

Exploitation of trophic resources by fish under stressful estuarine conditions

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ABSTRACT: Despite their high complexity and variability, estuaries are very productive and play an important role in fish feeding. We investigated how fish optimize their use of the available trophic resources by studying trophic preference variability and feeding strategies of some pelagic and demersal fish in the Gironde estuary (southwest France). Fish and their prey were collected approximately every 2 mo from July 2003 to June 2004 in the upstream area of the saline estuary. Stomach contents were analysed to assess the variability of fish feeding in relation to their size and the time of year. Intra- and interspecific food niche overlap was evaluated using Schoener's index, and a cross-calculation method was used to highlight general fish trends in predation strategy. Stomach content results showed interspecific and intraspecific variability in feeding by fish, which can be explained by their different or ontogenetically changing ecomorphology. Their diets are composed mainly of zooplankton and hyperbenthic crustaceans, with temporal variations in the consumed taxa. Optimization of available trophic resource use, a key element in estuarine resilience, is thus possible due to the temporal adaptation of this structural trophic web. However, in spite of their temporal adaptation capacity, most fish species exhibited a specialist feeding strategy. This result was not expected. Since zooplankton and hyperbenthic crustaceans exhibit a low specific richness in estuaries, especially in the high turbidity of the Gironde estuary, the loss of one of these species could affect the fish trophic web structure and hence the resilience of the system.

KEY WORDS: Pelagic and demersal fish · Stomach contents · Diet composition · Feeding strategy · Prey characteristics · Estuarine ecosystem · Gironde estuary

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INTRODUCTION

Estuaries are particular ecosystems, where the abiotic environment is characterized by rapid and large spatio-temporal fluctuations in physico-chemical characteristics (e.g. oxygen, temperature, salinity) in both water column and bed sediment dynamics (McLusky & Elliott 2004). This high environmental variability leads to a high spatio-temporal heterogeneity of the biological communities (McLusky & Elliott 2004, David et al. 2005), with a low diversity of all components, yet often with high abundances of adapted species (McLusky & Elliott 2004). Thus, this strong biological variability is

related to the ability of the estuarine biota to cope with natural stress, a key element in estuarine resilience (Elliott & Quintino 2007).

In addition, estuaries are generally exposed to high degrees of anthropogenic pressures that can modify their ecological status. Recent works underline the similarity between the features of organisms and assemblages in estuaries, subject to natural stress, and, those in anthropogenically stressed areas and, hence, the difficulty of distinguishing natural from human-induced stress in estuaries ('Estuarine quality paradox'; Elliott & Quintino 2007, Dauvin & Ruellet 2009).

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Because of these characteristics, monitoring and assessing the biodiversity and ecological status of marine ecosystems requires a substantial knowledge and a comprehensive understanding of properties across the entire biological system, in particular its structure (e.g. species composition) and functional properties (e.g. ecosystem processes; Hooper et al. 2005, de Jonge et al. 2006). Studying interactions between the biological compartments of an ecosystem, especially trophic relationships, provides a good picture of the biological community structure and is an essential step to understanding how an aquatic system functions (e.g. Elliott & Hemingway 2002, Livingston 2002, Pasquaud et al. 2007, 2008).

Topological approaches in trophic models are used to better understand estuarine ecological structure and functioning (Baird & Ulanowicz 1993, Wolff et al. 2000, Lin et al. 2007, Lobry et al. 2008). Most authors (in particular Lobry et al. 2008) suggest that estuarine communities have to optimize use of available trophic resources to successfully cope with stressful conditions. This suggests that: (1) a temporal adaptation of the trophic web would be observed and (2) most estuarine species would be opportunists. The present paper constitutes a preliminary investigation to test both of these assumptions by analyzing the food preferences and feeding strategies of the main fish species of the Gironde estuary.

The first objective was thus to describe the trophic relationship variability according to fish size and time of year of the main Gironde estuarine demersal and pelagic fish species using stomach content analysis, which appears to be the most reliable method to determine fish feeding (Pasquaud et al. 2007). The second objective was to analyze the dynamics of the fish feeding preferences using characteristics of their diet and of their prey population (abundance in the environment, mean weight).

MATERIALS AND METHODS

Study area. The Gironde estuary (45° 20' N, 0° 45' W; Fig. 1) is located in SW France and opens onto the Bay of Biscay. Its surface area is approximately 625 km² at high tide. It is 76 km long between the ocean and the Bec d'Ambès, where the Dordogne and Garonne Rivers meet and which generally constitutes the upstream salinity limit. The watershed covers 81 000 km², and the mean annual rate of freshwater discharge is around 760 m³ s⁻¹. These characteristics make it the largest estuary in western Europe (Salomon 2002, Lobry et al. 2003). The tidal range is 4.5 m at the mouth of the estuary and >5 m at Bordeaux. The Gironde is one of the most turbid estuaries in Europe (Sautour &

Castel 1995). River systems carry annually between 1.5 and 3 × 10⁶ t of suspended particulate matter (SPM; David et al. 2005) to the estuary, with a fairly permanent maximum turbidity zone (SPM about 1 g l⁻¹ at the surface and 10 g l⁻¹ near the bed; Sottolichio 1999). As a consequence, primary production in the Gironde is reduced (10 g C m⁻² yr⁻¹), and the food-web base consists, for the most part, of a varied nutritional pool containing a high proportion of detritus (Irigoiien & Castel 1995).

The climate of the region is temperate under oceanic influence. Typically, water temperature variability is moderate (between 2°C in January and 26°C in August) and monthly rainfall fluctuates between 50 mm in summer and 100 mm in winter (Klein Tank et al. 2002). During the sampling period (from July 2003 to June 2004), the water temperature ranged from 9.78°C in February to 25.42°C in July in the study area. The river flow remained very low from July to December 2003, in spite of a few strong freshwater inputs in December. The first half of 2004 was relatively dry, characterized only by episodes of flooding in January and April to May (authors' unpubl. data). Because of these hydrological conditions, a very strong marine intrusion was observed during summer 2003, with maximum salinity values in September (average salinity 11.43 in the sampling area), and low salinities were recorded in February (0.08), April (0.41) and June (3.48).

Fish sampling. To analyze temporal feeding variability, fish were collected approximately every 2 mo from

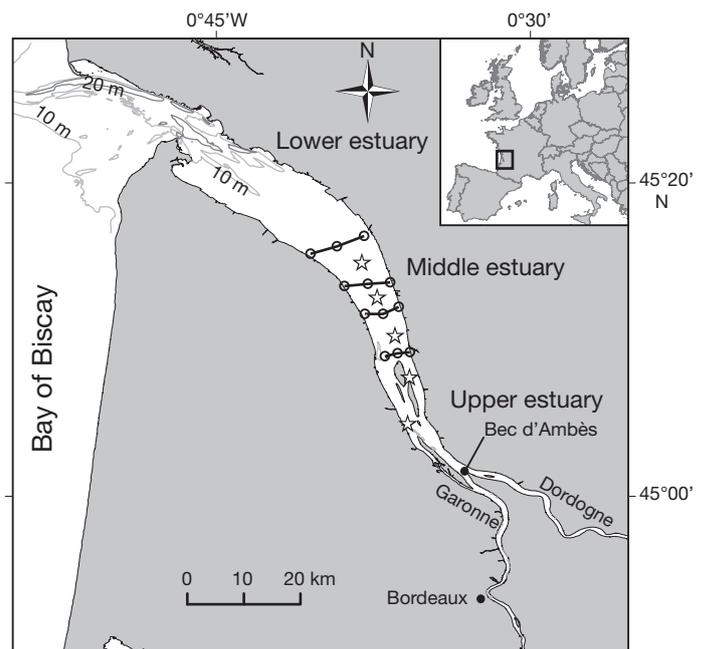


Fig. 1. Location of sampling stations in the Gironde estuary. Stars: fish; circles: shrimps; lines: the 4 transects

July 2003 to June 2004 in the upper and middle area of the Gironde estuarine haline part (Table 1, Fig. 1). Specimens were caught once per sampled month at 5 stations (Fig. 1) using an otter trawl (4 m opening and a cod-end with a mesh size of 8 mm). Trawling was restricted to daylight at high tide in order to standardize the samplings, and only when the tidal coefficient was <75 (trawling at a coefficient >80 in this system is not reliable). Haul duration was limited to 15 min to optimize the analysis of the stomach contents by minimizing regurgitation and feeding under abnormal conditions in the trawl (Pasquaud et al. 2007). All the sampled fish were identified, counted, measured (total length) and weighed. Fish <200 mm long were immediately placed on dry ice in order to stop the digestion processes. The digestive tract of the largest specimens was conserved on dry ice. The samples were stored at -18°C in the laboratory. Using this protocol, all the analyses could be carried out on fresh material, after defrosting, thus facilitating handling and also the identification of the fish species and their prey.

Stomach content analyses. The fish species analyzed were selected because they were considered typical of the estuarine ichthyofauna both in terms of occurrence and of functional guilds, i.e. ecological and feeding categories (see Lobry et al. 2003 for details; Table 1). Prey sampled in the system for which data were available (cf. 'prey data' paragraph) were zooplankton and hyperbenthos. We thus focused on their fish predator species.

The stomach contents of 538 individuals from the 8 fish species caught in the sampling area were analyzed (Table 1). A minimum of 5 specimens per taxa and per sampled month, with food items in their stomachs, were selected for analysis (minimum required to obtain a diet picture). Two size ranges were distinguished for *Pomatoschistus minutus* (small <40 mm; large ≥ 40 mm) and *Argyrosomus regius* (2 age classes) to test ontogenic changes in feeding. All the items in the stomachs were examined under a binocular microscope, identified to the highest possible taxonomic level, counted and weighed (dry weight, to nearest 10^{-4} g). Dietary analysis is traditionally assessed by occurrence (i.e. the percentage of non-empty stomachs where a certain prey item occurred), numerical and volumetric/gravimetric methods (see Hynes 1950, Hyslop 1980 for more details). Each of these measures provides a different insight into predator feeding habits (Cortès 1997). The numerical percentage of the prey (%N) is well adapted to our objective as it describes feeding behavior (Macdonald & Green 1983). This was calculated for each item consumed by a fish species per month.

The mean weight (\bar{W} in g) of each prey was also estimated from these stomach content analyses (average of the dry weights of each item consumed by a predator species per month).

Prey data. Sampling data for shrimps and zooplankton from the same estuarine area and the same months as the fish sampling data were used to characterize prey populations in the environment (Table 1).

Shrimps were collected from 4 transects, established since 1991 for monitoring the smaller components of the estuarine fauna around the Blayais nuclear power plant on a monthly basis (Lobry et al. 2006). Each transect consists of 3 sites, 1 close to each bank and 1 in the main channel of the estuary (Fig. 1). At each site, sampling was carried out simultaneously near the surface and near the bottom, with the water surface sampled using 2 pushnets located one on each side of the boat (section 4×1 m, stretched mesh of 1 mm in the cod-end) and the bottom sampled using a dragnet with a 2.0×1.2 m frame, kept at 0.2 m above the bed by runners. The net meshes were identical to those used for surface sampling. Sampling was carried out in daytime, between the halfway stage of the flood tide and high tide slack. Each tow lasted about 7 min. All the samples collected were preserved in 10% formaldehyde, before being identified and counted at the laboratory.

Table 1. Functional guilds (EG: ecological guild; TG: trophic guild) and number of fish used for stomach content analyses for each sampled month. N: number of sampled stations for fish, shrimp and zooplankton; S: small; L: large; ER: truly estuarine resident fish; MS: marine seasonal migrant fish; MJ: marine juvenile migrant fish; P: planktivore; IS: invertebrate feeder; IF: invertebrate and fish feeder

Organism	EG	TG	Jul 2003	Sep 2003	Nov 2003	Feb 2004	Apr 2004	Jun 2004
Fishes								
N			5	5	5	5	5	5
<i>Sprattus sprattus</i>	MS	P		5				
<i>Engraulis encrasicolus</i>	MS	P	27	9	6			
<i>Pomatoschistus microps</i>	ER	IS	20		10	11	15	
<i>Pomatoschistus minutus</i> (S)	ER	IS		15		21		15
<i>Pomatoschistus minutus</i> (L)	ER	IS	30	25	20	6		20
<i>Dicentrarchus labrax</i>	MJ	IF	6	5	9	26	11	
<i>Dicentrarchus punctatus</i>	MJ	IF					5	
<i>Argyrosomus regius</i> (S)	MS	IF	68					15
<i>Argyrosomus regius</i> (L)	MS	IF		29	36		20	40
<i>Merlangius merlangus</i>	MS	IF		5	8			
Shrimp								
N			12	12	12	12	12	12
Zooplankton								
N			23	22	16	12	16	16

Zooplankton was collected along the estuary every 3 units of salinity using a standard 200 μm WP-2 net for zooplankton and a 500 μm bongo net, which is better adapted to mysid and amphipod sampling. Vertical hauls were carried out at each station for each net. The catch was preserved in 5% seawater/formalin before being identified and counted at the laboratory.

Abundance of the different prey categories was calculated for each month, and expressed as the number of individuals per cubic meter of filtered water at the sampling site.

Data analyses. In order to determine whether the consumption of the different prey varied with time or predator size, permutation tests based on inertia analysis (Chessel et al. 2004), with a 0.05 significance level, were performed on matrices of the diet composition per each fish predator using the relative abundance (% N) of the prey items.

Intra- and interspecific food niche overlap was evaluated using Schoener's index (SI), defined as

$$SI_{xy} = 1 - 0.5 \left(\sum_{i=1}^n |N_{xi} - N_{yi}| \right) \quad (1)$$

where N_{xi} is the relative abundance of prey category i in the stomach content of species x and N_{yi} the same relative abundance in the species y (Hurlbert 1978). According to Wallace (1981) and Wallace & Ramsay (1983), overlap values >0.6 should be considered biologically significant.

The general trends in predation strategy for each species (or size group) and each sampled month were studied using the cross-calculation method described by Azémar et al. (2007). This method allows us to test if a predator diet can be determined by prey characteristics (e.g. abundance or mean weight/size) in the environment. It consists of: (1) ranking prey i of each fish of a predator group (species or size class) as a function of relative abundance (N) in the stomach contents (N_i ranks; e.g. for *Engraulis encrasicolus*, Stomach Content 1: $N_{Acartia}$ = Rank 1; Stomach Content 9: $N_{M. slabberi}$ = Rank 1, $N_{Cirripedes}$ = Rank 2, $N_{Acartia}$ = Rank 3), and (2) ranking these same prey according to their abundance (Ab ranks) and their mean weight (\bar{W} ranks) in the environment (e.g. in July, Ab $_{Acartia}$ = Rank 1, Ab $_{M. slabberi}$ = Rank 2, Ab $_{Cirripedes}$ = Rank 3). As only prey that appeared in the stomach contents are considered, predator feeding strategy is assessed within the context of its trophic niche. Moreover, non-sampled prey in the present study (e.g. nauplius crustacean stage) were excluded from the analysis. Next, (3) the frequencies (i.e. number of occurrences observed from all the stomach contents) of each combination N_i ranks \times Ab $_i$ ranks and N_i ranks \times W_i ranks were calculated for each prey of a predator group. Finally, (4) the shape of the distribution was tested using a Spearman rank test at $p < 0.05$. If these frequencies

increased or decreased as a function of the prey characteristic ranking (Ab or \bar{W}), the predation was considered to be selective according to prey abundance (Ab) or mean weight (\bar{W}); otherwise, the predation was unselective with regard to the prey characteristic considered (Ab or \bar{W}).

Three different types of predation strategy were determined: (1) generalist, when the Spearman correlation coefficient was not significant for either abundances or mean weights; (2) opportunistic, when frequencies increased significantly with abundances; and (3) specialist, when the highest frequencies were concentrated around a narrow mean weight (Fig. 2).

RESULTS

Interspecific feeding variability

Fish species showed different feeding ecology and strategy (Fig. 2, Table 2 & Appendix 1). Small marine pelagic fish *Sprattus sprattus* and *Engraulis encrasicolus* based their diet on mesozooplankton, feeding mainly on the nauplius stage of crustaceans and on copepods of the genus *Acartia*. However, their trophic niches did not overlap ($SI < 0.6$) and their predation strategy was different: *E. encrasicolus* was an opportunist, i.e. among its food spectrum, this species mainly consumed the most abundant prey in the system (e.g. *Acartia* in September), whereas *S. sprattus* was a specialist, focusing on prey of a specific weight (size) range (e.g. selection of cirriped larvae in September, not the most abundant prey).

Small estuarine resident species *Pomatoschistus minutus* and *P. microps* also consumed a high quantity of mesozooplankton, but their diet differed from that of *Sprattus sprattus* and *Engraulis encrasicolus* due to a high consumption of hyperbenthos, essentially the mysid *Mesopodopsis slabberi* and the amphipods *Gammarus* spp. (no overlap; $SI < 0.6$). The 2 species of *Pomatoschistus* were seldom present together in the area studied, and, if they were, they tended to show a trophic niche overlap (February, $SI > 0.8$). Both were characterized by specialist feeding, essentially on the largest zooplankton (the copepod *Eurytemora affinis*) and the smallest hyperbenthos (mysids *M. slabberi* and *Neomysis integer*).

Finally, the feeding of marine demersal fish (e.g. *Dicentrarchus labrax*, *D. punctatus*, *Argyrosomus regius* and *Merlangius merlangus*) was mainly characterized by hyperbenthic prey such as the mysids *Mesopodopsis slabberi* and *Neomysis integer*, the amphipods *Gammarus* spp. and the shrimps *Palaemon* spp.

The 2 species of *Dicentrarchus* did not show trophic niche overlap, and presented different predation strategies: *D. labrax* was a specialist and *D. punctatus*

Table 2. Predation strategy for each fish species according to size and time. Results were deduced from the form of N frequencies of prey versus abundances (Ab) and mean weights (\bar{W}). Three different types of food behavior were determined: (1) opportunistic when frequencies increased significantly with Ab , (2) generalist when the Spearman correlation coefficient was null, (3) specialist when the highest frequencies were concentrated around a narrow \bar{W} (cf. Fig. 2). See Fig. 2 for the definition of prey abbreviations; naup: nauplius larvae; copepods: other copepods. Prey range: the lowest and the highest weight (size) prey; ns: non-significant trend; *significant trend at $p < 0.05$

	Environment		Size (mm) (replicates)	Prey no. (range)	Prey strategy
	Available prey	Prey density (ind. l ⁻¹)			
<i>Engraulis encrasicolus</i> (Eenc)					
Jul 2003	10	7.8	38–127 (18)	6 (naup–Nint)	Opportunist*
Sep 2003	11	3.1	47–77 (9)	3 (cir–Msla)	Opportunist*
Nov 2003	5	5.0	47–62 (6)	4 (Ac–mysid)	Opportunist*
<i>Sprattus sprattus</i> (Sspr)					
Sep 2003	11	3.1	60–115 (5)	4 (naup–Eaff)	Specialist ^{ns}
<i>Pomatoschistus microps</i> (Pmic)					
Jul 2003	10	7.8	27–37 (15)	9 (eggs–pol)	Specialist ^{ns}
Nov 2003	5	5.0	27–38 (9)	6 (eggs–isop)	Specialist ^{ns}
Feb 2004	5	10.7	26–50 (11)	4 (eggs–amp)	Specialist ^{ns}
Apr 2004	9	18.6	33–39 (11)	5 (Ac–amp)	Specialist ^{ns}
<i>Pomatoschistus minutus</i> (small) (PminS)					
Sep 2003	11	3.1	23–39 (8)	5 (Ac–isop)	Specialist ^{ns}
Feb 2004	5	10.7	26–38 (21)	5 (eggs–amp)	Specialist ^{ns}
Jun 2004	10	13.1	21–39 (11)	2 (Nint–amp)	Specialist ^{ns}
<i>Pomatoschistus minutus</i> (large) (PminL)					
Jul 2003	10	7.8	40–73 (17)	9 (mol–shr)	Specialist ^{ns}
Sep 2003	11	3.1	40–65 (20)	5 (cops–amp)	Specialist ^{ns}
Nov 2003	5	5.0	41–65 (11)	5 (Msla–fish)	Opportunist*
Feb 2004	5	10.7	41–60 (5)	3 (eggs–amp)	Specialist ^{ns}
Jun 2004	10	13.1	40–55 (19)	3 (Nint–amp)	Opportunist*
<i>Argyrosomus regius</i> (small) (AregS)					
Jul 2003	10	7.8	30–104 (68)	9 (mol–fish)	Generalist ^{ns}
Jun 2004	10	13.1	30–52 (14)	7 (Eaff–fish)	Generalist ^{ns}
<i>Argyrosomus regius</i> (large) (AregL)					
Sep 2003	11	3.1	130–235 (25)	4 (Msla–fish)	Specialist ^{ns}
Nov 2003	5	5.0	130–249 (36)	6 (Msla–fish)	Specialist ^{ns}
Apr 2004	9	18.6	126–260 (20)	6 (Msla–shr)	Generalist ^{ns}
Jun 2004	10	13.1	118–263 (38)	9 (eggs–fish)	Specialist ^{ns}
<i>Merlangius merlangus</i> (Mmer)					
Sep 2003	11	3.1	90–102 (5)	3 (Ac–fish)	Specialist ^{ns}
Nov 2003	5	5.0	114–150 (6)	5 (Msla–fish)	Specialist ^{ns}
<i>Dicentrarchus labrax</i> (Dlab)					
Feb 2004	5	10.7	80–147 (21)	7 (Eaff–crab)	Specialist ^{ns}
Apr 2004	9	18.6	83–140 (8)	5 (cops–fish)	Specialist ^{ns}
<i>Dicentrarchus punctatus</i> (Dpun)					
Apr 2004	9	18.6	95–135 (8)	5 (Msla–pol)	Opportunist*

• For the 2003 cohort of *Argyrosomus regius*, the diet was dominated numerically by *Mesopodopsis slabberi* (78%) in July, by the shrimps *Palaemon* spp. in September (54%) and November (64%) and by *Neomysis integer* and *Gammarus* spp. in April (respectively, 44 and 28%) and June (31 and 59%). *A. regius* oscillated between a generalist and specialist feeding strategy.

• *Dicentrarchus labrax* fed essentially on the amphipods *Gammarus* spp. (24%) and the shrimps *Palaemon* spp. (32%) in February and on *Gammarus* spp. (57%) and *Neomysis integer* (14%) in April.

• The most abundant prey consumed by *Merlangius merlangus* were *Mesopodopsis slabberi* (88%) in September and *Palaemon* spp. (50%) in November. *Dicen-*

trarchus labrax and *M. merlangus* always showed a specialist feeding strategy.

Intraspecific feeding variability

Intra-specific feeding variability according to fish size was tested for *Pomatoschistus minutus* and *Argyrosomus regius*. No significant difference was observed between the diets of the 2 size groups for *P. minutus* (p -values > 0.05), in contrast to *A. regius*, e.g. only small specimens fed on small zooplankton. Moreover, whatever its size, *P. minutus* presented a specialist strategy, whereas *A. regius* exhibited generalist predation when small and specialist predation when large.

DISCUSSION

Sample representativeness

The present study was based on analyses, on the one hand, of fish stomach contents and, on the other hand, of hyperbenthic invertebrate samples, all from the same estuarine area, i.e. the upstream part of the saline Gironde estuary.

As in the saline areas of other European estuaries (Mees et al. 1995, McLusky & Elliott 2004), hyperbenthic invertebrate samples were characterized by a low specific diversity and high densities, features which vary significantly over time. In previous investigations, temporal variability has been linked to fluctuations in environmental factors (David et al. 2005, Lobry et al. 2006). In addition, the specific compositions observed in 2003 (David 2006, Lobry et al. 2006) were similar to those observed in other Gironde estuary studies (Castel 1981, Sorbe 1981, Mees et al. 1995): the copepods consisted predominantly of *Engraulis affinis* in the spring and *Acartia* spp. in summer; the suprabenthos consisted of *Neomysis integer* in the spring and *Mesopodopsis slabberri* and *Gammarus* spp. in summer, which was similar to in other European estuaries (Soetaert & van Rijswijk 1993, Mouny et al. 2000, Mouny & Dauvin 2002). The study area was also representative for zooplankton and estuarine suprabenthos, which were fairly homogenous (David 2006). Thus, the samples collected give a good picture of hyperbenthic prey availability in the brackish part of the estuary for the pelagic and demersal fish selected, i.e. those feeding mainly on these communities.

For some fish species chosen, only a few specimens were included in the analysis due to a small number of individuals collected and/or because few individuals had a non-empty stomach, e.g. *Sprattus sprattus* and *Dicentrarchus punctatus*. Moreover, these samples were sometimes collected from only one particular trawl, i.e. concerned only a small part of the study area. However, for various reasons, these data have been taken into consideration in the present study:

- These species showed a low intra-group feeding variability, which can be explained by the characteristic of consumed hyperbenthic communities, i.e. few species, high densities. The statistical minimum of 5 individuals would therefore appear sufficient to define the diet of these species.

- In the brackish part of the Gironde estuary, there was no significant spatial variability in the prey communities either in composition or density (David et al. 2005, David 2006). Whatever the location of the fish sampling, analysis of their stomach contents was representative of the feeding strategy in the area studied.

- The choice of these species allowed us to make strategy comparisons between fish exhibiting ecologi-

cal and feeding similarities, e.g. *Sprattus sprattus* and *Engraulis encrasicolus* and *Dicentrarchus punctatus* and *D. labrax*, and provided assumptions on the structuring mechanisms of fish communities in an estuarine environment.

Inter- and intraspecific fish feeding variability

Fish stomach content analyses provide more than just a snapshot of what and how much an individual has ingested at a given moment: they give essential information to help understanding of species feeding requirements and strategies.

Investigation of the diet compositions of the 8 main pelagic and demersal fish species during the study period in the Gironde estuary enabled us to show interspecific feeding variability. Despite the differences in taxa, geographical distribution and environmental conditions, similar feeding requirements have been observed in other estuarine and marine systems: the small pelagic fish *Sprattus sprattus* and *Engraulis encrasicolus* are zooplanktivores (e.g. Plounevez & Champalbert 1999, Maes & Ollevier 2002); demersal fish, represented by *Argyrosomus regius*, *Dicentrarchus labrax*, *D. punctatus* and *Merlangius merlangus*, consume hyperbenthos (Moore & Moore 1976, Ktari et al. 1978, Cabral & Ohmert 2001, Laffaille et al. 2001); and *Pomatoschistus minutus* and *P. microps* eat both mesozooplankton and hyperbenthic prey (Salgado et al. 2004, Leitão et al. 2006). This interspecific feeding variability could be linked to different body structures, i.e. ecomorphology or ecomorphology (Wootton 1990). Morphological characteristics (e.g. position, shape and size of the mouth, shape and ability to protrude the jaw, body form and size) determine position in the water column, locomotive abilities and the size of prey they can intake (e.g. Schafer et al. 2002).

The present study highlights the fact that species that have ecological and trophic similarities (e.g. *Sprattus sprattus* and *Engraulis encrasicolus*, or *Dicentrarchus labrax* and *D. punctatus*) do not necessarily show diet overlap. Moreover, they present different feeding strategies. For example, the small pelagic fish *S. sprattus* is a specialist, whereas *E. encrasicolus* shows opportunistic predation strategies, and the demersal fish *D. labrax* is a specialist, whereas *D. punctatus* is an opportunist. This feeding strategy variability could narrow diet overlap, minimize interspecific competition and allow the co-occurrence of these species (Oscoz et al. 2006).

For species presenting ecological and morphological similarities and the same feeding strategies. Either (1) there is no feeding niche overlap. These cases occur when the species considered do not belong to the same

size class, e.g. *Pomatoschistus minutus* and *P. microps* in November and February, *Argyrosomus regius* and *Merlangius merlangus* in September. Salgado et al. (2004) have already highlighted a decrease in feeding overlap between these 2 *Pomatoschistus* species due to an increased difference in length. Or (2) there is a feeding overlap when the resource is not limited, e.g. *Pomatoschistus minutus* and *P. microps* in February and *Argyrosomus regius* and *Merlangius merlangus* in November, the time of year when the environment is very poor in species numbers, but those that are present remain abundant, thus limiting any feeding competition.

Feeding variability according to size was tested only for *Pomatoschistus minutus* and *Argyrosomus regius*, and not for any other species, either because too few samples per species were available or because their size distribution was too uniform. No significant feeding variation was observed between the 2 size classes of *P. minutus* (small <40 mm; large \geq 40 mm). For this species, a dietary shift has already been highlighted for individuals with a total length >50 mm, with a progressive disappearance of copepods and a considerable increase in larger prey (Hamerlynck & Cattrijsse 1994, Salgado et al. 2004). This size range (\geq 50 mm) has not been differentiated in the present study because of the small number of specimens. A variation in feeding according to fish length was observed for *A. regius*, but also for *Merlangius merlangus* with their growth in time. Their diets varied, with larger fish showing an increased consumption of larger prey. Body size effects on feeding shifts have already been identified for these predators (Quéro & Vayne 1987, Pederson 1999, Cabral & Ohmert 2001), as well as for *Sprattus sprattus* (Arrhenius 1996, Casini et al. 2004), *Engraulis encrasicolus* (Conway et al. 1998) and *Dicentrarchus labrax* (Kennedy & Fitzmaurice 1972, Labourg & Stequert 1973). Diet variations according to fish size have already been explained by ontogenetic changes in morphology, especially by the increase in predator gape width and swimming speed with the increase in predator size (e.g. Garrison & Link 2000a, Pasquaud et al. 2004). The relative body size of the component species has often been identified as a major determinant of food-web structure (Warren & Lawton 1987). Garrison & Link (2000b) suggest that different size classes within a species may therefore be considered functionally as different species in terms of trophic dynamics. These diet changes are particularly marked when different ontogenetic stages are considered (e.g. Garrison & Link 2000a, Woodward & Hildrew 2002), but these have not been highlighted in this work.

The study of feeding strategies according to fish size reveals different behaviors for *Argyrosomus regius*

(generalist/specialist) and *Pomatoschistus minutus* (specialist/opportunist). Marshall & Elliott (1996), who studied the feeding ecology of the main fish species recorded in the Humber estuary (United Kingdom), also emphasized specialization by the largest specimens for some species and an increase in niche breadth with size for other species.

Temporal feeding variability

In relation to the naturally variable environmental conditions, estuarine biological communities exhibit distinctive temporal patterns at both low (David et al. 2005, 2006) and high trophic levels (see, for instance, Elliott & Hemingway 2002, Lobry et al. 2006), suggesting that the resilience of estuarine ecosystems is linked to the temporal trophic structure and perhaps to fish species' ability to adapt their diet according to available prey in the environment.

As in other estuarine systems (e.g. Hajisamae et al. 2003, Hampel et al. 2005, West et al. 2006, Reum & Essington 2008), the present work emphasizes a temporal variability in estuarine fish diets and thus in trophic topology. The use of the cross-calculation method enabled us to identify how fish exploit trophic resources according to time. As a result, most species were identified as specialist, whichever month is being considered. The present study therefore invalidates the common hypothesis that estuarine fish are generally opportunists (e.g. Moore & Moore 1976, Cabral & Ohmert 2001, Laffaille et al. 2001, Baldoa & Drake 2002, Elliott & Hemingway 2002). Only a minority of the pelagic and demersal fish community in the Gironde estuary—characterized by the marine juveniles *Engraulis encrasicolus* and *Dicentrarchus punctatus* and by the resident species *Pomatoschistus minutus*—were found to feed on the predominant abundant prey which differed from month to month.

This difference in conclusions, specialist versus opportunist, can be explained by the precision of the method used for the present study, as it enabled us to test whether, among all the prey that can be the most abundant in the system, a particular weight (size) range is selected. In the estuarine context, where specific diversities are low and densities are high, the use of this method to draw conclusions about fish feeding strategy would seem particularly appropriate.

It is interesting to note that this study reveals the specialist feeding strategy of *Pomatoschistus microps* and *P. minutus*, always described as opportunistic fish in the literature (e.g. Pihl 1985, Pasquaud et al. 2004, Leitão et al. 2006). Nevertheless, the dietary analysis for both size and time emphasizes the capacity of *P. minutus* to adapt its feeding strategy according to prey

availability. We can assume that the other resident species *P. microps* is able to adapt too.

The present study highlights the specialist feeding strategy of the *Sprattus sprattus*, *Merlangius merlangus* and *Dicentrarchus labrax* species, whatever the month considered. This strategy had already been shown for *S. sprattus*, which may have a major impact on the zooplankton community (Brooks & Dodson 1965, Rudstam et al. 1994, Casini et al. 2004). Thus, a decrease in the abundance of these 3 marine juvenile species or their absence from the system could be linked to a decrease in/disappearance of their preferential prey, associated with an increase in competition pressure (prey availability). For *S. sprattus*, a decrease in its zooplanktonic prey, as well as trophic competition pressure from *Engraulis encrasicolus* could explain its departure from the study area in November. The temporal segregation of *M. merlangus* and *D. labrax*, species that show feeding similarities, could also support this hypothesis. An ability to avoid niche overlap by spatio-temporal segregation has already been shown for these 2 species in relation to other fish species (Bromley et al. 1997, Cabral & Ohmert 2001). These results suggest a structuring of the fish communities according to prey–predator relationships.

However, as suggested by prey abundances, shrimps are probably not limited in winter. The absence of *Merlangius merlangus* and *Argyrosomus regius*—also specialist but trending towards generalist—in February could be correlated with environmental conditions, especially low salinities and low water temperatures (Quéro & Vayne 1987, Pasquaud 2006). These observations suggest that the fish assemblages in that brackish part of the estuary are structured more by abiotic factors than by trophic relationships during this period of the year. In other studies (e.g. Costa & Elliott 1991, Thiel et al. 1995, Kupschus & Tremain 2001, Harrison & Whitfield 2006, Lobry et al. 2006), this estuarine fish community structuring has also been related to environmental variables, especially temperature and salinity, which depend on temporal variations in water flow (Lobry et al. 2006).

The estuarine fish communities are structured in time, both by environmental conditions and trophic relationships (Marshall & Elliott 1996, Kimmerer 2002), but we can hypothesize that these structuring factors do not take effect on the same spatial scales as suggested by Martino & Able (2003): 'large-scale patterns in the structure of estuarine fish assemblage are primarily a result of individual species' responses to dominate environmental gradients, as well as ontogenetic migrations, whereas smaller-scale patterns appear to be the result of habitat associations that are most likely driven by foraging, competition, and/or predator avoidance'. This remark confirms theoretical views on community structure, which maintain that physiologi-

cal tolerances to environmental factors set up the community framework, while biotic interactions refine species distribution patterns within this structure (Weinstein et al. 1980, Menge & Olson 1990) and underlines the need to consider the spatial feeding variability, which was not studied in this work.

CONCLUSIONS

Analysis of fish stomach contents gave a picture of the temporal patterns of the Gironde estuary fish food web, describing interspecific and intraspecific trophic relationships and the dynamics of the food-web structure. Comparisons of the relative abundance of prey in the stomach contents, numerical abundance of these prey in the environment and mean weight appear particularly relevant for studying fish feeding strategy in estuaries and assessing the trophic functions provided by this system for these species.

The present study highlights a strong trophic dynamism and suggests a resource partitioning dependent on predator/prey size (according to predator/prey life cycle), prey availability and predator presence (according to predator life cycle and environmental conditions). Optimization of available trophic resource use, a key element in estuarine resilience (Elliott & Quintino 2007), is possible due to the temporal adaptation of this structural trophic web. This trophic dynamism could play a major role in the stability/resilience of this ecosystem (cf. Link 2002), as suggested by recent statements in the biodiversity–stability debate (see for instance Navarrete & Berlow 2006, Elliott & Quintino 2007).

In spite of their adaptation capacity, most fish species exhibited a specialist feeding strategy. In the Gironde estuary there are few invertebrate species. We can imagine that the loss of one species will affect the fish trophic web structure and hence the resilience of the system. Comparative spatial studies are envisaged, i.e. intra-system studies, or comparisons with other estuaries or marine systems, to examine whether our conclusions can be generalized, to give a better understanding of the mechanisms of prey–predator structuring and to ascertain the degree of marine fish species dependence on estuarine systems.

The present study has enabled us to go beyond the structural aspects of biological communities and access functional aspects, in accordance with some recent recommendations by de Jonge et al. (2006) and Elliott & Quintino (2007) concerning the implementation of monitoring programs in estuarine areas. In addition, this approach provides the data needed to develop and/or validate trophic models (i.e. Lobry et al. 2008), in order to identify keystone species (Libralato et al. 2006) and predict the development of these systems.

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