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To cite this version:
S. Pasquaud, M. Pillet, V. David, B. Sautour, Pierre Elie. Determination of fish trophic levels in an estuarine system. Estuarine, Coastal and Shelf Science, Elsevier, 2010, p. 237 - p. 246. hal-00473506
Determination of fish trophic levels in an estuarine system

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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 δ^{15}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.
Keywords: stomach contents; δ15N; predator-prey relationships; organic matter sources; fish

trophic levels; estuarine ecosystem

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 $^{13}C/^{12}C$ 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 $^{15}N/^{14}N$ 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 Hansoon, 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 $\delta^{13}C$ and $\delta^{15}N$ 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, $\delta^{15}N$ 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 $\delta^{15}N$ level than *Argyrosomus regius* which tends to be ichtyophagous. These observations can be explained by an enrichment of the $\delta^{15}N$ 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 $\delta^{15}N$ 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 $\delta^{15}N$ value taking into account the proportion of benthic/pelagic prey in their feeding and the $\delta^{15}N$ 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 km$^2$. 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 $\delta^{15}$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 δ¹⁵N 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 δ¹⁵N 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 δ¹⁵N values to characterize suspended matter, i.e. pelagic source. Consequently, averaged δ¹⁵N 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 δ¹⁵N 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:

$$\text{TL} = \left( \frac{\delta^{15}N_{\text{pred}} - \delta^{15}N_{\text{base}}}{\Delta \delta^{15}N} \right) + \text{TL}_{\text{base}},$$

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

Primary consumers (*Eurytemora affinis*, *Acartia* spp. and *Cerastoderma edule*) were used for that baseline. So, $\text{TL}_{\text{base}}$ 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 $\delta^{15}N_{\text{base}}$, calculated as:

$$\delta^{15}N_{\text{base}} = \left( \%V_B \times \delta^{15}N_B + \%V_H \times \delta^{15}N_H + \%V_D \times \delta^{15}N_D + \%V_I \times \delta^{15}N_I \right) / 100,$$

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. *Euterpinia acutifons*, 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 ± 0.39‰ and for *E. affinis* (pelagic/detritic food chain) and *Acartia* spp. (pelagic/phytoplanktonic food chain) the values are 7.13 ± 2.67‰ and 6.12 ± 1.51 ‰ 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 ± 0.50‰ for *Pomatoschistus* spp. and 13.60 ± 0.12‰ 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 δ¹⁵N 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; McCuthan 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

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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 $\delta^{15}N$ 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 $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$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 $\delta^{15}$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).
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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 δ¹⁵N 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,
- P: preys dependent of the pelagic source, - H: preys dependent of the phytoplankton, - D:
preys dependent of the detritus, - I: preys dependent of the intermediate pelagic source), mean
\( \delta^{15}N \) signatures (‰, ± Standard Deviation) of organisms, \( \delta^{15}N_{\text{base}} \) estimation (‰,) of the
trophic chain base to which fish species belong. TL: Trophic level of representative baseline
organisms and each fish species or size class. * = small size class and ** = large size class.
Pasquaud, S. et al. Determination of fish trophic levels in an estuarine system
Estuarine Coastal and Shelf Science, n° 86. p. 237-246. 2010
http://www.sciencedirect.com/science?_ob=PublicationURL&_tockey=%23TOC%236776%232010%239999139997%2331578281%23FLA%23&_cdi=6776&_pubType=J&_auth=y&_acct=C000037979&_version=1&_urlVersion=0&_userid=5403746&md5=bc7ab59f875c91f39987c5e4edc78dfe

Fig. 1.
Pasquaud, S. et al. Determination of fish trophic levels in an estuarine system
Estuarine Coastal and Shelf Science, n° 86. p. 237-246. 2010
http://www.sciencedirect.com/science?_ob=PublicationURL&_tockey=%23TOC%23236776%23232010%2323999139997%23231578281%23 Fla%23&_cdi=6776&_pubType=J&_auth=y&_acct=C000037979&_version=1&_urlVersion=0&_userid=5403746&md5=bc7ab59f875c91f39987c5e4edc78dfe

**Fig. 2.**
Table 1.

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Table 2
Table 2 (continued)

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**Metazooplankton**

- **Mysids**
  - 0.25
  - 0.59

- **Mollusc larvae**
- **Cypris larvae**
- **Nauplii**
  - 0.41

- **Fish larvae**
  - 20.78

**Fish**

- **Pomatoschistus spp.**
  - 1.08
  - 7.04
  - 2.20

- **Sprattus sprattus**
  - 0.00
  - 1.14

- **Solea solea**
  - 0.15

- **Engraulis encrasicolus**
  - 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**

- **Coscinodiscus sp.**
  - 6.45
- **Navicula sp.**
  - 0.23
- **Aulacoseira sp.**
  - 0.11
- **Skeletonema sp.**
  - 0.04
- **Plagiogramma sp.**
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- **Gyrosigma sp.**
  - 0.02
- **Thalassiosira sp.**
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- **Thalassionema sp.**
  - 0.01
- **Pediastrum sp.**
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- **Diatoma sp.**
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- **Dinoflagellate cyst**
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