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Exploitation of trophic resources by fish under stressful estuarine conditions

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ABSTRACT

Despite the high complexity and variability of estuaries, these ecosystems are very productive and play an important role in fish feeding. This paper constitutes a preliminary investigation to test how fish optimize the 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 two months from July 2003 to June 2004 in the upstream area of the saline estuary. Stomach content analyses were realized to describe the variability of fish feeding according 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 the general fish trends in predation strategy. Stomach content results showed interspecific and intraspecific variability in fish feeding, which can be explained by their different or evolutionary ecomorphology. Their diets are composed mainly of zooplankton and hyperbenthic crustaceans with temporal variations in the consumed taxa. Optimization of the 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.

Keywords: 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 especially characterized by fast and high 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 (Mc Lusky & 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 which can modify their ecological status. Recent works underline the similarity between the features of organisms and assemblages in estuaries and 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).

Because of these particularities, monitoring and assessing the biodiversity and ecological status of marine ecosystems require 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, Pasquaud et al. 2008).

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Topological approaches in trophic models are used to better understand estuarine ecological structure and functioning (e.g. 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 available trophic resources to successfully cope with stressful conditions This suggests that (1) a temporal adaptation of the trophic web would be observed, (2) most estuarine species would be opportunists. This paper constitutes a preliminary investigation to test both these assumptions by analysing the food preferences and the 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 (Lat. 45°20′N, Long. 0°45′W, Fig. 1) is located in South West France and opens onto the Bay of Biscay. Its surface area is approximately 625 km^2 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 km^2 and the mean annual rate of freshwater discharge is around 760 $m^3 s^{-1}$. These characteristics make it the biggest estuary in France and the largest in Western Europe (Salomon 2002). The tidal range is 4.5 m at the mouth of the estuary and over 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 $3x10^6$ 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 gC m^{-2} y^{-1}, Irigoien & Castel 1997) and the food web base consists, for the most part, of a varied nutritional pool containing a high proportion of detritus (Irigoien & 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 (Tank et al. 2002). During the sampling period (from July 2003 to June 2004) the water temperature oscillated between 9.78°C in February and 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-May (unpublished data). Because of these hydrological conditions, a very strong marine intrusion was observed during summer 2003, with maximum

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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 samplings

To analyze temporal feeding variability, fish were collected approximately every two months from 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 five 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 below 75 (trawling above coefficient 80 in this system is not reliable). Haul duration was limited to 15 minutes 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 smaller than 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 lab. 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 ichtyofauna 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 eight fish species caught in the sampling area were analyzed (Table 1). A minimum of five 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 size < 40mm; large size ≥ 40 mm) and *Argyrosomus regius* (two 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 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 ($\overline{W}$ 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 four 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 three sites, one close to each bank

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and one 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 two pushnets located on both sides of the boat (section 4 x 1 m, stretched mesh of 1mm in the cod-end) and the bottom sampled using a dragnet with a 2.0 x 1.2 m frame, kept at 0.2 m above the bed by runners. The net meshes are identical to those used for surface samplings. Sampling was carried out in daytime, between the halfway stage of the flood tide and high tide slack. Each tow lasted about 7 minutes. All the samples collected were preserved in 10% formaldehyde, before being identified and counted at the laboratory.

Zooplankton was collected along the study area every 3 units of salinity using a standard 200 µm WP-2net 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 m^3 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

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

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 as 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 the 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 *E. encrasicolus*, stomach content 1: $\mathrm{N}_{Arcartia}$ = rank1; stomach content 9: $\mathrm{N}_{M.slabberi}$ = rank1, $\mathrm{N}_{\mathrm{cirripeds}}$ = rank2, $\mathrm{N}_{Arcartia}$ = rank3), and (2) ranking these same prey according to their abundance (Ab-ranks) and their mean weight ($\overline{W}$-ranks) in the environment (e.g. in July, $\mathrm{Ab}_{Arcartia}$ = rank1, $\mathrm{Ab}_{M.slabberi}$ = rank2, $\mathrm{Ab}_{\mathrm{cirripeds}}$ = rank3). As only prey that appeared in the stomachs contents are considered, predator feeding strategy is assessed within the context of its trophic niche. Moreover, the non-sampled prey in this 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 X Ab*i*-ranks and N*i*-ranks X IB*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 $\overline{W}$) the predation was considered to be selective according to prey abundance (Ab) or mean weight ($\overline{W}$); otherwise the predation was unselective with regard to the prey characteristic considered (Ab or $\overline{W}$).

Three different types of predation strategy were determined: (1) generalist, when the Spearman correlation coefficient was not significant for either abundances or mean weights,

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(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; Tables 2 & 3). 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 *Pomatoschistus microps* also consumed a high quantity of mesozooplankton, but their diet varied from that of *S. sprattus* and *E. encrasicolus* due to a high consumption of hyperbenthos, essentially mysid *Mesopodopsis slabberi* and amphipods *Gammarus* spp (no overlap; SI < 0.6). The two 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 *N. integer*).

Finally, the feeding of marine demersal fish (e.g. *Dicentrarchus labrax, Dicentrarchus punctatus*, *Argyrosomus regius* and *Merlangius merlangus*) was mainly characterized by

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hyperbenthic prey such as the mysids *M. slabberi* and *Neomysis integer*, the amphipods *Gammarus* spp. and the shrimps *Palaemon* spp.

The two species of *Dicentrarchus* did not have a trophic niche overlap and presented different predation strategies, specialist for *D. labrax*, opportunistic for *D. punctatus*. In contrast to *Dicentrarchus* spp., the trophic niches of *A. regius* and *M. merlangus* did sometimes overlap, either together or with *P. minutus*. *M. merlangus* is a specialist predator, whereas *A. regius* was able to feed on either a wide range of prey (generalist) or a narrow range of prey (specialist).

Temporal feeding variability

Except for *P. microps*, all fish species showed a significant temporal feeding variability (p-values of the permutation tests < 0.05):

- *E. encrasicolus* consumed a large quantity of mollusk eggs (40%) and nauplius larvae (44%) in July, whereas it ate mostly the copepods *Acartia* (94%) in September and *E. affinis* (88%) in November. Its feeding strategy was opportunistic whatever the season.
- *P. microps* based its feeding essentially on eggs (indeterminate and mollusk eggs, respectively 40 and 24 %) in July and on *E. affinis* in November (55%), February (94%) and April (62%). However, this species showed no significant temporal feeding variability (p-value = 0.301). It was a specialist, focusing on prey from a specific weight (size) range whatever the considered month.
- The feeding of *P. minutus* consisted of mollusk eggs (39%) and the mysid *M. slaberri* (22%) in July, almost exclusively *M. slabberi* (60% for small individuals and 79% for large individuals) in September, *M. slaberri* (37%) and *Gammarus* (21%) in November, mainly *E. affinis* (84% for the small individuals and 82% for the large individuals) in February, and finally *Gammarus* (82 or 64%) and *N. integer* (18 or 28%) in June. Both size classes of *P.*

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minutus had specialist strategy, except in November when the numerous prey in their stomach were the most abundant in the system (opportunism).

- Concerning the 2003 cohort of *A. regius*, the diet was dominated numerically by *M. slabberi* (78%) in July, by the shrimps *Palaemon* in September (54%) and November (64%) and by *N. integer* and *Gammarus* in April (respectively 44% and 28%) and June (31% and 59%). *A. regius* oscillated between a generalist and a specialist feeding strategy.
- *D. labrax* fed essentially on the Amphipods *Gammarus* (24%) and the shrimps *Palaemon* (32%) in February and on *Gammarus* (57%) and *N. integer* (14%) in April.
- The most abundant prey consumed by *M. merlangus* were *M. slabberi* (88%) in September and *Palaemon* (50%) in November. *D. labrax* and *M. merlangus* always showed a specialist feeding strategy.

Intraspecific feeding variability

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

DISCUSSION

Sample representativeness

This study is 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, Mc Lusky & Elliott 2004), hyperbenthic invertebrate samples are 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 (Lobry et al. 2006, David 2006) were similar to those observed in other Gironde estuary studies (e.g. Castel 1981, Sorbe 1981, Mees et al. 1995): the copepods consisted predominantly of *E. affinis* in the spring and *Acartia* spp. in summer; the suprabenthos consisted of *N. integer* in the spring and *M. slaberri* and *Gammarus* spp. in summer, which was similar to other European estuaries (Mees et al. 1993, Soetaert & van Rijswik 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, few specimens were collected and/or had a non-empty stomach content, e.g. *Sprattus sprattus*, *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 this study:

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- 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 samplings, 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 ecological and feeding similarities, e.g. *S. sprattus* and *Engraulis encrasicolus, D. punctatus* and *Dicentrarchus 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 understand species feeding requirements and strategies.

Investigation of the diet compositions of the eight main pelagic and demersal fish species during the study period in the Gironde estuary enables us to show an interspecific feeding variability. Despite the differences in taxa, geographical distribution and environmental conditions, similar feeding requirements have been observed in other estuarine or marine systems: small pelagic fish, *S. sprattus* and *E. encrasicolus*, are zooplanktivores (e.g. Plounevez & Champalbert 1999, Maes & Ollevier 2002), demersal fish, represented by *Argyrosomus regius*, *D. labrax*, *D. punctatus* and *Merlangius merlangus*, consume hyperbenthos (Moore & Moore 1976, Ktari et al. 1978, Cabral & Ohmert 2001, Laffaille et al.

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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. ecotrophomorphology or ecomophology (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 intake (e.g. Schafer et al. 2002).

This study highlights the fact that species which have ecological and trophic similarities (e.g. *S. sprattus* and *E. encrasicolus* or *D. 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 there is no feeding niche overlap. These cases occur when the species considered do not belong to the same size class, e.g. *P. minutus* and *P. microps* in November and February, *A. regius* and *M. merlangus* in September. Salgado et al. (2004) have already highlighted a decrease in feeding overlap between these two *Pomatoschistus* species due to an increased difference in length.
- or there is a feeding overlap when the resource is not limited, e.g. *P. minutus* and *P. microps* in February, *A. regius* and *M. 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 *P. minutus* and *A. 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 two size classes of *P. minutus* (small size < 40mm; large size ≥ 40 mm). For this species, a dietary shift has already been highlighted for individuals with a total length greater than 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 (≥ 50 mm) has not been differentiated in this study because of the small number of specimens. A variation in feeding according to fish length was observed for *A. regius* but also for *M. 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 *S. sprattus* (Arrhenius 1996, Casini et al. 2004), *E. encrasicolus* (Conway et al. 1998) and *D. labrax* (Kennedy & Fitzmaurice 1972, Labourg & Stequert 1973). Diet variations according to fish size have already been explained by the evolution 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 *A. regius* (generalist/specialist) and *P. minutus* (specialist/opportunist). Marshall & Elliott (1996), who

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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, David et al. 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 the trophic resources according to time. As a result, most species were identified as specialist, whatever the month being considered. This study therefore invalidates the common hypothesis that estuarine fish are generally opportunists (e.g. Moore & Moore 1976, Cabral & Ohmert 2001, Laffaille et al. 2001, Baldó & Drake 2002, Elliott & Hemingway 2002). Only a minority of the pelagic and demersal fish community in the Gironde estuary - characterized by the marine juveniles *E. encrasicolus* and *D. punctatus* and by resident species *P. minutus* - were found to feed on the predominant abundant prey which differed from month to month.

This difference in conclusions, specialist vs opportunist, can be explained by the precision of the method used for this 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.

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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 *P. microps* and *P. minutus*, always described as opportunistic fish in the literature (e.g. Pilh 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.

This study highlights the specialist feeding strategy of the *S. sprattus*, *M. merlangus* and *D. 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 three 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 *E. 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 two 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 the prey abundances, shrimps are probably not limited in winter. The absence of *M. merlangus* and *A. regius* - also specialist but trending towards generalist - in February could be correlated with the environmental conditions, especially low salinities and low water temperatures (Quéro & Vayne 1987, Pasquaud 2006). These

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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 physiological 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.

This 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.

This 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 evolution of these systems.

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Captions

Fig. 1. Location of sampling stations – stars: fish, circles: shrimps (lines represent the four transects) - in the Gironde estuary.

Fig. 2. Examples of the cumulated frequencies of the relative abundance (N) ranks (Y axis) *versus* prey abundances (Ab) or mean weights ($\overline{W}$) in the environment for each predation strategy: *Argyrosomus regius* in July 2003 for generalist species (i.e. Spearman correlation coefficients were not significant for Ab and $\overline{W}$), *Engraulis encrasicolus* in September 2003 for opportunistic species (i.e. frequencies significantly increased with Ab), *Pomatoschistus minutus* in July 2003 for specialist species (i.e. the highest frequencies were concentrated around a narrow $\overline{W}$ value). Prey abbreviations: cir: cirriped larvae, mol: mollusc larvae, pol: polychaete larvae, Ac: *Acartia* spp., Eaff: *Eurytemora affinis*, mysis: mysis larvae, Nint: *Neomysis integer*, Msla: *Mesopodopsis slabberi*, mysid: other mysids, crev: shrimps, amp: amphipods essentially *Gammarus* spp., isop: isopods. Rg1, Rg2, Rg3 are the first, second and third N-ranks; n is the number of stomach contents used to calculate frequencies. Significant positive correlations between N-rank frequencies and an increase/decrease in the prey characteristic frequencies are shown on the right. Spearman rank correlation was applied to each of the cumulative series of the positive %N ranks, from the first and total N-rank; (** significant trend).

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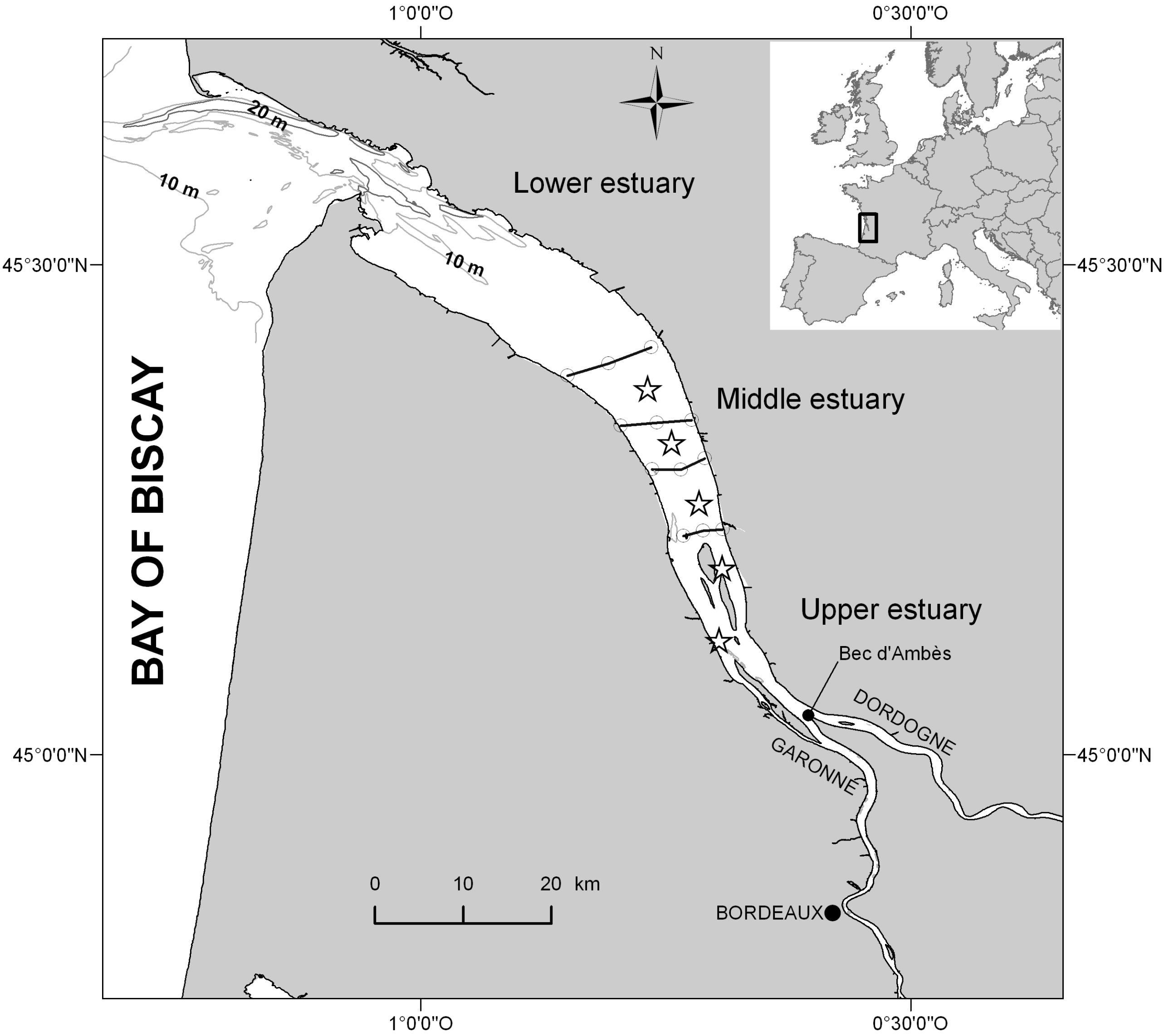

Fig. 1

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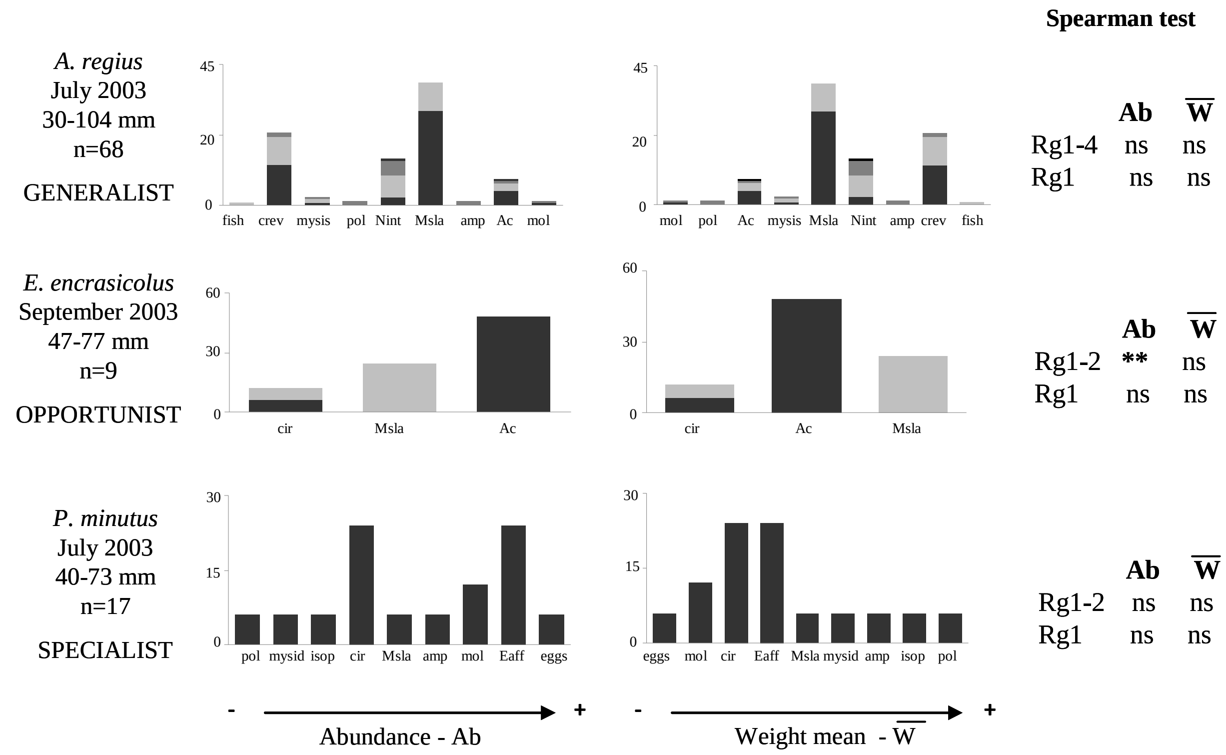

Fig. 2

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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. 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.

			July-03	**Sept-03**	**Nov-03**	**Feb-04**	**April-04**	**June-04**
Fish	**EG**	**TG**						
N			**5**	**5**	**5**	**5**	**5**	**5**
Sprattus sprattus	MS	P		5				
Engraulis encrasicolus	MS	P	27	9	6			
Pomatoschistus microps	ER	IS	20		10	11	15	
Pomatoschistus minutus (S)	ER	IS		15		21		15
Pomatoschistus minutus (L)	ER	IS	30	25	20	6		20
Dicentrarchus labrax	MJ	IF	6	5	9	26	11	
Dicentrarchus punctatus	MJ	IF					5	
Argyrosomus regius (S)	MS	IF	68					15
Argyrosomus regius (L)	MS	IF		29	36		20	40
Merlangius merlangus	MS	IF		5	8			
Shrimp								
N			**12**	**12**	**12**	**12**	**12**	**12**
Zooplankton								
N			**23**	**22**	**16**	**12**	**16**	**16**

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Table 2. Relative abundance diet composition (%N) of the main pelagic and demersal fish according to size and time in the upstream area of the saline Gironde estuary.

	July 2003				September 2003					
	Engraulis encrasicolus	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Argyrosomus regius*	*Engraulis encrasicolus*	*Sprattus sprattus*	*Pomatoschistus minutus*	*Pomatoschistus minutus*	*Argyrosomus regius*	*Merlangius merlangus*
Size range (TL ; mm)	38-127	27-37	40-73	30-104	45-77	60-115	23-39	40-65	130-235	90-102
Number of full stomach	18	15	17	68	9	5	8	20	29	5
Zooplankton										
Eggs		40								
Nauplius larvae	44.4		2.8		2.4	54.4				
Mysis larvae				1.7						
Mollusc eggs	39.6	24.4	38.9	0.3						
Mollusc larvae	1.5									
Polychaete larvae				0.2						
Cirriped larvae	8.3	11.1	2. 8			0.3				
Copepods										
E. affinis		13.3				3.9	10	3.4		
Acartia spp.	4.4			4.7	94	41.7	10			5.9
Copepods ind.								3.4		
Hyperbenthos										
Mysidacea										
Neomysis integer	1.5		11.1	4.3				10.3		
Mesopodopsis slabberi	0.8	2.2	22.2	78.5	3.6		60	79.3	22.2	88.2
Mysids ind.		2.2	8.3				10			
Isopoda										
Synidotea laticauda		2.2					10		6.4	
Isopods ind.			2.8							
Amphipoda										
Gammarus spp.		2.2	5.6	0.2				3.4		
Decapoda natantia										
Palaemon spp.				0.3					54.1	
Crangon crangon			2.8	9.5					9.2	
Nekton										
Teleost fishes				0.2					8.3	5.9
Benthos										
Annelida polychaeta										
Nereis succinea		2.2	2.8							
Other										
Pollen		0.1								

Table 2 (*continued*)

	November 2003					February 2004			
	Engraulis encrasicolus	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Argyrosomus regius*	*Merlangius merlangus*	*Pomatoschistus microps*	*Pomatoschistus minutus*	*Pomatoschistus minutus*	*Dicentrarchus labrax*
Size range (TL ; mm)	42-62	27-38	41-65	130-249	114-150	26-50	26-38	41-60	80-447
Number of full stomach	6	9	11	36	6	11	21	5	21
Zooplankton									
Eggs		38.5				4.2	1.4	15.4	
Copepods									
Eurytemora affinis	88.3	55.1				94	84.2	82.3	7.4
Acartia	7.4								
Copepods ind.		1. 3					13.7		
Hyperbenthos									
Mysidacea									
Neomysis integer			5.3	5.4					
Mesopodopsis slabberi	3.2		36.8	10	10	0.6	0.2		
Schystomysis spp.				1					
Mysids ind.	1.7	1.3	15.8	2.7					0.8
Isopoda									
Synidotea laticauda			15.8	3.6					
Amphipoda									
Gammarus spp.			21.5	1.8	10	1.2	0.4	2.3	24.4
Amphipods ind.									2.16
Decapoda natantia									
Palaemon spp.				64.5	50				31.6
Crangon crangon				10	18.2				6.1
Nekton									
Teleost fishes			5.3	1	10				
Epibenthos									
Isopoda									
Cyathura carinata		1.3							
Sphaeroma serratum									3.5
Amphipoda									
Corophium volutator		2.6							19.8
Decapoda brachyura									
Pachygrapsus marmoratus									1.5
Rhithropanopeus harrisii									0.8
Crabs ind.									0.8
Annelida polychaeta									
Nereis spp.									0.8
Polychaetes ind.					4.5				

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Table 2 (*continued*)

	April 2004				June 2004			
	Pomatoschistus microps	*Dicentrarchus labrax*	*Dicentrarchus punctatus*	*Argyrosomus regius*	*Pomatoschistus minutus*	*Pomatoschistus minutus*	*Argyrosomus regius*	*Argyrosomus regius*
Size range (TL ; mm)	33-39	83-140	92-135	125-260	21-39	40-55	30-52	118-263
Number of full stomach	11	8	5	20	11	19	14	38
Zooplankton								
Eggs								0.8
Mysis larvae							2.7	0. 7
Copepods								
Eurytemora affinis	62.2						18.9	
Acartia spp.	8.2							
Copepods ind.		7.1						
Ichtyoplankton							20.3	
Hyperbenthos								
Mysidacea								
Neomysis integer	5.4	14.3	17.6	44.1	17.6	28	36.5	31.4
Mesopodopsis slabberi			69.4	4.1			8. 2	0.3
Mysids ind.	5.4			1.4				0.13
Isopoda								
Synidotea laticauda		7.1	2.3	2.7				0.5
Sphaeroma serratum							4.5	
Amphipoda								
Gammarus spp.	18.9	57.1	8.2	27.6	82.3	64	9.5	59.2
Corophium volutator				3.4				
Bathyporeia spp.			1.2					
Amphipods ind.						8		
Decapoda natantia								
Palaemon spp.				6.9				0.5
Crangon crangon		7.1		10.3				5,1
Nekton								
Teleost fishes		7.1						1.6
Benthos								
Annelida polychaeta								
Nereis succinea			1.2					0.4

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Table 3. 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 ($\overline{W}$). 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 $\overline{W}$ (cf. Fig. 2). See Fig. 2 for the definition of prey abbreviations. ns: non-significant trend; * significant trend.

	July 2003	September 2003	November 2003	February 2004	April 2004	June 2004
Environment						
Available prey	10	11	5	5	9	10
Prey densities	7.8 ind L^{-1}	3.1 ind L^{-1}	5.0 ind L^{-1}	10.7 ind L^{-1}	18.6 ind L^{-1}	13.1 ind L^{-1}
E. encrasicolus						
Size (mm, replicates)	38-127 (18)	47-77 (9)	47-62 (6)			
Prey number (range)	6 (naup-*Nint*)	4 (naup-Msla)	4 (Ac-mysid)			
Spearman test	*	*	*			
Predation strategy	**OPPORTUNIST**	**OPPORTUNIST**	**OPPORTUNIST**			
S. sprattus						
Size (mm, replicates)		60-115 (5)				
Prey number		4 (naup-Eaf)				
Spearman test		ns				
Predation strategy		**SPECIALIST**				
P. microps						
Size (mm, replicates)	27-37 (15)		27-38 (9)	26-50 (11)	33-39 (11)	
Prey number	9 (eggs-pol)		6 (eggs-isop)	4 (eggs-amp)	5 (Ac-amp)	
Spearman test	ns		ns	ns	ns	
Predation strategy	**SPECIALIST**		**SPECIALIST**	**SPECIALIST**	**SPECIALIST**	
P. minutus						
•Small size		23-39 (8)		26-38 (21)		21-39 (11)
Prey number		5 (Ac-isop)		5 (eggs-amp)		2 (Nint-amp)
Spearman test		ns		ns		ns
Predation strategy		**SPECIALIST**		**SPECIALIST**		**SPECIALIST**
•Large size	40-73 (17)	40-65 (20)	41-65 (11)	41-60 (5)		40-55 (19)
Prey number	9 (mol-shr)	5 (cops-amp)	5 (Msla-fish)	3 (eggs-amp)		3 (Nint-amp)
Spearman test	ns	ns	*	ns		*
Predation strategy	**SPECIALIST**	**SPECIALIST**	**OPPORTUNIST**	**SPECIALIST**		**OPPORTUNIST**
A. regius						
•Small size	30-104 (68)					30-52 (14)
Prey number	9 (mol-fish)					7 (Eaff-fish)
Spearman test	ns					ns
Predation strategy	**GENERALIST**					**GENERALIST**
•Large size		130-235 (25)	130-249 (36)		125-260 (20)	118-263 (38)
Prey number		4 (Msla-fish)	6 (Msla-fish)		6 (Msla-shr)	9 (eggs-fish)
Spearman test		ns	ns		ns	ns
Predation strategy		**SPECIALIST**	**SPECIALIST**		**GENERALIST**	**SPECIALIST**
M. merlangus						
Size (mm, replicates)		90-102 (5)	114-150 (6)			
Prey number		3 (Ac-fish)	5 (Msla-fish)			
Spearman test		ns	ns			
Predation strategy		**SPECIALIST**	**SPECIALIST**			
D. labrax						
Size (mm, replicates)				80-147 (21)	83-140 (8)	
Prey number				7 (Eaf-crab)	5 (cops-fish)	
Spearman test				ns	ns	
Predation strategy				**SPECIALIST**	**SPECIALIST**	
D. punctatus						
Size (mm, replicates)					95-135 (8)	
Prey number					5 (Msla-pol)	
Spearman test					*	
Predation strategy					**OPPORTUNIST**	