2008a), combined with biological variables, including the timing of spawning seasons
72 and hence the influx and efflux of individuals to and from populations (Gibson et al., 1993),
73 food availability (Pasquaud et al., 2008), and predation pressure (Van der Veer and Bergman,
74 1987). However, there is still much confusion over which factor influences or controls biotic
75 temporal variations (Beyst et al., 2001) since numerous studies dealing with this topic were
76 based on only a limited part of the year, range of the system and specific species or
77 assemblages. Papers dealing with the seasonal variability of fauna almost exclusively
78 integrated physico-chemical factors, leading to poorly explained relationships ($\pm 20\%$, see
79 Selleslagh and Amara, 2008b for example) and suggested other predictors, such as predation or
80 competition (e.g. Marshall and Elliott, 1998). Understanding species variability requires a
81 study at a large temporal scale and, above all, knowledge of the dynamics of other species
82 because of interannual variations (Henderson and Bird, 2010) and biological interactions
83 (Monaco and Ulanowicz, 1997). With increased attention to the collection of multi-year data
84 sets, ecologists have better opportunities to test functional hypotheses driving temporal
85 dynamics. Studying interactions between the biological compartments of an ecosystem
86 provides a good picture of the biological community structure and is an essential step to
87 understanding how an aquatic system functions (Thrush et al., 1999; Pasquaud et al., 2010),
88 which is in turn essential for integrated estuarine management. It also provides a better
89 understanding of the dynamics of ecological networks (David et al., 2006).

90 The Gironde estuary, in south-west France, is the largest French estuary. It is known to
91 support a large number of fish, macrocrustacean (Lobry et al., 2006) and benthic (Bachelet,
92 1985) species. It is an important nursery area, a residence habitat for permanent species, as
93 well as a migration route for amphihaline species (e.g. Rochard et al., 2001) and is also of
94 important economic interest (G. Castelnaud, personal communication). As a consequence of
95 many studies, the Gironde estuary is one of the most surveyed estuarine systems in France.
96 Previous studies emphasized possible trophic implications of seasonal successions in biological
97 assemblages (e.g. David et al., 2005, 2006; Lobry et al., 2006; Pasquaud et al., 2010). Lobry et
98 al. (2008) first proposed an integrated picture of the whole Gironde estuarine food web using
99 an Ecopath modelling approach at the annual level. David et al. (2006) identified predator-prey
100 processes in the zooplankton food web and Pasquaud et al. (2010) described fish food webs at
101 various periods of the year. However, to date no studies have combined the seasonal dynamics

102 of all ecological compartments, particularly since macrozoobenthos sampling is recent. The
103 aims of this study were: (1) to describe the simultaneous seasonal dynamics of fish,
104 macrozoobenthos, shrimps and phyto- and zooplankton, considering dominant species; (2) to
105 relate their fluctuations to environmental variables, and (3) to discuss trophic interactions
106 structuring the seasonal dynamics of species. This work is the first analysis providing a
107 comprehensive overview of the recent seasonal succession of biological assemblages (fish,
108 macrozoobenthos, shrimps and plankton) in the Gironde estuary in the course of a year. The
109 temporal changes in the main biological components of the oligo-mesohaline area of the
110 Gironde were analyzed to test the hypothesis that trophic interactions have the important and
111 additional influence of physico-chemistry on the seasonal variability of estuarine communities.

112 **2. Materials and methods**

113 *2.1. Study area*

114 The Gironde estuary (45°20'N, 0°45'W; Fig. 1) is located in SW France and opens
115 onto the Atlantic Ocean. This is the largest estuary in France (Lobry et al., 2003), covering an
116 area of 625 km² at high tide. It is 12 km wide at the mouth and 76 km long to the upstream
117 salinity limit, where the Garonne and Dordogne rivers meet. The catchment covers 81,000
118 km² and the mean annual rate of freshwater flow is ca. 1,000 m³ s⁻¹ (Sottolichio and Castaing,
119 1999). The Gironde is a macrotidal estuary with a tidal range of 4.5 m at the mouth and over 5
120 m at Bordeaux. The hydrodynamic conditions are highly variable due to the interaction of
121 marine and fluvial flows, leading to strong temperature and salinity gradients. The Gironde is
122 one of the most turbid estuaries in Europe (SPM > 500 mg l⁻¹, Sautour and Castel, 1995).
123 Particulate matter is tidally resuspended and concentrations may exceed 1 g l⁻¹ at the upstream
124 limit of salinity intrusion (Allen et al., 1974). This zone of maximum turbidity, which is due
125 to an asymmetric tidal wave, migrates seasonally according to river flow and tidal cycles
126 (Sottolichio and Castaing, 1999). As a consequence of the high turbidity, primary production
127 is limited mainly to the upstream zone. However, there is a large zooplanktonic biomass
128 (Castel, 1993) and the food web seems to be based on the detritus pool (Irigoiien and Castel,
129 1995; Lobry et al., 2008). The Gironde estuary is notable amongst other French or European
130 estuaries in having a long-term (30 years) biological database. In this paper, the study area is
131 the zone between Blaye and Mortagne, covering the oligo-mesohaline area (Fig. 1).

132 *2.2. Sampling surveys*

133 As part of various ecological monitoring programmes (e.g. impact of a nuclear power
134 plant, monitoring of European sturgeon *Acipenser sturio*, European Water Framework
135 Directive WFD, Service d'Observation en Milieu Littoral SOMLIT), the main biological

136 compartments (fish, macrozoobenthos, shrimps and plankton) of the Gironde have been
137 surveyed and the environmental conditions measured regularly for several decades, except for
138 macrozoobenthos.

139 2.2.1. Fish and shrimp samplings

140 Fish and shrimps were collected using two types of sampling methods that use
141 different gears:

142 A 'Transect' survey was set up by the French Institute for Research in Environmental
143 Science and Technologies (Irstea) in 1979 to monitor small fish species or juvenile stages of
144 larger species and shrimps, around the Blayais nuclear power plant, and this survey is still
145 ongoing. Since 1991, it has been standardized (see for instance Pronier and Rochard, 1998
146 and Lobry et al., 2003). The sampling sites are located within four transects which cross the
147 estuary in the mesohaline and oligohaline sectors (Fig. 1). Each transect consists of three
148 sites, one close to each bank and one on the middle axis of the estuary (Fig. 1).
149 Simultaneously at each site, one fishing sample is taken near the surface and one near the
150 bottom. Surface samples are collected using two 4.0×1.0 m rectangular frame nets, equipped
151 with a flowmeter, fitted on both sides of the boat. The subconical nets have a stretched mesh
152 size of 18 mm in the main section and 2.8 mm in the cod end. For the benthic samples, a
153 dragnet with a 2.0×1.2 m frame is used. Runners keep the frame 0.2 m above the bed. The
154 net meshes are identical to those used for surface sampling. Sampling lasts between five and
155 seven minutes and is performed in daytime at high tide ± 3 h, with the gear being towed
156 against the current. The sampled fauna consists mainly of small pelagic and juveniles fish
157 species, as well as shrimps. The catch was preserved in 5% seawater buffered formalin. At the
158 laboratory, individuals were identified to species level (except for *Pomatoschistus* and
159 *Palaemon* genus) and counted. In order to standardize captures between samples, abundances
160 were expressed as number of individuals and biomass per $1,000 \text{ m}^3$ of filtered water. Total
161 biomass (fresh weight W, g) was measured by species at each station.

162 A second fish survey (so-called 'Sturat' survey) was set up by Irstea in 1994 in the
163 context of monitoring the European sturgeon *Acipenser sturio* in the Gironde estuary
164 (Rochard et al., 2001). Trawl surveys were performed once a month almost every year from
165 1994 to 2000. The sampling sites were located within fourteen zones in the oligohaline and
166 mesohaline sectors of the estuary (Fig. 1). Sampling was carried out during daylight hours on
167 the flood or ebb tide, using a wide-mouth bottom trawl (vertical opening 3.5 m and horizontal
168 opening 13 m and with a mesh size of 70 mm in the cod end). Trawl tows lasted 30 minutes
169 on average. Fish were identified, counted and measured to the nearest millimetre (FL) before

170 being returned to the water. The fish samples consisted mainly of large benthic-demersal
171 species. For each sample, species abundance was expressed as the number of individuals and
172 biomass per 100,000 m². In this study, biomass (fresh weight W, g) was determined for each
173 species using the equation $W = a TL^b$ (www.fishbase.org), where TL is the total length.

174 2.2.2. Macrozoobenthos sampling

175 Macrozoobenthic fauna has been sampled from 2004 at three sites (Lamarque, St-
176 Estèphe and St-Christoly) in the oligohaline and mesohaline sectors (Fig. 1). Samples were
177 collected every year at monthly intervals between April and November, and also in February
178 in the intertidal. Two stations were selected at each site: one at mid-tide level and one at a
179 depth of approximately 8 m (Fig. 1). Macrozoobenthos was sampled with a Smith-McIntyre
180 grab (0.1 m², 5 replicates) at subtidal stations and with a hand corer (0.0066 m², 10 replicates)
181 at intertidal stations. Samples were washed and sieved through a 0.5 mm mesh; the remaining
182 fraction was fixed in 4% buffered formalin and stained with Rose Bengal. In the laboratory,
183 macrozoobenthic fauna was sorted, identified to species level (except oligochaetes) and
184 counted using a binocular microscope. As intertidal and subtidal areas are not equal in the
185 estuarine zone considered (10 and 90%, respectively), abundances were balanced by the
186 relative percentage of intertidal and subtidal areas and expressed as number of individuals per
187 m².

188 2.2.3. Zooplankton sampling

189 As the copepods *Eurytemora affinis*, *Acartia bifilosa*, and *A. tonsa* and the mysids
190 *Neomysis integer* and *Mesopodopsis slabberi* accounted for the majority of zooplanktonic
191 abundance (>90%) in the oligo-mesohaline zone of the Gironde estuary, they were selected as
192 target species (David et al., 2005). Samples were collected during monthly cruises at different
193 locations along the estuary (Fig. 1). During each survey, three stations were regularly sampled
194 ten months per year (January and March to November): station K (off Lamarque), station E
195 (off St-Estèphe) and station F (off St-Christoly) (Fig. 1). Sampling was carried out at 3 h
196 intervals during the tidal cycle and at two levels (1 m below the surface and 1 m above the
197 bottom). From each depth, zooplankton was collected with a standard WP-2 net equipped
198 with a 200 µm mesh. The catch was preserved and fixed in buffered 5% seawater-
199 formaldehyde solution until identification and analyses. Abundances were expressed as
200 numbers of individuals per m³ based on average value of the surface and bottom samples over
201 the tidal cycle of the three stations.

202 2.3. Environmental data

203 Environmental factors (temperature, salinity, suspended particle matter [SPM]
204 concentration and chlorophyll *a* [Chl *a*] concentration) were measured at each tidal state and
205 each depth 10 months a year (January and March-November during the SOMLIT surveys)
206 from 1979. Water temperature and salinity were measured with a Valeport MK 108. SPM
207 concentrations (mg l^{-1}) were analysed gravimetrically according to conventional
208 oceanographic techniques: estuarine water samples were collected using Niskin bottles and
209 50-500 ml were filtered through GF/F Whatman filters. After filtration, filters were
210 immediately dried at 60°C and stored until analysis. SPM concentrations were determined as
211 weight differences before and after filtration. Chlorophyll *a* content ($\mu\text{g l}^{-1}$) was measured by
212 spectrometry and was used as a proxy for phytoplankton biomass. In addition, flow data from
213 the Bordeaux Harbour Authorities were used.

214 2.4. Data selection and analysis

215 The main goal of this study was to provide a comprehensive overview of the present
216 seasonal dynamics of the main biological compartments of the estuarine food web of the
217 Gironde. We thus focused on data collected in the oligo-mesohaline area between 2004 and
218 2008, corresponding to the location and period with the most recent available data for each
219 component. Large fish were the exception and for them we took data from January 1998 to
220 December 2000 since the ‘Sturat’ surveys stopped in 2000. During these periods, sampling
221 protocols were standardized and we assumed that time intervals were sufficiently short for no
222 major changes in biological dynamics to have occurred (David et al., 2005; Henderson and
223 Bird, 2010; Henderson et al., 2011).

224 As we focused on main dynamics, we selected only the most representative species for
225 each compartment. Concerning ‘Transect’ data, we only took into account dominant small
226 fish and shrimp species that occurred in more than 50% of the samples and with an abundance
227 $>2 \text{ ind. } 1,000 \text{ m}^{-3}$. In the same way, only species with an occurrence $>50\%$ and a mean
228 abundance $>1 \text{ ind. } 100,000 \text{ m}^{-2}$ were considered in the ‘Sturat’ data. For macrozoobenthos,
229 only species with an occurrence $>50\%$ and a mean abundance $>5 \text{ ind. m}^{-2}$ were considered.
230 Thus, only 9 macrozoobenthic species (of the 47 species represented in the database)
231 remained and were included in the analyses. Due to their low abundance, crabs were not
232 considered. A preliminary procedure was carried out in order to group sympatric fish and
233 macrozoobenthos species with the same temporal pattern (*Alosa alosa* and *Alosa fallax* called
234 *Alosa* spp; *Bathyporeia pilosa*, *Gammarus salinus* and *G. zaddachi* called *Bathyporeia* +
235 *Gammarus*). Finally, we considered the 5 main zooplankton species (*Eurytemora affinis*,

236 *Acartia bifilosa*, *A. tonsa*, *Neomysis integer*, *Mesopodopsis slabberi*; Castel, 1993) in our
237 analyses.

238 The database analysed was composed of monthly values of environmental factors
239 (temperature, salinity, river flow, SPM) and biological factors (phytoplankton biomass (Chl *a*
240 concentrations), abundance and/or biomass of zooplankton, macrozoobenthos, shrimp and
241 fish species). Canonical correspondence analysis (CCA) was performed in order to assess
242 environmental influences on biological components. Square-root transformation was applied
243 to species abundances and Monte Carlo permutations were used to test the significance of
244 analysis. Ascendant Hierarchical Clustering analysis (AHC) was performed to group species
245 according to their temporal dynamics. The aggregation criterion used was Ward's criterion.
246 Multivariate analyses were performed with R software (R Development Core Team, 2005).

247 **3. Results**

248 *3.1. Environmental conditions*

249 All selected environmental variables showed classical seasonal variations (Fig. 2).
250 Highest water temperature was observed in summer months (from June to September) with a
251 maximum of $22.3 \pm 0.2^\circ\text{C}$ in July and the lowest values during winter with a minimum of 7.7
252 $\pm 0.2^\circ\text{C}$ in January. Salinity and river flow showed inverse variations. Low salinities were
253 observed between January and May (minimum average value = 5.4 ± 0.9 in May) when river
254 flow was highest ($>1,000 \text{ m}^3 \text{ s}^{-1}$) while high salinities were observed in summer and autumn
255 when river flows were low. SPM showed a seasonal pattern with lowest concentrations
256 between January and July (around 500 mg l^{-1}) and high concentrations from August to
257 November (around $1,200 \text{ mg l}^{-1}$).

258 *3.2. Seasonal dynamics of biological components*

259 *3.2.1. Phytoplankton biomass*

260 Chlorophyll *a* concentrations ranged from $1.5 \pm 0.2 \mu\text{g l}^{-1}$ in January to $6.0 \pm 1.5 \mu\text{g l}^{-1}$
261 in August with two peaks, one in spring ($5.3 \pm 0.9 \mu\text{g l}^{-1}$) and another in summer ($6.0 \pm 1.5 \mu\text{g}$
262 l^{-1}).

263 *3.2.2. Zooplankton*

264 Zooplankton abundance showed strong intra-annual changes (Fig. 3). *Eurytemora*
265 *affinis* was the most abundant zooplanktonic species throughout the year with a minimum
266 average abundance $>3,400 \text{ ind. m}^{-3}$ in January. Very high abundances of *E. affinis* occurred in
267 spring ($24,005 \text{ ind. m}^{-3}$ in March) with decreasing values until summer and autumn. *Acartia*
268 showed a clear successional pattern, with *A. bifilosa* occurring essentially during June and
269 July with a peak of abundance in June (699 ind. m^{-3}) and *A. tonsa* being more abundant from

270 August to October with a peak of abundance in September (6,631 ind. m⁻³). Mysids
271 *Mesopodopsis slabberi* and *Neomysis integer* were mainly present from April to October,
272 with a maximum abundance in summer (120 ind. m⁻³ in July for *M. slabberi* and 367 ind. m⁻³
273 in June for *N. integer*).

274 3.2.3. Macrozoobenthos

275 Oligochaetes were by far the most abundant benthic taxa in the Gironde estuary
276 throughout the year with abundance >400 ind. m⁻² (Fig. 4). Abundances of the amphipod
277 *Corophium volutator* (intertidal), the polychaete *Streblospio shrubsolii* and the gastropod
278 *Hydrobia ulvae* (intertidal) showed marked seasonal changes with a peak in September
279 (>5,000 ind. m⁻², >300 ind. m⁻² and >80 ind. m⁻² respectively, Fig. 4). The polychaete
280 *Heteromastus filiformis* and the amphipods *Bathyporeia pilosa* + *Gammarus* spp. were more
281 abundant in spring and/or early summer (April-July) with mean densities of 139 and 21 ind.
282 m⁻², respectively, whereas the polychaete *Hediste diversicolor* was more abundant in summer
283 and autumn (August to November). In contrast, the isopod *Cyathura carinata* and the bivalve
284 *Scrobicularia plana* were abundant only during winter months (October-February, Fig. 4)
285 with a peak in density of 178 ind. m⁻² and 147 ind. m⁻² respectively in October.

286 3.2.4. Shrimps

287 White shrimps *Palaemon* spp. were more abundant from August to December while
288 the brown shrimp *Crangon crangon* showed marked seasonal changes with peak densities
289 (>45 ind. 1,000 m⁻³) occurring in warm months (July and August). For both shrimp species
290 biomass fluctuations paralleled those of abundance, with a biomass peak of 27.2 g 1,000 m⁻³
291 and 7.8 g 1,000 m⁻³ for *Palaemon* spp. and *C. crangon*, respectively (Fig. 5).

292 3.2.5. Fishes

293 Although 65 fish species were collected during the study period, only 12 were
294 considered in the analysis. Small pelagic fish species showed marked seasonal variations in
295 abundances with different dates of abundance peaks (Fig. 6). While *S. sprattus* occurred
296 essentially during late spring-early summer (May-June) with densities of ca. 10 ind. 1,000 m⁻³
297 ³, the abundance peak of anchovy *E. encrasicolus* occurred later, in August-September (>40
298 ind. 1,000 m⁻³). Regarding other small fish, abundances of *Syngnathus acus* and
299 *Pomatoschistus* spp. showed clear intra-annual changes, with peaks in August (71.7 and 193.3
300 ind. m⁻³, respectively; Fig. 6). Variability in fish biomass paralleled that of abundance for
301 most species, with however a delay of one month in the peak of biomass for *E. encrasicolus*
302 (15.8 g 1,000 m⁻³) and *S. acus* (16.2 g 1,000 m⁻³) (Fig. 6), reflecting individual growth. *S.*
303 *sprattus* showed a second peak of biomass which was not observed for abundance.

304 Concerning larger fish (Fig. 7), *Alosa* spp. showed important seasonal changes and
305 were more abundant during winter months (December-February) with ca. 10 ind. 100,000 m⁻².
306 There was a considerable difference in the timing between the biomass and density peaks for
307 *Alosa* spp. with biomass peaks in May (276.1 g 100,000 m⁻²) and September (363.6 g 100,000
308 m⁻²; Fig. 6). The most abundant fish species on an annual scale, *Liza ramada*, also showed
309 higher densities between December and February (>200-300 ind. 100,000 m⁻²) and also in
310 April (Fig. 7). Cooler months were also marked by the presence of *Merlangius merlangus*
311 with a peak of density occurring in February (Fig. 7). Abundances of *Argyrosomus regius*
312 showed clear intra-annual changes with peaks occurring in August (86.0 ind. 100,000 m⁻²),
313 whereas densities of *Dicentrarchus labrax* decreased steadily until August, followed by a
314 peak (10.2 ind. 100,000 m⁻²) in September (Fig. 7). The biomass of *D. labrax* paralleled
315 abundance, although with a delay of one month (2,778.1 g 100,000 m⁻² in October) (Fig. 7),
316 and peaked again in July which was not the case for abundance. On the other hand, *Solea*
317 *solea* was present throughout the year with abundances ranging from 0.3 ind. 100,000 m⁻² in
318 December to 39.6 ind. 100,000 m⁻² in September. These flatfishes displayed higher (but
319 variable) abundances and biomass during the summer and autumn months. *Anguilla anguilla*
320 and the flatfish *Platichthys flesus*, however, showed no clear temporal pattern, with
321 considerable variability in their abundances from month to month. Both species occurred
322 throughout the year with abundances ranging from 15.1 ind. 100,000 m⁻² in August to 64.9
323 ind. 100,000 m⁻² in May for *P. flesus* and from 0.4 ind. 100,000 m⁻² in August to 6.9 ind.
324 100,000 m⁻² in July for *A. anguilla* (Fig. 7).

325 3.3. Species associations and relation with environmental variables

326 The seasonal changes in the abundance of phyto- and zooplanktonic,
327 macrozoobenthic, shrimps and fish species and their relationships with environmental
328 variables were analyzed using multivariate analyses. The ascendant hierarchical clustering
329 (AHC) showed a division into four distinct groups of species according to their seasonal
330 abundance. Cluster 1 was associated with spring months and was composed of phytoplankton,
331 *Eurytemora affinis*, *Acartia bifilosa*, *Mesopodopsis slabberi*, *Bathyporeia* + *Gammarus*,
332 *Heteromastus filiformis*, *Sprattus sprattus*, *Platichthys flesus* and *Anguilla anguilla*. Cluster 2,
333 associated with summer months, was composed of *Neomysis integer*, *Corophium volutator*,
334 *Crangon crangon*, *Argyrosomus regius*, *Syngnathus acus*, *Pomatoschistus* spp., *Engraulis*
335 *encrasicolus* and *Solea solea*. Cluster 3, associated with late autumn, was composed of
336 *Cyathura carinata*, *Scrobicularia plana* and *Merlangius merlangus*. Cluster 4, associated with

337 autumn months, was composed of *Acartia tonsa*, *Hydrobia ulvae*, *Streblospio shrubsolii*,
338 *Hediste diversicolor*, *Palaemon* spp. *Dicentrarchus labrax* and *Alosa* spp. (reported in Fig. 8).

339 The CCA analysis indicated that the environmental variables measured (temperature,
340 salinity, spm and flow) significantly explained 25.5% of the species abundance variations in
341 the Gironde estuary. Axes 1 and 2 accounted for 71.8% of the variability explained (Fig. 8).
342 Considering their vector length and correlation with axes, salinity (best correlated with axis 1,
343 $r = 0.97$) and temperature (best correlated with axis 2, $r = -0.81$) are the most important
344 environmental variables influencing the species seasonal variations (Fig. 8). Group 1 species
345 are more abundant during months of low salinity and high flow, Group 3 and 4 species are
346 more abundant during months of low temperature and either intermediate or high salinity,
347 respectively, whereas both temperature and salinity have a positive effect on Group 2 species
348 (Fig. 8).

349 **4. Discussion**

350 *4.1. Relevance of biological data*

351 In the Gironde estuary, numerous studies have described the structure and spatio-
352 temporal variability of biotic compartments considered separately (e.g. Santos et al., 1996 for
353 meiofauna; David et al., 2005 for zooplankton; Lobry et al., 2003, 2006 for fish; Béguer et al.,
354 2010 for white shrimp), as well as the trophic interactions between a small number of trophic
355 levels (e.g. David et al., 2006; Lobry et al., 2008; Pasquaud et al., 2010). However, studies on
356 the biological groups considered here have never been conducted until now, partly because of
357 the lack of any recent long-term survey of the macrozoobenthic communities. Therefore,
358 using the present analysis, based on a five-year period (2004-2008, except for large fishes)
359 and monthly sampling, it is possible for the first time to characterize and synthesize the
360 comparative dynamics of representative biological components of the Gironde estuary:
361 plankton (both zooplankton and phytoplankton, described by Chl *a*), macrozoobenthos,
362 shrimps and fish. In addition, environmental data for this study were gathered simultaneously.

363 From available data on these biological groups, the present paper also identifies data
364 gaps and emphasizes the need to improve knowledge about specific groups or parts of the
365 estuary. Sampling of the main biotic groups in the Gironde estuary is restricted to the oligo-
366 mesohaline area. Whereas investigations are conducted on large fish throughout the estuary
367 (from Blaye to Royan) during ‘Sturat’ surveys, very few data exist on small fish and shrimps
368 (‘Transect’ surveys), or on zooplankton and benthos in the polyhaline sector; these were
369 therefore not considered in the present study. Thus our conclusions cannot be extrapolated to
370 the entire estuary or must be given careful consideration even if ongoing studies indicate that

371 polyhaline communities do not differ strongly from those in the oligo-mesohaline area; this is
372 the case at least for fish and shrimps (Irstea, unpublished data). Regarding zooplankton and
373 macrozoobenthos, winter data are lacking because long-term monitoring is usually from April
374 to November. Four months (December-March) were therefore deleted from the database
375 since, values were missing for at least one of the species considered, resulting in a lack of
376 information (see for example Selleslagh and Amara, 2008b) in the global multivariate
377 analysis. Nevertheless, the seasonal pattern highlighted by the analysis is ecologically
378 significant as the period considered in the analysis represents the most productive period in
379 the Gironde estuary (Sautour and Castel, 1995). Furthermore, results are consistent with
380 previous results (e.g. Lobry et al., 2006 for fish and David et al., 2005 for zooplankton).
381 Investigations on large fishes were conducted throughout the estuary during ‘Sturat’ surveys,
382 including the polyhaline sector, until 2000; we therefore used the three most recent years
383 (1998-2000) to estimate and analyse the temporal dynamics of large fish in the oligo-
384 mesohaline area of the Gironde estuary.

385 While the selectivity of the sampling gears used in this study is perhaps not well
386 adapted to all fish species (for instance, the selectivity of otter trawl for benthic/epibenthic
387 species such as *Anguilla anguilla*, *Platichthys flesus* and *Solea solea* is sometimes questioned;
388 Lobry, 2004), the use of different sampling methods (trawling and transect) that overlap in
389 terms of selectivity allows for a good description of the fish composition and abundance, as
390 recommended by several authors (e.g. Whitfield and Marais, 1999; Selleslagh and Amara,
391 2008b). The present study is based on the largest biological database available for the Gironde
392 estuary, including investigation of the most important biological groups at monthly intervals,
393 data which are rather scarce in other French and European estuaries. Furthermore, it focused
394 on a period for which the different protocols (gears, number of stations, sampling frequency,
395 etc.) were well standardized.

396 4.2. *Composition, temporal dynamics and relation with environment*

397 The small number of abundant species occupying the Gironde estuary (i.e. twelve fish
398 and 9 macrozoobenthos dominant species against a total of 65 and 47 species, respectively)
399 was attributed to the wide variation in annual water temperature (about 15°C), as reported by
400 Lazzari et al. (1999) in temperate regions. The composition and dynamics of fish, as well as
401 of their potential prey, emphasized the feeding, residence, migratory and nursery functions of
402 the Gironde estuary (Rochard et al., 2001; Lobry et al., 2006; Pasquaud et al., 2010). In the
403 present study, most species use the estuary during the spring and summer, providing evidence
404 that many marine species use it as a transitory key habitat (Gili, 2002) and in particular as a

405 nursery habitat for fish. This is true in other shallow water systems for Clupeidae, flatfish and
406 bass (Beyst et al., 2001; Selleslagh and Amara, 2008b; Henderson and Bird, 2010) or mysids
407 (Hamerlynck and Mees, 1991). During the settlement period, which has been related to the
408 timing of spawning and the planktonic phase (DeMartini, 1999) a sharp decrease in
409 abundances was observed for many species. This may be the result of a variety of factors,
410 including response to declining temperature (Clark et al., 1996; Beyst et al., 2001),
411 movements between feeding grounds, the need to leave the estuary to breed or predation
412 (Henderson and Bird, 2010).

413 Temporal fluctuations in biological communities were particularly marked and show a
414 discrimination of species into four seasonal groups. This seasonal pattern is characteristic of
415 estuarine or coastal species and has been observed in many other temperate systems for
416 different biological compartments (e.g. Ross et al., 1987; Clark et al., 1996; Maes et al., 1998;
417 Ramos et al., 2006; Modéran et al., 2010). From an ecological point of view, two distinctive
418 ecological seasons can be discriminated. Results show a clear shift occurring in July,
419 indicating a biomass transfer from a “planktonic phase” to a “benthic-demersal phase” with
420 the former distinguished by very high densities of plankton, in particular the copepod
421 *Eurytemora affinis*. This planktonic phase is characterized by the arrival of sprat *Sprattus*
422 *sprattus* juveniles, the growth of *Alosa* spp. and the development of mysid populations, and
423 corresponds overall to low densities of macrozoobenthos and fish. After July, corresponding
424 to maximal temperature, the transition to high salinities and the beginning of a period of
425 maximum turbidity, plankton decreases sharply while benthic and demersal species grow,
426 particularly in September-October. This second phase is characterized by the recruitment and
427 development of numerous macrozoobenthic species, the growth of *Palaemon* spp. and higher
428 densities of *Crangon crangon*. This period also corresponds to an increase in *Pomatoschistus*
429 spp., *Syngnathus acus*, *Dicentrarchus labrax*, *Solea solea*, *Engraulis encrasicolus* and
430 *Argyrosomus regius* abundances. Between the two phases, a transition period may be
431 identified, characterized by the absence or low density of the main species and a noticeable
432 abundance of species such as *Merlangius merlangus* or *Liza ramada*; corresponding to the
433 poorly documented “winter period” from November to March. Shrimps, *Platichthys flesus*, *L.*
434 *ramada* and, to a lesser extent, *D. labrax* are still abundant in this transition period. This is
435 consistent with previous studies which suggested a benthic pattern of trophic interactions in
436 winter (Lobry et al., 2006; Pasquaud et al., 2010). The hypothesis of two different trophic
437 flow structures during the year needs to be explored more deeply by constructing and
438 comparing seasonal food web models, as suggested by Lobry et al. (2008). In this way, by

439 providing important elements on biological dynamics, the present study not only provides a
440 better understanding of the functioning of the Gironde estuary but also lays the foundations
441 for seasonal trophic modelling of this kind.

442 In shallow habitats, temperature and salinity are often considered to control the
443 seasonal patterns of species occurrence (e.g. Thiel et al., 1995; David et al., 2005, among
444 others). Results from the present study indicated these two parameters as the most structuring
445 variables of temporal distribution of phytoplankton, zooplankton, macrozoobenthos, shrimps
446 and fish species. According to CCA, *Eurytemora affinis* was positively correlated with river
447 flow and negatively with salinity. This is in accordance with David et al. (2005) who
448 explained that it results from its seasonal cycle and ecological requirements, with maxima
449 occurring in winter-early spring, corresponding to periods of high river flow. In agreement
450 with other authors, mysids *Mesopodopsis slabberi* and *Neomysis integer* showed positive
451 correlations with temperature (Sorbe, 1981; David et al., 2005). The same trend was observed
452 for other species, i.e. *Crangon crangon*, *Argyrosomus regius* and *Syngnathus acus*, in other
453 marine or estuarine ecosystems (e.g. Quéro and Vayne, 1987; Beyst et al., 2001; Selleslagh
454 and Amara, 2007, 2008a). Phytoplankton, *E. affinis* and *M. slabberi* were clustered together;
455 this agrees with the common view that chlorophyll *a* influences the use of estuaries by
456 copepods and mysids (Gasparini and Castel, 1997; David et al., 2005). SPM has been
457 identified as a structuring variable for species seasonal variations, in particular for
458 zooplankton (David et al., 2005). In the present study, *Acartia tonsa* was correlated with
459 SPM, as reported by David et al. (2005). High turbidities (high SPM) affect its survival by
460 limiting selective feeding (Gasparini and Castel, 1997). Regarding macrozoobenthos, species
461 variations and abundances are indicative of main recruitment periods, which accords with
462 previous works on benthic population dynamics (Bachelet, 1981; Bachelet and Yacine-
463 Kassab, 1987).

464 Results indicated that the main temporal changes in the structure and density of fish,
465 macrozoobenthos, shrimps and phyto- and zooplankton reflect the different times of
466 recruitment of species and their relations with physico-chemical variables, but also to other
467 variables with regard to the high unexplained variability. The CCA analysis indicated that
468 measured environmental variables (temperature, salinity, spm and river flow) explained
469 25.5% of the species abundance variations in the Gironde estuary. The great majority of
470 papers dealing with the seasonal variability of fauna almost exclusively integrated physico-
471 chemical factors, leading to poorly explained relationships ($\pm 20\%$ as in the present case) and
472 they suggested other predictors, such as predation or competition (e.g. Marshall and Elliott,

473 1998). David et al. (2005) showed that the summer decrease in the copepod *E. affinis* is
474 controlled by a combined effect of temperature and predation. Similarly, Selleslagh and
475 Amara (2008b) showed that biotic variables (potential predators or preys for fish) have an
476 additional influence to abiotic variables on fish abundances in the Canche estuary. In addition,
477 studies dealing with seasonal variability of fauna were based on specific species or
478 assemblages, yet understanding species variability requires knowledge of the dynamics of
479 other species because of biological interactions (Monaco and Ulanowicz, 1997).

480 4.3. Influence of trophic interactions

481 Describing seasonal dynamics from primary producers to top predators gives a better
482 understanding of estuarine functioning and a first overview of the dynamics of trophic
483 interactions between species in the estuary. Sharp decreases following abundance peaks,
484 seasonal successions of species with trophic similarities, coincidence between the increase of
485 one species and the decline of another or parallel patterns observed between species suggest
486 trophic implications such as mortality due to predation or competition.

487 In the Gironde estuary, high secondary production explains the occurrence during the same
488 period of many fish species, especially those using estuaries as a nursery area (Lobry et al.,
489 2006, 2008). Copepods, in particular *Eurytemora affinis*, play a significant role in estuarine
490 food webs as an important food supply for many fishes, shrimps and mysids (Sorbe, 1983;
491 Fockedey and Mees, 1999; Lobry et al., 2008; Pasquaud et al., 2008). In the present study, *E.*
492 *affinis* showed maximum densities from March to May and then decreased in summer.
493 Probably in relation to this, *Neomysis integer* also showed maximum densities during June,
494 one month later, suggesting predation by *N. integer* on copepods, with a possible food
495 limitation (David et al., 2006). *N. integer* is known to control the copepod biomass in some
496 estuarine ecosystems (Roff et al., 1988; Irvine et al., 1995) and *E. affinis* is known to be the
497 main prey in the diet of *N. integer*, as shown by stomach content analysis (Fockedey and
498 Mees, 1999) or laboratory experiments (Winkler and Greve, 2004). Recently, David et al.
499 (2005) related the seasonal variation of *N. integer* to the temporal distribution of copepods in
500 the Gironde, which was verified thereafter by David et al. (2006) using a prey-predator
501 model. In addition, the mysid *N. integer* can constitute an important prey for fish, demersal
502 fishes in particular. *Argyrosomus regius*, the largest demersal fish in the Gironde estuary,
503 feeds on hyperbenthic species: *Crangon crangon* and *Pomatoschistus* spp. and a large
504 proportion of mysids (Pasquaud et al., 2008, 2010). These trophic interactions are observed in
505 multivariate analysis where *N. integer*, *C. crangon* and *A. regius* showed a similar trend and
506 were grouped together. The seasonal dynamics of the meagre could thus explain the decrease

507 in density of both *N. integer* and *C. crangon* in summer due to predation. It is also likely that
508 the migration of *A. regius* to marine waters in late summer explains the peak in abundance of
509 *Pomatoschistus* spp. one month later because of limited predation. In the same way, the
510 seasonal pattern of *Sprattus sprattus* in relation to *E. affinis* and *Acartia bifilosa*,
511 *Dicentrarchus labrax* in relation to *Palaemon* spp., and *Engraulis encrasicolus*, in relation to
512 *A. tonsa*, can be partially explained.

513 Flatfishes are known to prey upon epibenthic species, especially polychaetes, which
514 influence their distribution and migration behaviour in shallow water areas (Gibson, 1994;
515 Vinagre et al., 2006; Nicolas et al., 2007). In the Vilaine estuary, Nicolas et al. (2007)
516 reported that the density of juvenile sole was positively affected by the benthic invertebrate
517 biomass. Although *Solea solea* and *Platichthys flesus* consume polychaetes, benthic isopods
518 and shrimps in the Gironde estuary (Pasquaud et al., 2008), such interactions were not
519 suggested by the present study. Conversely, although a high correlation was observed
520 between *S. solea* and the benthic amphipod *Corophium volutator*, a common prey of *S. solea*
521 (Nicolas et al., 2007; Vinagre et al., 2008), few individuals were retrieved from fish stomachs
522 by Pasquaud et al. (2008).

523 Competition seems possible for species which exhibit a specialist feeding strategy in
524 the case of food limitation (Pasquaud et al., 2010) and it can play a determining role in
525 temporal partitioning in estuarine fish (Henderson and Holmes, 1991; Ogburn-Matthews and
526 Allen, 1993). The present results presume such a trophic partitioning for the small pelagic fish
527 *Sprattus sprattus* and *Engraulis encrasicolus*, which are both known to be zooplanktivores
528 (Pasquaud et al., 2008, 2010). These findings agree with Henderson and Holmes (1991), who
529 reported that the differing occupancy of flatfishes in the lower Severn estuary reduced
530 potential inter-specific competition. Due to different assemblages of prey consumed by fish
531 (Pasquaud et al., 2008) and a recognized degree of plasticity in prey item choice, inter-
532 specific competition for food appears relatively limited in the Gironde. Pasquaud et al. (2008)
533 suggested a considerable sharing of resources which would limit inter-specific competition
534 for access to food resources. Several studies have shown that prey are generally not a limiting
535 resource in estuaries (Lobry et al., 2008; Selleslagh et al., 2011, 2012), discarding the trophic
536 competition hypothesis. The life cycle of *S. sprattus* and *E. encrasicolus*, which have different
537 spawning periods, is probably the reason for the time-lag observed between these two species
538 rather than a competitive partitioning of resources, considering the very high abundance of
539 copepods in the Gironde estuary. Furthermore, *S. sprattus* and *E. encrasicolus* display
540 different feeding strategies, which could narrow diet overlap, minimize inter-specific

541 competition and allow the co-occurrence of species (Pasquaud et al., 2010). Although trophic
542 competition seems relatively low regarding these concerns, this process needs to be explored
543 further since the ‘seasonal trophic bottleneck’ seems to be a non negligible phenomenon
544 controlling estuarine dynamic patterns.

545 Taking all these considerations into account, the present study shows that the temporal
546 variability of estuarine species is predominantly influenced by physico-chemical variables and
547 trophic interactions, most notably predation. In future, it will be interesting to carry out
548 further analysis of dependence of the species seasonal dynamic on prey (or conversely on
549 predators) fitting predator-prey models, especially between mysids and the meagre *A. regius*.

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826 **Figure legends**

827

828 Figure 1. Map of the Gironde estuary and location of the sampling stations and areas.

829

830 Figure 2. Mean monthly variations of environmental variables in the Gironde estuary
831 averaged for 2004-2008. Vertical bars indicate standard errors of the means.

832

833 Figure 3. Mean (\pm SE) monthly abundance (ind. m^{-3}) of zooplanktonic species averaged for
834 2004-2008.

835

836 Figure 4. Mean (\pm SE) monthly abundance (ind. m^{-2}) of macrozoobenthic species averaged for
837 2004-2008. For species exclusively collected and abundant in the intertidal zone, mean
838 abundance was calculated only with intertidal samples. For other species mean was
839 calculated with both subtidal and intertidal samples, taking into account a ratio
840 subtidal:intertidal area 9:1.

841

842 Figure 5. Mean (\pm SE) monthly abundance (full line, ind. m^{-2}) and biomass (hatched line, g
843 $1,000 m^{-3}$) of shrimps averaged for 2004-2008.

844

845 Figure 6. Mean (\pm SE) monthly abundance (full line, ind. $1,000 m^{-3}$) and biomass (hatched
846 line, g $1,000 m^{-3}$) of small fish species averaged for 2004-2008.

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848 Figure 7. Mean (\pm SE) monthly abundance (full line, ind. $100,000 m^{-2}$) and biomass (hatched
849 line, g $100,000 m^{-2}$) of large fish species averaged for 1998-2000.

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851 Figure 8. CCA ordination diagram based on species abundances, with environmental
852 parameters represented by vectors.

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