Determination of fish trophic levels in an estuarine system

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Abstract

The concept of trophic level is particularly relevant in order to improve knowledge of the structure and the functioning of an ecosystem. A precise estimation of fish trophic levels based on nitrogen isotopic signatures in environments as complex and fluctuant as estuaries requires a good description of the pelagic and benthic trophic chains and a knowledge of organic matter sources at the bottom. In this study these points are considered in the case of the Gironde estuary (south west France, Europe). To obtain a good picture of the food web, fish stomach content analyses and a bibliographic synthesis of the prey feeding ecology were carried out. Fish trophic levels were calculated from these results and $\delta^{15}\text{N}$ data. The feeding link investigation enabled us to identify qualitatively and quantitatively the different preys consumed by each fish group studied, to distinguish the prey feeding on benthos from those feeding on pelagos and to characterize the different nutritive pools at the base of the system. Among the species studied, only *Liza ramada* and the flatfish (*Platichthys flesus* and *Solea solea*) depend mainly on benthic trophic compartments. All the other fish groups depend on several trophic (benthic and/or pelagic) sources. These results enabled us to correct the calculation of fish trophic levels which are coherent with their feeding ecology data obtained from the nitrogen isotopic integrative period. The present work shows that trophic positions are linked with the feeding ecology of fish species and vary according to individual size. Ecological data also allow the correction of the isotopic data by eliminating absurd results and showing the complementarity of the two methods. This work is the first to consider source variability in the fish food web. This is an indispensable step for trophic studies in a dynamic environment. The investigation of matter fluxes and recycling processes at the food web base would provide an useful improvement in future estuarine food web research.

39 *Keywords:* stomach contents; $\delta^{15}\text{N}$; predator-prey relationships; organic matter sources; fish

40 trophic levels; estuarine ecosystem

41 *Regional index terms:* Europe; France; Gironde estuary; Lat. 45°20'N; Long. 0°45'W

1. Introduction

In recent years, there has been increased interest in use of carbon and nitrogen stable isotopes to characterize the trophic web structure and the energy flows of aquatic ecosystems (e.g. Kwak and Zedler, 1997). For a living being, the carbon isotope ratio $^{13}\text{C}/^{12}\text{C}$ provides an estimate of the origin of the assimilated organic matter (De Niro and Epstein, 1978; Fry and Sherr, 1984; Post, 2002) and the nitrogen carbon ratio $^{15}\text{N}/^{14}\text{N}$ gives its trophic level (De Niro and Epstein, 1981; Minagawa and Wada, 1984; Hesslein et al., 1991; Wada et al., 1991).

For fish, stable isotope analysis represents a complementary approach to traditional feeding studies: stomach contents reflect the qualitative and quantitative ingestion of species at a given time whereas stable isotope analyses represent an integrative record of the food that has really been assimilated by the fish during a period prior to the sampling (e.g. Persson and Hansson, 1999; Davenport and Bax, 2002; West et al., 2003; Winemiller et al., 2007). The isotopic integrative time varies from days to years according to the ecosystem, the species, their growth rate and the tissue considered (Tieszen et al., 1983; Hesslein et al., 1993; Guelinckx et al., 2007; Church et al., 2009; Suring and Wing, 2009). For example, Perga & Gerdeaux (2003) have estimated that the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of muscle tissue only reflected the food consumed during the spring and summer growth period.

The combined use of these two methods can provide a detailed picture of the structure of an estuarine fish food web by i) describing trophic relationships between different biological compartments (stomach contents analyses) and ii) estimating the trophic position of species one alongside the other (nitrogen stable isotope analyses) (e.g. West et al., 2003; Akin and Winemiller, 2008).

In the Gironde estuary, $\delta^{15}\text{N}$ seemed to be a good marker to improve knowledge of the food web structure, even if anomalies in fish trophic positions have been identified (Pasquaud

et al., 2008). For example, *Platichthys flesus*, a predator of small benthic crustaceans has a higher average $\delta^{15}\text{N}$ level than *Argyrosomus regius* which tends to be ichthyophagous. These observations can be explained by an enrichment of the $\delta^{15}\text{N}$ signatures in benthic species compared to pelagic species for an equivalent trophic position (e.g. Sherwood and Rose, 2005). Moreover, a precise estimation of the fish trophic positions requires knowledge of sources at the bottom of the food chains (Vander Zanden et al., 1997; Vander Zanden and Rasmussen, 1999; Sherwood and Rose, 2005; Pasquaud et al., 2008).

The aim of the present study was to characterize fish trophic levels precisely according to their size class from $\delta^{15}\text{N}$ values, taking account of variability. Hence, the objectives were (1) to determine the food chains during the nitrogen isotopic integrative period in the Gironde estuary from fish stomach content analyses and from literature data for the prey; (2) to attribute to each fish species (or size class) studied a baseline $\delta^{15}\text{N}$ value taking into account the proportion of benthic/pelagic prey in their feeding and the $\delta^{15}\text{N}$ signatures of the nutritive pool identified, and (3) use this information to calculate fish/size class trophic levels.

2. Materials and methods

2.1. Study area

The Gironde estuary is located in South West France (45°20'N, 0°45'W; Fig. 1). It is 12 km wide at the mouth and 76 km long between the ocean and the Bec d'Ambès, where the Garonne and Dordogne rivers meet and which also constitutes the upstream salinity limit. The watershed of this system represents an area of 81 000 km². The hydrodynamic conditions are highly variable due to the interactions of marine and fluvial flows, leading to temperature and salinity gradients. There are also considerable seasonal variations. During the period under

consideration (April to September 2004), discharge values varied widely with a flood event in spring (up to 3,600 m.s⁻³ in May) and an important drought period in summer (about 250 m.s⁻³ from July to September; unpublished data). In consequence, salinity values varied and were especially low in June 2004. Temperatures stayed relatively high in summer, fluctuating between 13.1 and 24.7°C. The dynamic conditions involved high turbidity values reaching 500 mg.L⁻¹ (Sottolichio and Castaing, 1999; David et al., 2007) and a restricted light penetration. In consequence, primary production was reduced and the food web seems based on the detritus pool (Lobry et al., 2008). In spite of these constraining conditions, the Gironde estuary shows a high biodiversity and seems to be a particularly well-preserved ecosystem.

2.2. Sampling surveys

Fish were sampled approximately bimonthly from April 2004 to September 2004, across ten stations located in the upstream area of the saline Gironde estuary (Fig. 1). An otter trawl (4 m opening and a cod-end with a mesh size of 8 mm) was used. Fish sampling was carried out during daylight hours at high tide and was restricted to 15-minute episodes in order to limit regurgitation or abnormal feeding. All the sampled fish were identified, counted, weighed, measured and finally frozen until laboratory analysis could be carried out. Some of the most abundant fish species or genus, separated in some cases into size classes, are presented here (Table 1). Only cohorts spending the totality of their spring and summer growth period (i.e. period considered in that study, see paragraph 2.3.) inside the system were selected.

2.3. Fish stomach content analyses

The fish stomach contents were analyzed in order to describe their trophic relationships during the nitrogen isotopic integrative time in the Gironde estuary (Table 1). Crossing literature information (Tieszen et al., 1983; Perga and Gerdeaux, 2005; Miller, 2006; Guelinckx et al., 2007), we have estimated that the $\delta^{15}\text{N}$ of the muscle tissue (used in these isotopic analyses, see Pasquaud et al., 2008 for more details) reflected the food consumed during the warm growth period, i.e. from April to September. It is important to note that we only selected specimens belonging to the same cohorts during the period considered, i.e. we took account for the individual growth along the integrative time.

The different items were examined under binocular microscope and identified to the highest possible taxonomic separation. The volume of each prey was estimated using the point method described by Pillay (1952) and Hyslop (1980).

For *Liza ramada*, only the stomach contents collected in September 2004 were analyzed. Even if these data do not provide this species food variability over the isotopic integrative period, they were nevertheless considered to give data elements on its feeding ecology and thus to estimate the origin of the organic matter at the base of its trophic chain in the Gironde estuary.

Due to this species' specific diet, a particular methodology was used, adapted from Almeida et al. (1993) and Laffaille et al. (2002): a 200 mg sample was removed from the stomach and suspended in 5 ml of formaldehyde (5%). First, the samples were analyzed under binocular microscope to identify zooplanktonic organisms. Next, a known volume (0.03 ml) was pipetted onto a slide for microscopic observation ($\times 500$). Items were identified using diatoms and phytoplankton determination keys (Cupp, 1943; Prygiel and Coste, 2000). Diatom volumes were estimated from literature data (Padisak and Adrian, 1999) and zooplankton volumes were calculated from their length. The volumetric percentage was then estimated for each item identified.

2.4. Prey feeding ecology

A bibliographic review was carried out to identify general feeding ecology of benthic prey (molluscs, annelid polychaetes and crabs), hyperbenthic prey (amphipods, isopods and shrimps) and pelagic prey (mysids, copepods and diverse metazooplankton) in order to characterize the main source of organic matter on which they eat in the Gironde estuary. The fish feeding ecology was estimated from the stomach content analysis results obtained in the present study and a published work (Pasquaud et al., 2008).

2.5. Available data

The $\delta^{15}\text{N}$ signatures of fish species (or size classes) measured by Pasquaud et al. (2008) and of their prey (unpublished data) were used in this study (Table 1).

Since the benthic trophic chain is generally richer in $\delta^{15}\text{N}$ than the pelagic trophic chain (Sherwood and Rose, 2005), a distinction was made between isotopic values from the benthic organic matter and the pelagic matter. Due to sampling constraints, our isotope data set did not include sufficient $\delta^{15}\text{N}$ values to characterize suspended matter, i.e. pelagic source. Consequently, averaged $\delta^{15}\text{N}$ signatures of two primary consumers characterizing two different pelagic nutritive pools during the considered period were chosen, one detritivorous *Eurytemora affinis* and the other phytoplanktivorous *Acartia* spp. The averaged $\delta^{15}\text{N}$ signature of a benthic primary consumer, *Cerastoderma edule*, was used to characterize the benthic baseline.

2.6. Fish trophic level

Fish trophic level (TL) was estimated as: $TL = [(\delta^{15}N_{pred} - \delta^{15}N_{base}) / \Delta\delta^{15}N] + TL_{base}$,

where $\delta^{15}N_{pred}$ is the $\delta^{15}N$ signature of the predator in question, $\delta^{15}N_{base}$ is the $\delta^{15}N$ signature of a representative baseline for the predator and TL_{base} is the trophic level of that baseline.

Primary consumers (*Eurytemora affinis*, *Acartia* spp. and *Cerastoderma edule*) were used for that baseline. So, TL_{base} is equal to 2. $\Delta\delta^{15}N$ represents the trophic fractionation of $\delta^{15}N$, estimated at 3.4‰ (Post, 2002).

The fish preys feed on benthic and/or pelagic food chains (phytoplanktonic and/or detritic) and/or intermediate food chains (mixing of the two pelagic sources), determined from their feeding ecology. The fish species or size class studied present different diets. Thus from the knowledge of the food chains, we estimated for each fish predator group the $\delta^{15}N_{base}$, calculated as: $\delta^{15}N_{base} = (\%V_B \times \delta^{15}N_B + \%V_H \times \delta^{15}N_H + \%V_D \times \delta^{15}N_D + \%V_I \times \delta^{15}N_I) / 100$, where %V is the volumetric percentage of the prey B, H, D or I in the stomachs of a predator; B groups together all the prey feeding almost exclusively on the benthic food chain, H the prey feeding almost exclusively on the phytoplanktonic food chain, D the prey feeding almost exclusively on the detritic (pelagic) food chain, and I the prey feeding both on detritic and phytoplanktonic food chains.

3. Results

3.1. Fish trophic ecology

The diet of each fish species was identified during their growth period (warm period) from stomach content analyses and expressed as a volumetric percentage (%V; Table 2).

A large proportion of *Liza ramada* stomach contents was composed of organic debris (%V = 86.53%). The rest was predominantly micro-algae in volume (essentially diatoms).

The flatfish, *Solea solea* and *Platichthys flesus*, fed on the benthic and suprabenthic compartments. The diet of *P. flesus* consisted mainly of the bivalve *Cerastoderma edule* (72.62%) and the isopod *Synidotea laticauda* (11.68%). *S. solea* fed more on the polychaetes *Neanthes succinea* (13.69%) and *Pectinaria koreni* (12.02%), the amphipods *Gammarus* spp. (19.46%) and the shrimp *Crangon crangon* (10.35%). Some vegetal debris (11.59%) was found in its diet.

Pomatoschistus spp. fed mainly on the suprabenthic compartment. The majority of their stomach contents consisted of *Gammarus* spp. (66.67%) and the mysid *Neomysis integer* (26.19%).

All other species (*Dicentrarchus labrax*, *Argyrosomus regius*, *Anguilla anguilla* and *Dicentrarchus punctatus*) had a more diversified diet, feeding from the supra-, epibenthic and pelagic compartments on organisms such as amphipods, isopods, shrimps and copepods. They also are ichthyophagous. Large and small *A. regius* fed especially on *Gammarus* spp. (respectively 14.92 and 11.87%), *C. crangon* (35.76 and 17.96%) and *N. integer* (12.15 and 17.16%). Moreover, small *A. regius* consumed the mysids *M. slabberi* (23.52%) and fish larvae (20.78%), whereas large *A. regius* fed on the shrimp *Palaemon* spp. (13.02%). *S. laticauda* was the preferential prey for large *D. labrax* (11.90%), *A. anguilla* (25.59%) and *D. punctatus* (44.30%). The other preferential prey of *D. punctatus* was *M. slabberi* (18.37%). The diet of *A. anguilla* was also composed of *Gammarus* spp. (33.71%) and *Palaemon* spp. (12.75%). Large *D. labrax* had the most diversified diet, eating many preys such as *Gammarus* spp. (38.89%), *C. crangon* (11.72%), *N. integer* (12.89%), copepods (12.50%) and fish (12.10%). Finally, small *D. labrax* did not have the same diet as large individuals.

Their stomach contents were composed of a large proportion of *C. crangon* (25%), *Palaemon* spp. (28.30%), *Acartia* spp. (16.67%) and fish (16.67%).

Results represented ingested biomasses and from these the most important prey was determined (% V>10%; Table 2; Fig. 2).

3.2. Prey trophic ecology

A bibliographic review provides information on prey trophic ecology in the Gironde estuary or in similar estuarine systems (Table 3).

Organisms living on or in the sediment have diverse types of food habits: bivalves are suspension feeders (*C. edule*), deposit feeders (*Macoma balthica*) or grazers (*Littorina saxatilis*); polychaeta are carnivorous (*Nephtys* spp. or *Neanthes* spp.) or deposit feeders (*Polydora* spp., *Notomastus latericeus*, *Heteromastus filiformis*, *Pectinaria koreni*) and crabs are carnivorous. Some isopods (*Sphaeroma serratum* and *Cyathura carinata*), amphipods (*Bathyporeia* spp and *Corophium volutator*), shrimps (*C. crangon*) and copepods (*Acanthocyclops trajani*) also live on the sediment. However, all these species also use the sediment as a source of organic matter. In the pelagic compartment, organisms feed on phytoplankton, detritus or both. A few organisms, such as *M. slabberi*, *Schistomysis* spp., *Gastrosaccus* spp. and *Acartia* spp., are exclusively herbivorous and depend on phytoplankton as a source of organic matter. Others, such as *Eurytemora affinis*, depend exclusively on detritus at the food web baseline. Most of the pelagic organisms consume both phytoplankton and detritus (e.g. *Euterpina acutifrons*, the crustacean larvae).

From this trophic knowledge, the base of the fish food chains could be characterized (sources of organic matter; Fig. 2; Table 4).

3.3. Fish trophic levels

The characterization of fish and prey diets gives a good picture of the Gironde food web (Fig. 2). It highlights the fact that the fish species studied use diverse sources of organic matter by eating prey with different food habits. Moreover, from the feeding ecology information of preys and their $\delta^{15}\text{N}$ values, we observed an enrichment of the $\delta^{15}\text{N}$ signatures for the benthic species compared to the pelagic ones for an equivalent trophic position. In addition, an organism feeding on a detritic pelagic source got a higher $\delta^{15}\text{N}$ signatures compared to the ones using a phytoplanktonic source.

To identify a $\delta^{15}\text{N}_{\text{base}}$ for each fish group (genus, species or size class), the relative proportion of each category of prey (B, H, D, I; cf. definitions part 2.6) in the diet was estimated (Table 4). All the fish fed on both pelagic and benthic food chains, but in different proportions. For example, *Pomatoschistus* spp. ate only 3.57% of benthic prey whereas small *D. labrax* ate 37.53%. *P. flesus*, *S. solea* and *L. ramada* ate mostly from the benthic compartment, with 79.96, 59.41 and 94.68% of their diet respectively depending on this food chain.

The $\delta^{15}\text{N}$ value of *C. edule*, used to characterize the benthic organic matter, is $7.97 \pm 0.39\text{‰}$ and for *E. affinis* (pelagic/detritic food chain) and *Acartia* spp. (pelagic/phytoplanktonic food chain) the values are $7.13 \pm 2.67\text{‰}$ and $6.12 \pm 1.51 \text{‰}$ respectively. We assume that these three representative baseline organisms are primary consumers and have a position of 2. Fish $\delta^{15}\text{N}$ signatures have higher values, varying between $10.70 \pm 0.50\text{‰}$ for *Pomatoschistus* spp. and $13.60 \pm 0.12\text{‰}$ for large *D. labrax*.

The $\delta^{15}\text{N}_{\text{base}}$ signature for each fish species (or size class) were estimated and from this their trophic levels were calculated (TL; Table 4). Large predators, such as large *D. labrax* and *A. anguilla*, were positioned at the higher TL (respectively 3.98 and 3.89), followed by *D.*

punctatus and large *A. regius* (3.58). *L. ramada* (2.87), and *Pomatoschistus* spp. (3.14) were found at the lower TL. Small *A. regius* and *D. labrax* and benthic fish *S. solea* and *P. flesus* were at the intermediate position, at TL = 3.15, TL = 3.43; TL = 3.30 and TL = 3.36 respectively.

4. Discussion

4.1. Trophic web of the Gironde estuary

A precise estimation of fish trophic levels based on $\delta^{15}\text{N}$ values requires a good knowledge of the trophic web in order to characterize the different nutritive pools at the base of the system and to describe food linkages allow us to distinguish pelagic food chains from benthic ones (Vander Zanden and Rasmussen, 1999; Mc Cuthan et al., 2003).

In environment as complex and fluctuant as estuaries, it appears necessary to consider the temporal feeding ecology of the nitrogen isotopic integrative period. Crossing bibliographic data, this time was estimated for fish to their warm growth period. Nevertheless, this time is species and life-stage specific (e.g. Miller, 2006; Guelinckx et al., 2007). It will be interesting to complete this study by an experimental approach to define precisely the different turnover times.

Fish stomach content analyses were carried out the warm period and enabled us to identify qualitatively and quantitatively the different preys consumed by each fish group studied. For both small and large groups of *D. labrax*, *D. punctatus* and *L. ramada*, the number of samples was reduced and/or limited to a restricted part of the period studied compared to other species, which led to less accurate results. Nevertheless, they were considered because they give information on these species diets in the Gironde estuary. In

addition, the trophic positions of these species obtained in that study are coherent with the description of their feeding ecology (Cf. following paragraph).

The general diet trends in their preys have been characterized from bibliographic data, mainly coming from Gironde estuary, to estimate the origin and the importance of each source for fish groups. Due to available isotopic data, one benthic baseline and two pelagic ones were distinguished. The knowledge of food chains and the $\delta^{15}\text{N}$ data of different compartments confirm the isotopic enrichment in benthic species compared to pelagic ones for an equivalent trophic position and also highlight an enrichment of the detritic pelagic chains compared to phytoplanktonic ones. Recycling processes of the detritic organic matter could explained these enrichments (Hughes et al., 2000; David et al., 2006).

Considering the pelagic chains, a prey may not have a clear detritic or phytoplanktonic origin, but rather have a mixed origin of both. For zooplanktonic species which feed on the two sources, an intermediate source has been attributed to them. It would be interesting to determine the relative importance of these sources for these species. Fatty acids would allow an identification of the different nutritive pools and produce a better estimate (David et al., 2006). However, the differentiation of the diverse pelagic sources described in the present work provides a realistic estimation of the fish trophic levels and of the importance of the phytoplanktonic source in the functioning of the system, which may be underestimated in previous studies.

During the warm period, the trophic organization of the Gironde appears to be based both on detritic and phytoplanktonic sources. Moreover, the pelagic organic matter sources seem to be more used than benthic ones. These observations on the functioning of the Gironde confirms the assumption put forward for this period of the year in a previous work using a mass-balanced trophic model (Lobry et al., 2008).

4.2. Validity of the fish trophic levels obtained

By describing the bottom of the food chains and their sources we were able to calculate the trophic levels of some main fish groups (species, genus or size class) in the Gironde estuary from $\delta^{15}\text{N}$ values. The data from fish stomach content analyses obtained in the nitrogen isotopic integrative period, or part of this period, led to a discussion about the validity of results.

In this study, *L. ramada* presents the lowest trophic level. Its feeding ecology differs from that of other species as it consumes a high level of primary producers (micro-algae) and detritus. Its grazing behaviour in brackish water, as previously described in other estuarine and coastal systems (Laffaille et al., 2002; Almeida, 2003), is confirmed here by its diet composed principally of benthic diatoms such as *Coscinodiscus*, *Melosira*, *Raphoneis*, *Girosigma* or *Navicula* (Almeida et al., 1993; Laffaille et al., 2002; Almeida, 2003).

Among the fish studied, *Pomatoschistus* spp. and the two flatfish *S. solea* and *P. flesus* have intermediate trophic levels. The genus *Pomatoschistus* is described in this study as a small crustacean feeder, which is in agreement with a previous work on the Gironde (Pasquaud et al., 2004) or other estuaries (e.g. Hamerlynck and Cattrijsse, 1994; Salgado et al., 2004; Leitão et al., 2006). *P. flesus* feeds especially on primary consumers, including a very large quantity of molluscs (*C. edule*) which were not found in their stomach contents the previous year (Pasquaud et al., 2008). Several studies (e.g. Summers, 1980; Hampel et al., 2005) indicate that the diet of *P. flesus* is very flexible, depending on benthic prey availability in the environment. However, some authors emphasize this fish species' strong preference for molluscs (Jones, 1962; Vinagre et al., 2008). *S. solea* tends to eat carnivorous prey such as polychaetes, *Gammarus* spp. and some decapods, as previously described in estuaries (Vinagre et al., 2005; Pasquaud et al., 2008). The diet of the two flatfish species is

distinguished from that of *Pomatoschistus* by fish consumption and this may explain their higher trophic levels. The lower trophic level of *S. solea* compared to *P. flesus* may be due to the fact that vegetal debris is found in its stomach contents.

A. anguilla, *D. punctatus*, *D. labrax* and *A. regius* have the highest trophic levels.

They could be considered as the top predators of this system because of their carnivorous feeding behaviour, feeding on a high diversity of crustaceans (amphipods, isopods, shrimps, mysids), and especially because of their piscivorous trend. The diets of these species show similarities with the results of the previous year in the Gironde estuary (Pasquaud et al., 2008) and with those observed in other estuarine systems (Costa, 1988; Cabral and Costa, 2001; Cabral and Ohmert, 2001). The quantitative differences could be explained by variations in prey availability in the environment.

This study also shows an increase in trophic levels in parallel with an increase in the size of individuals for the two species tested, *D. labrax* and *A. regius*. The same observation was made from the analysis of $\delta^{15}\text{N}$ values (Pasquaud et al., 2008). This result suggests that a species can play different functions in the ecosystem and emphasizes the importance of considering size criteria in studies of trophic dynamics (Garrison and Link, 2000).

Thus the trophic levels of fish groups, calculated from $\delta^{15}\text{N}$ values, are representative of their feeding ecology. This method allows us to correct the work of Pasquaud et al. (2008), and therefore redefine the trophic position of the benthic fish.

5. Conclusions

This study demonstrates the necessity of a good knowledge of estuarine trophic webs, i.e. qualitative and quantitative fish trophic relationships, benthic/pelagic food chains, sources of organic matter, in order to calculate fish trophic levels from $\delta^{15}\text{N}$ values and validate them.

Due to the considerable variability of these systems, it is essential to use complementarily stable isotope and stomach contents analyses during the whole integration period in fish. With this method, the variability of the feeding ecology during the considered period is taken into account and a possible inter-annual variability in the feeding ecology of some species (e.g. *P. flesus*) is palliated.

This approach developed to identify fish trophic levels in estuaries appears particularly appropriate, giving more accurate results than those produced by the Ecopath model developed in the Gironde estuary (see Lobry et al., 2008). This type of data could help to validate trophic models (Dame and Christian, 2008).

For future research, it would be interesting to estimate more precisely the different matter fluxes at the food web base and to study in details the recycling processes in order to see the relative importance of the sources in the system and thus obtain a better understanding of the functioning of estuarine fish food webs.

Acknowledgements

This investigation was supported by the French Institute of Agricultural and Environmental Engineering Research (Cemagref). The authors would like to thank Maria Cellamare (Cemagref-Bordeaux), Maud Cottet (Cemagref-Bordeaux), Michel Coste (Cemagref-Bordeaux), Nicolas Savoye (University of Bordeaux 1) and Pierre Richard (CNRS-CRELA, l'Houmeau).

References

- Akin, S., Winemiller, K.O., 2008. Body size and trophic position in a temperate estuarine food web. *Acta Oecologica-International Journal of Ecology* 33, 144-153.
- Almeida, P.R., 2003. Feeding ecology of *Liza ramada* (Risso, 1810) (Pisces, Mugilidae) in a south-western estuary of Portugal. *Estuarine, Coastal and Shelf Science* 57, 313-323.
- Almeida, P.R., Moreira, F., Costa, J.L., Assis, C.A., Costa, M.J., 1993. The feeding strategies of *Liza ramada* (Risso, 1826) in fresh and brackish water in the River Tagus, Portugal. *Journal of Fish Biology* 42, 95-107.
- Bachelet, G., 1981. Données préliminaires sur l'organisation trophique d'un peuplement benthique marin. *Vie et Milieux* 31, 205-213.
- Cabral, H., Costa, M.J., 2001. Abundance, feeding ecology and growth of 0-group sea bass, *Dicentrarchus labrax*, within the nursery areas of the Tagus estuary. *Journal of the Marine Biological Association of the United Kingdom* 81, 679-682.
- Cabral, H.N., Ohmert, B., 2001. Diet of juvenile meagre, *Argyrosomus regius*, within the Tagus estuary. *Cahiers de Biologie Marine* 42, 289-293.
- Cammen, L.M., 1980. A Method for Measuring Ingestion Rate Deposit Feeders and its Use with the Polychaete *Nereis succinea*. *Estuaries* 3, 55-60.
- Cannicci, S., Gomei, M., Boddi, B., Vannini, M., 2002. Feeding Habits And Natural Diet of the Intertidal Crab *Pachygrapsus marmoratus*: Opportunistic Browser or Selective Feeder? *Estuarine, Coastal and Shelf Science* 54, 983-1001.
- Castel, J., Bachelet, G., Rochard, E., Elie, P., 1994. La biologie de l'estuaire, Estuaire de la Gironde, livre blanc. Agence de l'Eau Adour Garonne, IFREMER, pp. 115.

408 Church, M.R., Ebersole, J.L., Rensmeyer, K.M., Couture, R.B., Barrows, F.T., Noakes,
 409 D.L.G., 2009. Mucus: a new tissue fraction for rapid determination of fish diet switching
 410 using stable isotope analysis. Canadian Journal of Fisheries and Aquatic Sciences 66, 1-5.
 411 Cohen, A.N., Carlton, J.T., Fountain, M.C., 1995. Introduction, dispersal and potential
 412 impacts of the green crab *Carcinus maenas* in San Francisco Bay, California. Marine Biology
 413 122, 225-237.
 414 Costa, M.J., 1988. Ecologie alimentaire des poissons de l'estuaire du Tage. Cybium 12, 301-
 415 320.
 416 Cupp, E.E., 1943. Marine plankton diatoms of the west coast of North America. University of
 417 California press Berkeley and Los Angeles.
 418 Dame, J.K., Christian, R.R., 2008. Evaluation of ecological network analysis: Validation of
 419 output. Ecological Modelling 210, 327-338.
 420 Davenport, S.R., Bax, N.J., 2002. A trophic study of a marine ecosystem off southeastern
 421 Australia using stable isotopes of carbon and nitrogen. Canadian Journal of Fisheries and
 422 Aquatic Sciences 59, 514-530.
 423 David, V., Sautour, B., Chardy, P., 2007. Successful colonization of the calanoid copepod
 424 *Acartia tonsa* in the oligo-mesohaline area of the Gironde estuary (SW France) - Natural or
 425 anthropogenic forcing? Estuarine Coastal and Shelf Science 71, 429-442.
 426 David, V., Sautour, B., Galois, R., Chardy, P., 2006. The paradox high zooplankton biomass-
 427 low vegetal particulate organic matter in high turbidity zones: What way for energy transfer?
 428 Journal of Experimental Marine Biology and Ecology 333, 202-218.
 429 De Niro, M.J., Epstein, S., 1978. Influence of diet on the distribution of carbon isotopes in
 430 animals. Geochimica et Cosmochimica Acta 42, 495-506.
 431 De Niro, M.J., Epstein, S., 1981. Influence of the diet on the distribution of nitrogen isotopes
 432 in animals. Geochimica et Cosmochimica Acta 45, 341-351.

- 433 Fauchald, K., Jumars, P.A., 1979. The diet of worms: a study of polychaete feeding guilds.
 434 Oceanographic marine biology. Annual Review 17, 193-284.
- 435 Focke, N., Mees, J., 1999. Feeding of the hyperbenthic mysid *Neomysis integer* in the
 436 maximum turbidity zone of the Elbe, Westerschelde and Gironde estuaries. Marine Systems
 437 22, 207-228.
- 438 Fry, B., Sherr, E.B., 1984. $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and
 439 freshwater ecosystems. Contributions in Marine Science 27, 13-47.
- 440 Garrison, L.P., Link, J.S., 2000. Dietary guild structure of the fish community in the
 441 Northeast United States continental shelf ecosystem. Marine Ecology Progress Series 202,
 442 231-240.
- 443 Gerdol, V., Hughes, R.G., 1994. Feeding behaviour and diet of *Corophium volutator* in an
 444 estuary in southeastern England. Marine Ecology Progress Series 114, 103-108.
- 445 Grall, J., Le Loc'h, F., Guyonnet, B., Riera, P., 2006. Community structure and food web
 446 based on stable isotopes ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) analysis of a North Eastern Atlantic maerl bed.
 447 Journal of Experimental Marine Biology and Ecology 338, 1-15.
- 448 Grosholz, E.D., Ruiz, G.M., 1996. Predicting the impact of introduced marine species:
 449 Lessons from the multiple invasion of the European green crab *Carcinus maenas*. Biological
 450 Conservation 78, 59-66.
- 451 Guelinckx, J., Maes, J., Van Den Driessche, P., Geysen, B., Dehairs, F., Ollevier, F., 2007.
 452 Changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in different tissues of juvenile sand goby
 453 *Pomatoschistus minutus*: a laboratory diet-switch experiment. Marine Ecology-Progress
 454 Series 341, 205-215.
- 455 Hamerlynck, O., Cattrijsse, A., 1994. The food of *Pomatoschistus minutus* (Pisces, Gobiidae)
 456 in Belgian coastal waters, and a comparison with the food of its potential competitor *P.*
 457 *lozanoi*. Journal of Fish Biology 44, 753-771.

458 Hampel, H., Cattrijsse, A., Elliott, M., 2005. Feeding habits of young predatory fishes in
 459 marsh creeks situated along the salinity gradient of the Schelde estuary, Belgium and The
 460 Netherlands. *Helgoland Marine Research* 59, 151-162.

461 Herman, P.M.J., Middelburg, J.J., Widdows, J., Lucas, C.H., Heip, C.H.R., 2000. Stable
 462 isotopes as trophic tracers: combining field sampling and manipulative labelling of food
 463 resources for macrobenthos. *Marine Ecology Progress Series* 204, 79-92.

464 Hesslein, R.H., Capel, M.J., Fox, D.E., Hallard, K.A., 1991. Stable isotopes of sulfur, carbon,
 465 and nitrogen as indicators of trophic level and fish migration in the lower Mackenzie river
 466 basin, Canada. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 2258-2265.

467 Hesslein, R.H., Hallard, K.A., Ramlal, P., 1993. Replacement of Sulfur, carbon and nitrogen
 468 in tissue of Growing broad Whitefish (*Coregonus nasus*) in response to a change in diet
 469 traced by delta 34S, delta 13C and delta 15N. *Canadian Journal of Fisheries and Aquatic*
 470 *Sciences* 50, 2071-2076.

471 Hughes, J.E., Deegan, L.A., Peterson, B.J., Holmes, R.M., Fry, B., 2000. Nitrogen flow
 472 through the food web in the oligohaline zone of a new England estuary. *Ecology* 81, 433-452.

473 Hyslop, E.J., 1980. Stomach contents analysis - a review of methods and their application.
 474 *Journal of Fish Biology* 17, 411-429.

475 Jones, N.S., 1962. The bottom fauna and the food of flatfish of the Cumberland Coast. *Journal*
 476 *of Animal Ecology* 21, 182-205.

477 Kwak, T., Zedler, J.B., 1997. Food web analysis of southern California coastal wetlands using
 478 multiple stable isotopes. *Oecologia* 110, 262-277.

479 Laffaille, P., Feunteun, E., Lefebvre, C., Radureau, A., Sagan, G., Lefevre, J.-C., 2002. Can
 480 Thin-lipped Mullet Directly Exploit the Primary and Detritic Production of European
 481 Macrotidal Salt Marshes? *Estuarine, Coastal and Shelf Science* 54, 729-736.

- 482 Laurand, S., Riera, P., 2006. Trophic ecology of the supralittoral rocky shore (Roscoff,
483 France): A dual stable isotope ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) and experimental approach. Journal of Sea
484 Research 56, 27-36.
- 485 Leitão, R., Martinho, E., Neto, J.M., Cabral, H., Marques, J.C., Pardal, M.A., 2006. Feeding
486 ecology, population structure and distribution of *Pomatoschistus microps* (Kroyer, 1838) and
487 *Pomatoschistus minutus* (Pallas, 1770) in a temperate estuary, Portugal. Estuarine Coastal and
488 Shelf Science 66, 231-239.
- 489 Lobry, J., David, V., Pasquaud, S., Lepage, M., Sautour, B., Rochard, E., 2008. Diversity and
490 stability of an estuarine trophic network. Marine Ecology Progress Series 358, 13-25.
- 491 Marchand, J., 1981. Observations sur l'écologie de *Crangon crangon* (Linné) et *Palaemon*
492 *longirostris* H. Milne Edwards (Crustacea, Decapoda, Natantia) dans l'estuaire interne de la
493 Loire (France). Vie et Milieu 31, 83-92.
- 494 Mc Cuthan, J.H., Lewis, W.M., Kendall, C., Mc Grath, C.C., 2003. Variation in trophic shift
495 for stable isotope ratios of carbon, nitrogen, and sulfur. Oikos 102, 378-390.
- 496 Miller, T.W., 2006. Tissue-specific response of delta N-15 in adult Pacific herring (*Clupea*
497 *pallasi*) following an isotopic shift in diet. Environmental Biology of Fishes 76, 177-189.
- 498 Minagawa, M., Wada, E., 1984. Stepwise enrichment of ^{15}N along food chains: further
499 evidence and the relation between $\delta^{15}\text{N}$ and animal age. Geochimica et Cosmochimica Acta
500 48, 1135-1140.
- 501 Mouny, P., Dauvin, J.C., Bessineton, C., Elkaim, B., Simon, S., 1998. Biological components
502 from the Seine estuary: first results. Hydrobiologia 374, 333-347.
- 503 Ólafsson, E.B., Persson, L.-E., 1986. Distribution, life cycle and demography in a brackish
504 water population of the isopod *Cyathura carinata* (Kröyer) (Crustacea). Estuarine, Coastal
505 and Shelf Science 23, 673-687.

- 506 Padisak, J., Adrian, R., 1999. Biovolumen. In: Tümping, W. and Friedrich, G. (Eds),
 507 Biologische Gewässeruntersuchung. Fisher, G., pp. 334-368.
- 508 Pasquaud, S., Elie, P., Jeantet, C., Billy, I., Martinez, P., Girardin, M., 2008. A preliminary
 509 investigation of the fish food web in the Gironde estuary, France, using dietary and stable
 510 isotope analyses. Estuarine, Coastal and Shelf Science 78, 267-279.
- 511 Pasquaud, S., Girardin, M., Elie, P., 2004. Diet of gobies of the genus *Pomatoschistus* (*P.*
 512 *microps* and *P. minutus*), in the Gironde estuary (France). Cybium 28, 99-106.
- 513 Perga, M.E., Gerdeaux, D., 2003. Using the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of whitefish scales for
 514 retrospective ecological studies: Changes in isotope signatures during the restoration of Lake
 515 Geneva, 1980-2001. Journal of Fish Biology 63, 1197-1207.
- 516 Perga, M.E., Gerdeaux, D., 2005. 'Are fish what they eat' all year round? Oecologia 144, 598-
 517 606.
- 518 Persson, A., Hansoon, L.A., 1999. Diet shift in fish following competitive release. Canadian
 519 Journal of Fisheries and Aquatic Sciences 56, 70-78.
- 520 Pillay, T.V.R., 1952. A critique of the methods of study of food of fishes. Journal of the
 521 Zoological Society of India 4, 185-200.
- 522 Post, D.M., 2002. Using stable isotopes to estimate trophic position: Models, methods, and
 523 assumptions. Ecology 83, 703-718.
- 524 Prygiel, J., Coste, M., 2000. Guide méthodologique pour la mise en œuvre de l'indice
 525 biologique Diatomées. Agences de l'eau, MATE, Cemagref Bordeaux, 134 pp.
- 526 Salgado, J.P., Cabral, H.N., Costa, M.J., 2004. Feeding ecology of the gobies *Pomatoschistus*
 527 *minutus* (Pallas, 1770) and *Pomatoschistus microps* (Kroyer, 1838) in the upper Tagus
 528 estuary, Portugal. Scientia Marina 68, 425-434.

- 529 Sauriau, P.G., Mouret, V., Rince, J.P., 1989. Organisation trophique de la malacofaune
 530 benthique non cultivée du bassin ostréicole de Marennes-Oléron. *Oceanologica Acta* 12, 193-
 531 204.
- 532 Sherwood, G.D., Rose, G.A., 2005. Stable isotope analysis of some representative fish and
 533 invertebrates of the Newfoundland and Labrador continental shelf food web. *Estuarine,*
 534 *Coastal and Shelf Science* 63, 537-549.
- 535 Sorbe, J.-C., 1983. Les décapodes natantia de l'estuaire de la Gironde (France). Contribution à
 536 l'étude morphologique et biologique de *Palaemon longirostris*. H. Milne Edwards, 1837.
 537 *Crustaceana* 44, 251-270.
- 538 Sottolichio, A., Castaing, P., 1999. A synthesis on seasonal dynamics of highly-concentrated
 539 structures in the Gironde estuary. *Comptes rendus de l'Académie des Sciences Série II*
 540 *Fascicule a- Sciences de la Terre et des Planètes* 329, 795-800.
- 541 Summers, R.W., 1980. The diet and feeding behaviour of the flounder *Platichthys flesus* (L.)
 542 in the Ythan estuary, Aberdeenshire, Scotland. *Estuarine and Coastal Marine Science* 11, 217-
 543 232.
- 544 Suring, E., Wing, S.R., 2009. Isotopic turnover rate and fractionation in multiple tissues of red
 545 rock lobster (*Jasus edwardsii*) and blue cod (*Parapercis colias*): Consequences for ecological
 546 studies. *Journal of Experimental Marine Biology and Ecology* 370, 56-63.
- 547 Thiébaud, E., Lagadeuc, Y., Olivier, F., Dauvin, J.C., Retière, C., 1998. Do hydrodynamic
 548 factors affect the recruitment of marine invertebrates in a macrotidal area? *Hydrobiologia*
 549 375-376, 165-176.
- 550 Tieszen, L.L., Boutton, T.W., Tesdahl, K.G., 1983. Fractionation and turnover of stable
 551 carbon isotopes in animal tissues: implication for $\delta^{13}\text{C}$ analysis of diet. *Oecologia* 57, 32-37.

- 552 Vander Zanden, M.J., Cabana, G., Rasmussen, J.B., 1997. Comparing trophic position of
 553 freshwater fish calculated using stable nitrogen isotope ratios ($\delta^{15}\text{N}$) and literature dietary
 554 data. Canadian Journal of Fisheries and Aquatic Sciences 54, 1142-1158.
- 555 Vander Zanden, M.J., Rasmussen, J.B., 1999. Primary consumer $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ and the
 556 trophic position of aquatic consumers. Ecology 80, 1395-1404.
- 557 Vinagre, C., Cabral, H., Costa, M.J., 2008. Prey selection by flounder, *Platichthys flesus*, in
 558 the Douro estuary, Portugal. Journal of Applied Ichthyology 24, 238-243.
- 559 Vinagre, C., Franca, S., Costa, M.J., Cabral, H.N., 2005. Niche overlap between juvenile
 560 flatfishes, *Platichthys flesus* and *Solea solea*, in a southern European estuary and adjacent
 561 coastal waters. Journal of Applied Ichthyology 21, 114-120.
- 562 Wada, E., Mizutani, H., Minagawa, M., 1991. The use of stable isotopes for food web
 563 analysis. Critical Reviews in Food Science and Nutrition 30, 361-371.
- 564 Wägele, J.W., Welsch, U., Müller, W., 1981. Fine structure and function of the digestive tract
 565 of *Cyathura carinata* (Krøyer) (Crustacea, Isopoda). Zoomorphology 98, 69-88.
- 566 West, J.M., Williams, G.D., Madon, S.P., Zedler, J.B., 2003. Integrating spatial and temporal
 567 variability into the analysis of fish food web linkages in Tijuana Estuary. Environmental
 568 Biology of Fishes 67, 297-309.
- 569 Wieking, G., Kröncke, I., 2005. Is benthic trophic structure affected by food quality? The
 570 Dogger Bank example. Marine Biology 146, 387-400.
- 571 Winemiller, K.O., Akin, S., Zeug, S.C., 2007. Production sources and food web structure of a
 572 temperate tidal estuary: integration of dietary and stable isotope data. Marine Ecology-
 573 Progress Series 343, 63-76.
- 574 Ysebaert, T., Herman, P.M.J., 2002. Spatial and temporal variation in benthic macrofauna and
 575 relationships with environmental variables in an estuarine, intertidal soft-sediment
 576 environment. Marine Ecology Progress Series 244, 105-124.

Captions

Fig. 1. Map of the Gironde estuary showing the fish sampling stations (stars) for dietary and stable isotope analyses.

Fig. 2. Synthesis of the Gironde estuary trophic web knowledge during the investigation period. Relationships between fish (simple line box) and their preys (dashed box) result from data of fish stomach content analyses (present study). The thicker the arrow, the greater the trophic link. Relationships between preys and sources of organic matter (double lines box) were established from bibliographic work. Excepted for *S. laticauda*, all these data come from the Gironde estuary. The different compartments were localised according to their trophic position, from TL results for fish, from feeding ecology information for prey. The mean $\delta^{15}\text{N}$ signature (‰) of each taxon, obtained in that study, is indicated in grey.

Table 1. Size class and total number (n) of fish analysed for the Stable Isotope Analyses (SIA) and the Stomach Content Analyses (SCA).

Table 2. Volumetric percentage diet composition of fish collected during their growth period in the Gironde estuary; n: total number of full stomachs; *: small size class; **: large size class and bold type denotes preferential preys (%V>10%).

Table 3. Diet of the different preys examined in fish Stomach Content Analysis (SCA) and trophic chain to which preys belong.

Table 4. Volumetric percentage diet composition of fish species (or size class) on each trophic chain (%V = volumetric percentage of - B: preys dependent of the sediment as organic matter,

603 - P: preys dependent of the pelagic source, - H: preys dependent of the phytoplankton,- D:
 604 preys dependent of the detritus, - I: preys dependent of the intermediate pelagic source), mean
 605 $\delta^{15}\text{N}$ signatures (‰, $\pm$ Standard Deviation) of organisms, $\delta^{15}\text{N}_{\text{base}}$ estimation (‰,) of the
 606 trophic chain base to which fish species belong. TL: Trophic level of representative baseline
 607 organisms and each fish species or size class. * = small size class and ** = large size class.

Fig. 1.

Fig. 2.

624 Table 1.

Species	n (SCA)	size class (mm) for SCA	n (SIA)	size class (mm) for SIA
<i>Anguilla anguilla</i>	36	267-643	21	267-760
<i>Dicentrarchus labrax</i> **	13	195-231	2	180-200
<i>Dicentrarchus labrax</i> *	6	79-109	4	70-100
<i>Dicentrarchus punctatus</i>	13	75-183	5	75-189
<i>Argyrosomus regius</i> **	82	237-309	9	220-300
<i>Argyrosomus regius</i> *	35	53-166	11	54-160
<i>Platichthys flesus</i>	22	147-333	11	121-333
<i>Solea solea</i>	52	117-197	12	90-198
<i>Pomatoschistus</i> spp.	35	57-65	7	29-65
<i>Liza ramada</i>	17	65-112	8	78-188

625

Species	<i>L. ramada</i>	<i>S. solea</i>	<i>P. flesus</i>	<i>Pomatoschistus</i> spp.	<i>D. labrax</i> *	<i>A. regius</i> *	<i>A. regius</i> **	<i>D. punctatus</i>	<i>A. anguilla</i>	<i>D. labrax</i> **
size (mm)	65-112	117-197	147-333	57-65	79-109	53-166	237-309	75-183	267-643	195-231
n	17	52	17	28	6	35	82	13	36	8
Bivalves										
<i>Cerastoderma edule</i>			72.62							
<i>Macoma balthica</i>		0.10	0.53							
<i>Littorina saxatilis</i>			0.01							
Annelida polychaetes										
<i>Nereis</i> spp.					3.30			7.57		
<i>Hediste diversicolor</i>		1.29								
<i>Neanthes succinea</i>		13.69					0.40			
<i>Polydora</i> spp.		4.83								
<i>Nephtys</i> spp.			0.31							
<i>Notomastus latericeus</i>			0.38							
<i>Heteromastus filiformis</i>			0.19							
<i>Pectinaria koreni</i>		12.02								
Polychaetes undetermined		6.09							0.27	
Crabs										
<i>Carcinus maenas</i>		0.32							2.08	
<i>Pachygrapsus marmoratus</i>									1.39	
<i>Liocarcinus</i> spp.		0.50								
Amphipods										
<i>Gammarus</i> spp.		19.46		66.67		11.87	14.92	8.24	33.71	38.89
<i>Bathyporeia</i> spp.		0.51		3.57			0.05	0.15		
<i>Corophium volutator</i>		3.61	5.88					1.87		
Amphipod undetermined				3.57						
Isopods										
<i>Synidotea laticauda</i>		4.83	11.68			2.37	8.13	44.30	25.59	11.90
<i>Sphaeroma serratum</i>					9.23	3.25				
<i>Cyathura carinata</i>		6.08	0.04							
<i>Idotea</i> spp.		1.48			0.18					
Shrimps										
<i>Crangon crangon</i>		10.35			25.00	17.96	35.76		7.40	11.72
<i>Palaemon</i> spp.		2.36			28.30	0.69	13.02	0.10	12.75	
Mysids										
<i>Mesopodopsis slabberi</i>					0.33	23.52	3.88	18.37	0.10	
<i>Neomysis integer</i>				26.19		17.16	12.15	3.31	9.10	12.89
<i>Shistomysis</i> spp.										
<i>Gastrosaccus</i> spp.							0.05			
Mysids undetermined							0.95		0.09	
Copepods ind.										
<i>Acartia</i> spp.	1.73				16.67	0.03				
<i>Eurytemora affinis</i>						0.63				
<i>Acanthocyclops trajani</i>								8.33		
<i>Euterpina acutifrons</i>	2.60									
Copepods undetermined	0.57									12.50

Table 2

628 Table 2 (continued)

Species	<i>L. ramada</i>	<i>S. solea</i>	<i>P. flesus</i>	<i>Pomatoschistus</i> spp.	<i>D. labrax</i> *	<i>A. regius</i> *	<i>A. regius</i> **	<i>D. punctatus</i>	<i>A. anguilla</i>	<i>D. labrax</i> **
size (mm)	65-112	117-197	147-333	57-65	79-109	53-166	237-309	75-183	267-643	195-231
n	17	52	17	28	6	35	82	13	36	8
Metazooplankton										
Mysids						0.25	0.59			
Mollusc larvae										
Cypris larvae										
Nauplii	0.41									
Fish larvae						20.78				
Fish		0.87	6.08		16.67		1.52	7.58	2.01	12.10
<i>Pomatoschistus</i> spp.						1.08	7.04		2.20	
<i>Sprattus sprattus</i>							0.00		1.14	
<i>Solea solea</i>							0.15			
<i>Engraulis encrasicolus</i>							0.84			
Divers										
Eggs			0.07	0.16	0.33	0.41	0.06	0.01	0.00	
Vegetal debris		11.59	2.20	0.08			0.48	0.17	2.16	
Pollen										
Organic debris	86.53									
Micro-algae										
<i>Coscinodiscus</i> sp.	6.45									
<i>Navicula</i> sp.	0.23									
<i>Aulacoseira</i> sp.	0.11									
<i>Skeletonema</i> sp.	0.04									
<i>Plagiogramma</i> sp.	0.14									
<i>Gyrosigma</i> sp.	0.02									
<i>Thalassiosira</i> sp.	0.09									
<i>Thalassionema</i> sp.	0.01									
<i>Pediastrum</i> sp.	0.21									
<i>Diatoma</i> sp.	0.01									
Dinoflagellate cyst	0.37									
<i>Prorocentrum</i> sp.	0.01									
<i>Raphoneis</i> sp.	0.01									
<i>Nitzschia</i> sp.	0.15									
<i>Fragilaria</i> sp.	0.01									
<i>Cyclotella</i> sp.	0.30									

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Table 3

Species	Diet	References	Gironde data (*)	Source of organic matter
Bivalves				
<i>Cerastoderma edule</i>	active suspension feeder	Bachelet, 1981; Sauriau et al., 1989; Ysebaert & Herman, 2002	*	sediment
<i>Macoma balthica</i>	surface deposit and filter-feeder	Bachelet, 1981; Sauriau et al., 1989; Castel et al., 1994; Ysebaert & Herman, 2002	*	sediment
<i>Littorina saxatilis</i>	grazer	Laurand & Riera, 2006		sediment
Annelid polychaetes				
<i>Neanthes</i> spp.	carnivorous, omnivorous	Bachelet, 1981	*	sediment
<i>Hediste diversicolor</i>	carnivorous, omnivorous	Fauchald & Jumars, 1979; Cammen, 1980; Ysebaert & Herman, 2002		sediment
<i>Neanthes succinea</i>	carnivorous, omnivorous	Fauchald & Jumars, 1979; Ysebaert & Herman, 2002		sediment
<i>Polydora</i> spp.	carnivorous, omnivorous	Fauchald & Jumars, 1979; Cammen, 1980		sediment
<i>Nephtys</i> spp.	surface deposit feeder	Fauchald & Jumars, 1979		sediment
<i>Notomastus latericeus</i>	carnivorous, omnivorous	Fauchald & Jumars, 1979		sediment
<i>Heteromastus filiformis</i>	subsurface deposit feeder	Fauchald & Jumars, 1979; Grall et al., 2006		sediment
<i>Pectinaria koreni</i>	subsurface deposit feeder	Fauchald & Jumars, 1979; Ysebaert & Herman, 2002		sediment
	subsurface deposit feeder	Fauchald & Jumars, 1979; Thiébaud et al., 1998		sediment
Crabs				
<i>Carcinus maenas</i>	carnivorous, omnivorous	Cohen et al., 1995; Grosholz & Ruiz, 1996		sediment
<i>Pachygrapsus marmoratus</i>	carnivorous, omnivorous	Cannicci et al., 2002		sediment
<i>Liocarcinus</i> spp.	carnivorous, omnivorous	Grall et al., 2006		sediment
Amphipods				
<i>Gammarus</i> spp.	carnivorous, omnivorous	Unpublished data	*	intermediate
<i>Bathyporeia</i> spp.	suspension and surface deposit feeder	Herman et al., 2000; Wieking & Kröncke, 2005		intermediate
<i>Corophium volutator</i>	deposit and filter feeder	Castel et al., 1994; Gerdol & Hugues, 1994; Ysebaert & Herman, 2002	*	sediment
Isopods				
<i>Synidotea laticauda</i>	phytoplanktivorous, detritivorous			intermediate
<i>Sphaeroma serratum</i>	phytoplanktivorous, detritivorous			sediment
<i>Cyathura carinata</i>	carnivorous	Wägele et al., 1981; Olafsson & Persson, 1986		sediment
<i>Idotea</i> spp.	phytoplanktivorous, detritivorous			intermediate
Shrimps				
<i>Crangon crangon</i>	carnivorous, macro-benthivorous	Marchand, 1981		sediment
<i>Palaemon</i> spp.	carnivorous, mysid feeder	Marchand, 1981; Sorbe, 1983; Castel et al., 1994; Mouny et al., 1998	*	intermediate
Mysids				
<i>Mesopodopsis slabberi</i>	phytoplanktivorous	Unpublished data	*	phytoplankton
<i>Neomysis integer</i>	detritivorous	Castel et al., 1994; Focke & Mees, 1999	*	detritus
<i>Shistomysis</i> spp.	deposit and filter feeder	Unpublished data	*	phytoplankton
<i>Gastrosaccus</i> spp.	deposit and filter feeder	Unpublished data	*	phytoplankton

Table 3 (Continued)

Species	Diet	References	Gironde data (*)	Source of organic matter
Copépods				
<i>Acartia</i> spp.	phytoplanktivorous	Unpublished data	*	phytoplankton
<i>Eurytemora affinis</i>	detritivorous	Castel et al., 1994; Unpublished data	*	detritus
<i>Acanthocyclops trajani</i>	-	Unpublished data	*	sediment
<i>Euterpina acutifrons</i>	-	Unpublished data	*	intermediate
Metazooplankton				
Mysids	planktivorous	Castel et al., 1994	*	intermediate
Mollusc larvae	planktivorous	Castel et al., 1994	*	intermediate
Cypris larvae	planktivorous	Castel et al., 1994	*	intermediate
Nauplii	planktivorous	Castel et al., 1994	*	intermediate
Fish larvae	planktivorous	Castel et al., 1994	*	intermediate
Fish				
<i>Pomatoschistus</i> spp.	planktivorous	present work	*	intermediate
<i>Sprattus sprattus</i>	planktivorous	Pasquaud et al., 2008	*	intermediate
<i>Solea solea</i>	hyperbenthophagous, piscivorous	present work	*	sediment
<i>Engraulis encrasicolus</i>	planktivorous	Pasquaud et al., 2008	*	intermediate
Divers				
Eggs	-			detritus
Vegetal debris	-			detritus
Pollen	-			detritus

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Table 4.

SCA		Trophic data			SIA				
Species	V% _B	V% _P			Trophic chain (source)	δ ¹⁵ N ± SD	δ ¹⁵ N _{base} estimation	TL _{base} estimation	TL
		% V _H	% V _D	% V _I					
<i>C. edule</i>					benthic	7.97 ± 0.39		2.00	
<i>Acartia</i> spp.					pelagic (phytoplanktonic)	6.12 ± 1.51		2.00	
<i>E. affinis</i>					pelagic (detritic)	7.13 ± 2.67		2.00	
Intermediate					pelagic	6.63 ± 0.72		2.00	
<i>D. labrax</i> **	11.72	0.00	12.89	75.39	mixed	13.60 ± 0.12	6.85		3.98
<i>A. anguilla</i>	11.14	0.10	11.27	77.50	mixed	13.26 ± 0.69	6.83		3.89
<i>D. punctatus</i>	17.92	18.37	3.48	60.22	mixed	12.18 ± 0.90	6.79		3.58
<i>A. regius</i> **	36.36	3.93	12.69	47.02	mixed	12.55 ± 0.68	7.16		3.58
<i>D. labrax</i> *	37.53	17.00	0.33	45.15	mixed	11.91 ± 0.81	7.05		3.43
<i>P. flesus</i>	79.96	0.00	2.27	17.77	benthic	12.34 ± 0.95	7.71		3.36
<i>S. solea</i>	59.41	0.00	11.59	29.00	benthic	11.91 ± 1.01	7.48		3.30
<i>A. regius</i> *	21.21	23.55	18.20	37.04	mixed	10.80 ± 1.07	6.88		3.15
<i>Pomatoschistus</i> spp.	3.57	0.00	26.44	70.24	mixed	10.70 ± 0.50	6.83		3.14
<i>L. ramado</i>	94.68	1.73	0.00	3.58	benthic	10.85 ± 1.43	7.89		2.87

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