Available online at www.sciencedirect.com
SCIENCE DIRECT®
Aquat. Living Resour. 16 (2003) 47–58
Aquatic Living Resources
www.elsevier.com/locate/aquliv

Structure of the Gironde estuarine fish assemblages: a comparison of European estuaries perspective

Jérémy Lobry *, Laetitia Mourand, Eric Rochard, Pierre Elie

Cemagref, Groupement de Bordeaux, Unité Ressources aquatiques continentales, 50, avenue de Verdun, 33612 Cestas cedex, France

Received 16 May 2002; accepted 3 March 2003

Abstract

An estuary is an ecotone. It plays various vital roles in the functioning of the different fish species encountered. Each estuary has its own geographical, hydraulic, sedimentological and biological characteristics. These specific features influence the makeup and structure of the fish assemblages and the dynamics of the fish populations. The Gironde estuary is the biggest estuary in France and one of the largest in Europe. It is considered to be relatively unspoilt. The aim of this study is to provide an initial reference document on the specific composition of its fish assemblage. This study establishes a list of the fish species sampled by two different and complementary methods which have been regularly undertaken since 1979. A typology is recognized according to a series of ecological criteria. The relative proportion of fish species that spend all their life cycle in the Gironde estuary is very small. Moreover, the Gironde would appear to be the European estuary with the largest migratory amphihaline fish assemblage. Considering the study made by Elliott and Dewailly (1995), the Gironde estuarine fish population can be compared to those of 17 other European estuaries. The classification we obtained, raised a number of questions on the particularities of estuarine environment, with regard to ecological diagnostics and comparisons. Important points include the need for an inter-calibration of sampling practices, the relevance of taking into account the physical dimension of the environment (tidal range, upstream limit of saline intrusion, etc.), the degree of anthropogenic influence and its evolution.

Résumé

Structures des assemblages de poissons estuariens de la Gironde : en perspective avec les autres estuaires d'Europe. Un estuaire est un écotone. Il assure des fonctions écologiques diverses pour les espèces piscicoles qui le fréquentent. Chaque estuaire possède ses caractéristiques géographiques, démographiques, hydrauliques, sédimentologiques et biologiques propres. Ces spécificités influencent la composition et la structure de l'ichtyofaune qui fréquente le milieu. La Gironde est le plus grand estuaire français et un des plus grands d'Europe. Il est souvent présenté comme l'un des plus préservés. Ce travail a pour but de représenter un premier document de référence sur son état écologique actuel à travers la composition spécifique de son cortège ichtyologique. Une liste faunistique est établie sur la base des données issues des deux protocoles d'échantillonnage scientifique différents et complémentaires qui sont régulièrement mis en œuvre depuis de nombreuses années. Une typologie du peuplement est ainsi réalisée suivant différents critères écologiques. On aborde ainsi l'utilisation de l'estuaire par les populations ichtyologiques. La Gironde est notamment caractérisée par une proportion relativement faible d'espèces effectuant l'ensemble de leur cycle en estuaire par rapport au nombre d'espèces migratrices essentiellement d'origine marine. En particulier, elle apparaît comme l'estuaire d'Europe de l'ouest avec le plus grand cortège de migrateurs amphihalins. En reprenant un travail effectué par Elliott et Dewailly (1995), on compare la typologie du peuplement girondin à celles de 17 autres estuaires européens. La classification effectuée soulève un certain nombre de questions concernant la particularité des milieux estuariens pour ce type de diagnostics comparatifs. Ils nécessitent une intercalibration des protocoles d'échantillonnage, une prise en compte de la dimension physique du milieu (marnage, limite amont de l'intrusion saline), du degré d'anthropisation et de son évolution.

Keywords: Estuary; Population typology; Ecological state; Fish guilds; Classification

* Corresponding author.
E-mail address: jeremy.lobry@bordeaux.cemagref.fr (J. Lobry).

DOI: 10.1016/S0990-7440(03)00031-7

1. Introduction

Fish communities are more frequently used to assess quality or to monitor environmental changes in estuarine environments (Pomfret et al., 1991; Rebelo, 1992; Thiel et al., 1995; Maes et al., 1998; Marshall and Elliott, 1998; Mathieson et al., 2000; Methven et al., 2001). The estuarine environment, owing to its dual marine and fresh water characteristics, supports a wide faunal diversity (Dreux, 1986; Mauvais and Guillaud, 1994; Bachelet et al., 1997) and its biological productivity is high (Potter et al., 1986; Castel, 1993; Bachelet et al., 1997). Fish assemblages are very varied, composed of true estuarine, amphihaline or euryhaline species (Marchand and Elie, 1983; Elie et al., 1990; Mauvais and Guillaud, 1994; Elliott and Dewailly, 1995; Methven et al., 2001). Estuaries play a vital role in the functioning of both marine and inland aquatic systems by providing many marine, migratory or estuarine species with basic requirements for their life cycle (Potter et al., 1986; Elie et al., 1990), such as key habitats for reproduction, feeding, growth or physiological preparation for migration (Mc Dowall, 1988). Due to their position within the drainage basin, these environments are among the most impacted by human activities (e.g., Hostens and Hamerlynck, 1994; Maes, 2000; Cabral et al., 2001).

The main aim of this study is to provide an initial reference document on the Gironde estuarine fish assemblage. Since the early 1980s, various methods have been implemented to monitor and sample the fauna. However, since Sorbe (1980) and Boigontier and Mounié (1984), no other study has examined the system as a whole. The first step is to provide a description of the fish assemblage based on extensive sampling across space and time. The second step is to compare the Gironde to several other European estuaries by using some of the characteristics of its fish assemblage. Elliott and Dewailly (1995) proposed a classification of 17 European estuaries (excluding Gironde) using the structure of their fish assemblages based on guilds. This work places the results in context with those reported by these authors.

This study, which to a large extent ignores the space and time dimensions of the data, is an initial and preliminary approach to take stock of the ecological status of the Gironde estuary. In a context in which environmental quality tends to be evaluated increasingly in terms of the quality of fish assemblages (Deegan et al., 1997), it seems important to classify each ecosystem in comparison with neighbouring ecosystems of a similar type.

2. Materials and methods

2.1. General presentation of the Gironde estuary

The Gironde is a macrotidal estuary. The tidal range is 4.5 m at the mouth and over 5 m at Bordeaux. The estuary is the result of the confluence of the Garonne and Dordogne rivers at the Bec d'Ambès. The watershed covers 81,000 km^2 and the mean annual rate of freshwater discharge is around 1000 m^3 s^{-1} (Allen, 1972; Sottolichio and Castaing, 1999). In this paper, the "Gironde estuary" will mean the area between the upstream salinity limit (Bec d'Ambès) and the ocean (seaward of a transect drawn between Pointe de Grave and Pointe de Suzac; Fig. 1). This area includes a polyhaline sector (salinity between 18 and 30), a mesohaline sector (salinity between 5 and 18) and an oligohaline sector (salinity between 0 and 5), the geographical limits of which vary according to the season (Maurice, 1994).

The study area is 76 km long. It varies in width from 2 km at the Bec d'Ambès to 11 km at its widest part (Mauvais and Guillaud, 1994). Its surface area is approximately 625 km^2 at high tide. It is the biggest estuary in France and one of the largest in Western Europe. The bottom of the estuary is mainly a mixture of sand and mud, with the sandiest part in the lower sectors and the muddiest part in the upper sectors (Latouche and Jouanneau, 1994). There is a more or less permanent turbidity maximum zone (silt plug) with suspended matter concentrations of about 1 g l^{-1} at the surface and 10 g l^{-1} near the bed (Latouche and Jouanneau, 1994; Sottolichio and Castaing, 1999). Owing to the turbidity, primary production is low. However, there is a large plankton biomass (Castel, 1993). There is little pollution as the surrounding area supports limited anthropic activities, predominately tourism and wine-growing (Mauvais and Guillaud, 1994). In 1994, Mauvais and Guillaud estimated that compared to the Seine, Loire, Rhône, Vilaine, Rhine and Po estuaries, the Gironde contained the least phosphates and had

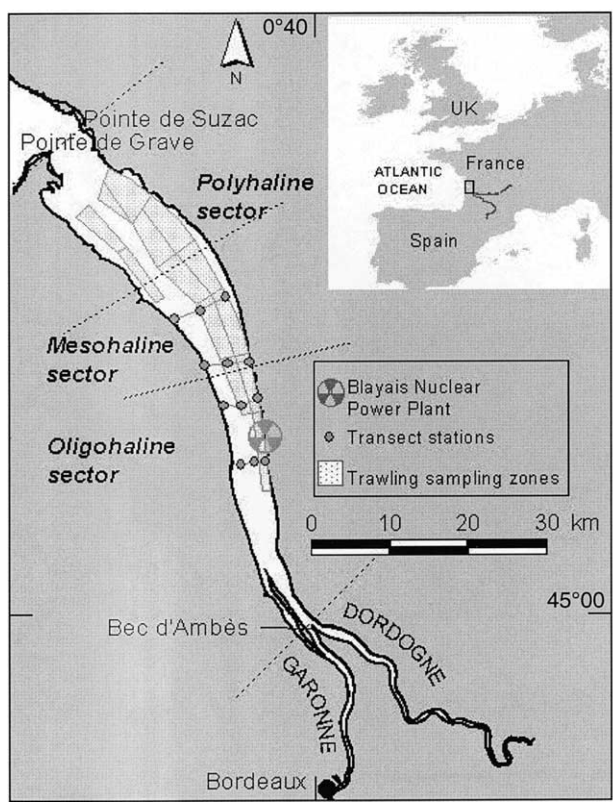

Fig. 1. Location of sampling points and area n the Gironde estuary.

the second lowest nitrogen content (quantity in comparison with the surface of its watershed).

2.2. Origin of the data

As part of the fauna monitoring and surveillance schemes, the waters of the Gironde have been sampled regularly. Data collected have involved the use of two types of sampling methods that utilize different gears.

2.2.1. Frame sampling surveys

Transect surveys were undertaken at least once a month since 1979 to monitor the smaller components of the estuarine fauna around the Blayais nuclear power plant (Elie and Rochard, 1994; Pronier and Rochard, 1998). The fauna consisted mainly of small fish species or the younger stages of larger species. The sampling stations were located on four transects, which cross the estuary in the mesohaline and oligohaline sectors (Fig. 1). Each transect consisted of three surface sites and three benthic sites, one site close to each bank and one on the median axis of the estuary. Surface samples were taken using two 4.0 × 1.0 m rectangular frame nets, fitted either side of the boat. The subconical nets have a stretched mesh of 18 mm in the main section and 2.8 mm in the terminal section. For the benthic samples, a dragnet with a 2.0 × 1.2 m frame was used. The frame was kept 0.2 m from the bed by runners (Albiges et al., 1985). The net meshes were identical to those used at the surface. Fish caught were preserved in buffered formalin.

2.2.2. The trawling sampling surveys

Trawling was used to monitor the population of European sturgeon (*Acipenser sturio*). This is a rare and endangered European species, which has been sampled (see Rochard, 2001 for details) as part of the European Life Nature programme (Elie, 1997). From 1994, sampling was conducted over most of the estuary (Fig. 1). Each trawl lasted an average of 30 min, and 20 benthic trawls were performed per month. Sampling was carried out during the day on the flood or ebb tide using a wide-mouth bottom trawl (terminal mesh 70 mm, vertical opening 3 m, horizontal opening 13 m). The fish were identified, counted, measured and returned to the water (Elie, 1997; Williot et al., 1997).

2.3. Division into ecotrophic guilds

We used the data from the period 1979–1999 for the frame samples and 1994–1999 for the trawling samples. We compiled a list of the fish species obtained by the two methods and calculated their frequency in the samples. Each species was classified according to the characteristics defined by Elliott and Dewailly (1995). They proposed a classification into ecotrophic guilds according to a series of criteria: vertical distribution, ecological type, reproduction type, substratum preference and food type (Table 1). Using this classification, the Gironde estuary can be compared to 17 European estuaries as described by Elliott and Dewailly (Fig. 2). However, we have taken a critical view of this typology, specifically the ecological guilds of the species. Some corrections have therefore been made with regard to the ecology of the fish species present in the Gironde estuary.

Table 1
Definition of the different ecotrophic guilds described by Elliott and Dewailly (1995)

Guild categories		Guild components
Ecological guilds	ER	Truly estuarine resident fish
	MA	Marine adventitious visitors
	CA	Diadromous migrant fish
	MS	Marine seasonal migrant fish
	MJ	Marine juvenile migrant fish
	FW	Freshwater adventitious fish
Vertical distribution guilds	P	Pelagic fish, living in the main water column
	B	Benthic fish, living on or in the substratum
	D	Demersal fish, living in the water layer just above the bed
Substratum preference guilds	S	Sandy bottom
	F	Soft bottom
	R	Rough bottom
	M	Mixed or various bottom
	V	For species living above or among the vegetation V can be added concurrently to S, F, R, M for species living among the vegetation on a certain bottom type (SV, FV, RV, MV)
Feeding guilds		As fish feed on
	P	Plankton
	I	Invertebrate
	F	Fish
	V	Aquatic plants
	D	Detritus
		Possible combinations:
		PS, FS, IS, VS, DS: fishes feeding strictly on plankton, fishes, etc.
	CS	Carnivorous fish other than PS, IS
	OV	Omnivorous fish
	HC	Fish partly herbivorous, partly carnivorous, but not omnivorous
Reproductive guilds	V	Viviparous
	W	Ovoviviparous
	O	Oviparous with:
	Op	Pelagic eggs
	Og	Eggs guarded by parents
	Ob	Benthic eggs
	Os	Eggs shed/protected in a nest
	Ov	Eggs deposited in/stuck to vegetation

2.4. Data processing

The typology obtained can be compared with the typologies formulated by Elliott and Dewailly (1995). Like these authors, we used classification techniques to analyse similarities in fish assemblage structures between estuaries. The results from the two classification methods were compared in order to test the robustness of the patterns obtained.

Initially, we used the same method as Elliott and Dewailly, adding the Gironde to their classification. The technique is based on calculating a matrix of inter-estuarine distances

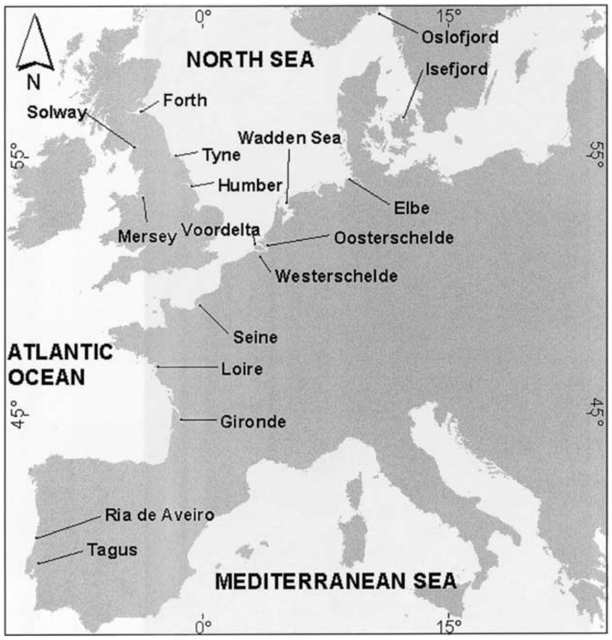

Fig. 2. Localization of the 17 estuaries analysed by Elliott and Dewailly (1995). We added the Gironde estuary and the Seine estuary.

determined by computing the Bray-Curtis (BC) coefficient (Legendre and Legendre, 1984). From this matrix, we produced a dendrogram using group average sorting. In parallel, a factor-based ascendant hierarchical classification (AHC) was made. This technique was used to classify a set of individuals characterized by their prime factorial coordinates, as created by a factorial analysis procedure. The aggregation criterion used was Ward's criterion.

BC analyses were performed using SYSTAT 10 (SYSTAT 10 Copyright © SPSS Inc., 2000). Spad 4.01 (Spad 4.01 Copyright © CISIA-CERESTA, 1987–1999) was used for AHC.

3. Results

3.1. Species identified in the Gironde estuary

The two sampling databases included 75 fish species (Table 2), making the Gironde estuary the second richest of the 18 European estuaries studied. The species were classified into the categories defined by Elliott and Dewailly (1995). Eight species were encountered only in the Gironde were: the spotted bass *Dicentrarchus punctatus*, the pumpkinseed *Lepomis gibbosus*, the black bullhead *Ameiurus melas*, the red mullet *Mullus barbatus*, the painted ray *Raja microocellata*, the cuckoo ray *Raja naevus*, the undulate ray *Raja undulata* and the ombrine *Umbrina cirrosa*. These species were therefore reclassified based on our own knowledge and a review of related literature. We also calculated the frequency of each guild in all the samples for the two sampling methods (Table 3).

3.2. Relative importance of each guild in the Gironde estuary

From the list of fish in the Gironde ecosystem, we established the relative importance of each of the guilds in the different categories (Fig. 3). The Gironde population typology can be compared to the average typology described by Elliott and Dewailly (1995), based on the 17 estuaries that the authors used as a reference and named the "typical European estuary".

The results were compared between the guilds. A comparison between the proportion of species in each category, in the Gironde, and the average proportion ± standard deviation in the 17 estuaries, indicated certain disparities (Fig. 4).

- In terms of ecology, the relative proportion of the species that complete their entire life cycle in the estuary is smaller in the Gironde than in other European estuaries. Conversely, the proportion of freshwater species is higher.
- With regard to reproduction, no viviparous species were found in the Gironde, while the proportions of ovoviviparous species and species whose eggs are protected, were higher than in a typical European estuary.
- The proportion of species whose diet is exclusively composed of invertebrates is smaller than in the other estuaries, while the proportion of omnivores was greater.
- The "substrate" category had no distinguishing features compared to the mean of other estuaries.
- In terms of vertical distribution, our data showed more pelagic and demersal species in the Gironde than elsewhere in Europe and proportionally fewer benthic species.

3.3. Estuary classification

The dendrogram produced by Elliott and Dewailly (1995) after combining all guilds together indicated an overall similarity of more than 75%. They described three groups with the Solway, exhibiting slightly different characteristics from all other areas (Fig. 5a). The first group contained the Dutch Delta areas (Oosterschelde, Westerschelde, Voordelta) and the Humber. The second group contained the Iberian estuaries and the Loire estuary. The third one consisted of the Wadden Sea (Dutch and German), UK estuaries (such as Forth, Tyne and Mersey) and Scandinavian areas (Isefjord and Oslofjord). But this latter cluster can be divided into two groups with the Tyne, Mersey and Elbe estuaries in one group and the Wadden Sea, the Forth estuary and the Scandinavian areas in the other. The inclusion of the Gironde does little to change the classification obtained by Elliott and Dewailly (Fig. 5b), hence fitting the Gironde into the Mersey–Tyne–Elbe group.

Depending on the classification method used, the results were not strictly identical (Figs. 5 and 6) but they were relatively similar. The factor-based ascending AHC performed on the data revealed four groups (Fig. 6) that were

Table 2
Fish species encountered in the Gironde estuary and guild characteristics from Elliott and Dewailly (1995). See Table 1 for explanation of abbreviations. Terminology is conformed to Bauchot and Pras (1980) and Keith and Allardi (2001). For each species, frequency in trawling samples and in frame samples is noted. ++++, frequency >75%; +++, 50–75%; ++, 12.5–50%; +, <12.5%; –, absent

Scientific name	Common name	Ecology	Vertical distribution	Bottom	Food	Reproduction	Frequency in trawling samples	Frequency in transect samples
Acipenser sturio	European sturgeon	CA	D00	S	IF	Ob	+	+
Alosa alosa	Allis shad	CA	P	/	PS	Ob	++	++
Alosa fallax	Twaite shad	CA	P	/	CS	Ob	++	++
Anguilla anguilla	European eel	CA	B	F	CS	Op	++	++
Gasterosteus aculeatus	Three-spined stickleback	CA	P	/	IF	Og	—	++
Lampetra fluviatilis	River lamprey	CA	B	F	FS	Os	+	+
Liza ramada	Thin-lipped grey mullet	CA	P	/	HC	Op	++	++
Osmerus eperlanus	Smelt	CA	P	/	IF	Ob	+	++
Petromyzon marinus	Sea lamprey	CA	B	F	FS	Os	+	+
Salmo salar	Atlantic salmon	CA	P	/	CS	Os	+	+
Salmo trutta	Sea trout	CA	P	/	CS	Os	+	+
Ammodytes tobianus	Lesser sand eel	ER	B	S	PS	Ob	—	+
Gobius niger	Black goby	ER	B	FV	CS	Ob	—	+
Nerophis ophidion	Straight-nosed pipefish	ER	D	MV	IS	Og	—	+
Platichthys flesus	Flounder	ER	B	F	IF	Op	++	+
Pomatoschistus minutus	Sand goby	ER	B	S	IS	Ob	—	++++
Syngnathus rostellatus	Nilsson's pipefish	ER	B	SV	IS	Os	—	+++
Abramis brama	Common bream	FW	D	MV	CS	Ov	—	+
Ameiurus melas	Black bullhead	FW	B	F	HC	Ob	+	—
Barbus barbus	Barbel	FW	D	S	CS	Ob	+	—
Blicca bjoerkna	Silver bream	FW	P	/	HC	Ov	—	+
Carassius carassius	Crucian carp	FW	P	/	OV	Ov	+	—
Cottus gobio	Bullhead	FW	B	R	IF	Og	—	+
Cyprinus carpio	Common carp	FW	D	MV	OV	Ov	+	+
Esox lucius	Pike	FW	D	MV	IF	Op	—	+
Gambusia affinis	Mosquito fish	FW	D	R	IS	W	—	+
Lepomis gibbosus	Pumpkinseed	FW	P	/	IS	Ov	—	+
Perca fluviatilis	Perch	FW	P	/	CS	Ov	+	—
Rutilus rutilus	Roach	FW	P	/	HC	Ov	+	+
Scardinius erythrophthalmus	Rudd	FW	P	/	CS	Ov	—	+
Stizostedion lucioperca	Zander	FW	D	R	IF	Ob	+	+
Tinca tinca	Tench	FW	P	/	CS	Ov	—	+
Argyrosomus regius	Meagre	MA	P	/	IF	Op	++	+
Conger conger	Conger eel	MA	B	R	IF	Op	+	—
Galeorhinus galeus	Tope	MA	D	S	IF	W	+	—
Hippocampus hippocampus	Short-snouted seahorse	MA	D	MV	IS	W	—	+
Labrus bergylta	Ballan wrasse	MA	D	RV	IS	Os	—	+
Lophius piscatorius	Angler fish	MA	B	M	FS	Os	+	—
Merluccius merluccius	Hake	MA	D	M	FS	Op	+	—
Mullus barbatus	Striped mullet	MA	B	S	IF	Op	+	—
Mullus surmuletus	Red mullet	MA	B	R	IS	Op	—	+
Raja clavata	Thornback ray	MA	B	S	IS	Os	+	—
Raja microocellata	Painted ray	MA	B	F	IF	Os	+	—
Raja naevus	Cuckoo ray	MA	B	F	IS	Os	+	—
Raja undulata	Undulate ray	MA	B	F	IF	Os	+	—
Scomber scombrus	Mackerel	MA	P	/	IF	Op	+	—
Solea lascaris	Sand sole	MA	D	F	IS	Op	+	—
Sparus aurata	Gilt-head	MA	B	FV	OV	Ob	+	—
Torpedo marmorata	Marbled electric ray	MA	B	S	IF	Os	+	—
Trachurus trachurus	Horse mackerel	MA	D	S	IF	Op	+	+
Atherina presbyter	Sand smelt	MJ	P	/	IF	Ov	—	+
Clupea harengus	Herring	MJ	P	/	IF	Ob	+	+
Dicentrarchus labrax	Bass	MJ	D	M	IF	Op	++	++
Dicentrarchus punctatus	Spotted bass	MJ	D	M	IF	Op	+	+

Table 2
(continued)

Scientific name	Common name	Ecology	Vertical distribution	Bottom	Food	Reproduction	Frequency in trawling samples	Frequency in transect samples
Dicologlossa cuneata	Wedge sole	MJ	D	S	IS	Ob	—	—
Diplodus sargus	White seabream	MJ	D	MV	OV	Ob	+	—
Gadus morhua	Cod	MJ	D	F	IF	Op	+	—
Merlangius merlangus	Whiting	MJ	D	F	IF	Ob	++	+
Pleuronectes platessa	Plaice	MJ	B	F	IS	Op	+	—
Psetta maxima	Turbot	MJ	B	F	FS	Op	+	+
Scophthalmus rhombus	Brill	MJ	B	F	IF	Ob	+	—
Solea senegalensis	Senegalese sole	MJ	D	F	IS	Ob	+	—
Solea vulgaris	Sole	MJ	B	F	IS	Op	++	+
Spondyliosoma cantharus	Black seabream	MJ	B	MV	OV	Og	+	—
Trigla lucerna	Tub gurnard	MJ	D	F	IF	Ob	+	—
Trisopterus luscus	Bib	MJ	D	M	IF	Ob	+	—
Umbrina cirrosa	Shi drum	MJ	D	SR	IF	Op	+	+
Belone belone	Garpike	MS	P	/	IF	Ov	+	+
Chelon labrosus	Thick-lipped grey mullet	MS	D	RV	CS	Op	+	—
Ciliata mustela	Five-bearded rockling	MS	B	M	IF	Op	+	+
Dasyatis pastinaca	Sting ray	MS	B	F	IF	W	+	—
Engraulis encrasicolus	European anchovy	MS	P	/	PS	Op	+	++
Liza auratus	Golden mullet	MS	P	/	HC	Op	+	—
Sardina pilchardus	Pilchard	MS	P	/	CS	Op	+	+
Sprattus sprattus	Sprat	MS	P	/	PS	Op	+	++

approximately the same as those obtained using similarity analysis (BC). There are, however, several points to note:

- The Solway, which is clearly distinguishable from all the other estuaries in the BC similarity analysis, is in the same group as the Dutch estuaries (Oosterschelde, Westerschelde and Voordelta) and the Humber in the AHC.
- The right-hand section of the two dendrograms is ostensibly different: the variance breakdown is not the same using the two methods, but both arrive at the same four final groups.
- It should be noted that the three final groups distinguished by Elliott and Dewailly cannot be superimposed on the results obtained with the AHC.
- The Loire estuary changed group in the AHC. On the factorial maps (Fig. 6a), the Loire is in an intermediate position between the Iberian estuaries (Tagus, Ria de Aveiro and El Abra) and the Mersey–Tyne–Elbe group. It can also be seen that El Abra is clearly different from the other estuaries.

Table 3
Frequencies of each ecological guild in the lower (Low), middle (Mid) and the upper (Upp) parts of the estuary, in the samples. ++++, >75%; +++, 50–75%; ++, 12.5–50%; +, < 12.5%; –, 0%

Ecological guilds	Winter			Spring			Summer			Autumn			Total
	Low	Mid	Upp	Low	Mid	Upp	Low	Mid	Upp	Low	Mid	Upp	
(a) Small fish fauna													
Diadromous species (CA)	Ø	++++	++++	Ø	++++	++++	Ø	++++	++++	Ø	++++	++++	++++
Estuarine resident species (ER)	Ø	++++	++++	Ø	++++	++++	Ø	++++	++++	Ø	++++	++++	++++
Freshwater species (FW)	Ø	–	+	Ø	+	+	Ø	+	+	Ø	+	+	+
Marine adventitious species (MA)	Ø	—	—	Ø	—	+	Ø	—	—	Ø	—	—	+
Marine juvenile species (MJ)	Ø	++	++	Ø	++	++	Ø	++	++	Ø	++	++	++
Marine seasonal species (MS)	Ø	++	+	Ø	+++	++	Ø	++++	+++	Ø	+++	++	++
(b) The larger fish fauna													
Diadromous species (CA)	+++	+++	+++	++	+++	+++	++	++	+++	++++	+++	+++	+++
Estuarine resident species (ER)	+++	+++	++	++	+++	++	++	+++	++	++	+++	++	++
Freshwater species (FW)	—	+	+	—	+	+	—	+	+	—	+	+	+
Marine adventitious species (MA)	++	++	++	++++	++	++	++++	++	++	++	++	++	++
Marine juvenile species (MJ)	+++	+++	+++	++	+++	+++	++	++	+++	+++	+++	+++	+++
Marine seasonal species (MS)	++	+	++	+	+	+	+	+	+	++	++	++	++

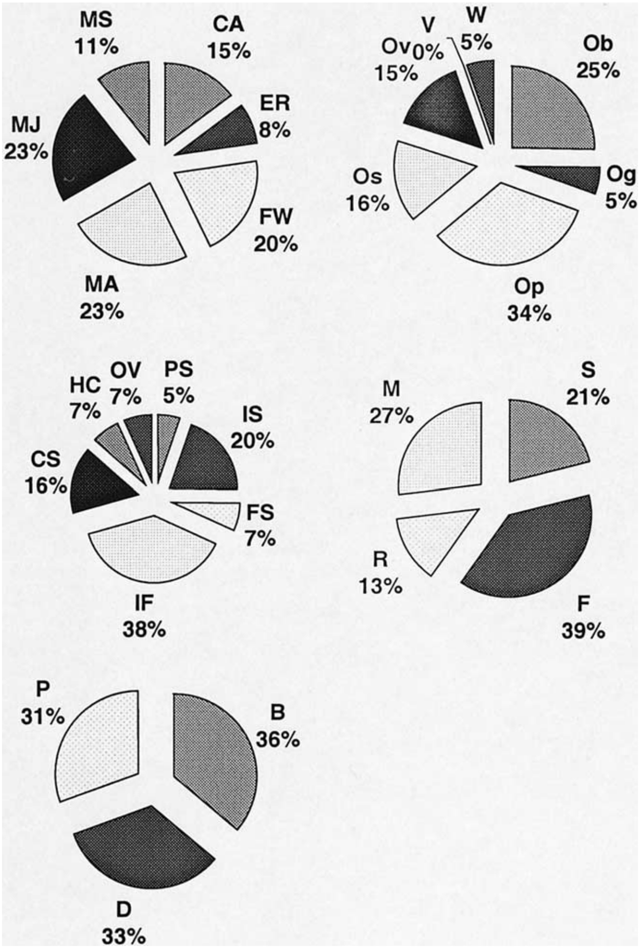

Fig. 3. Structure of the fish assemblages in the Gironde estuary. Percentage of each of the components of Elliott and Dewailly's guilds (1995) in the Gironde estuary. Abbreviations are listed in Table 1.

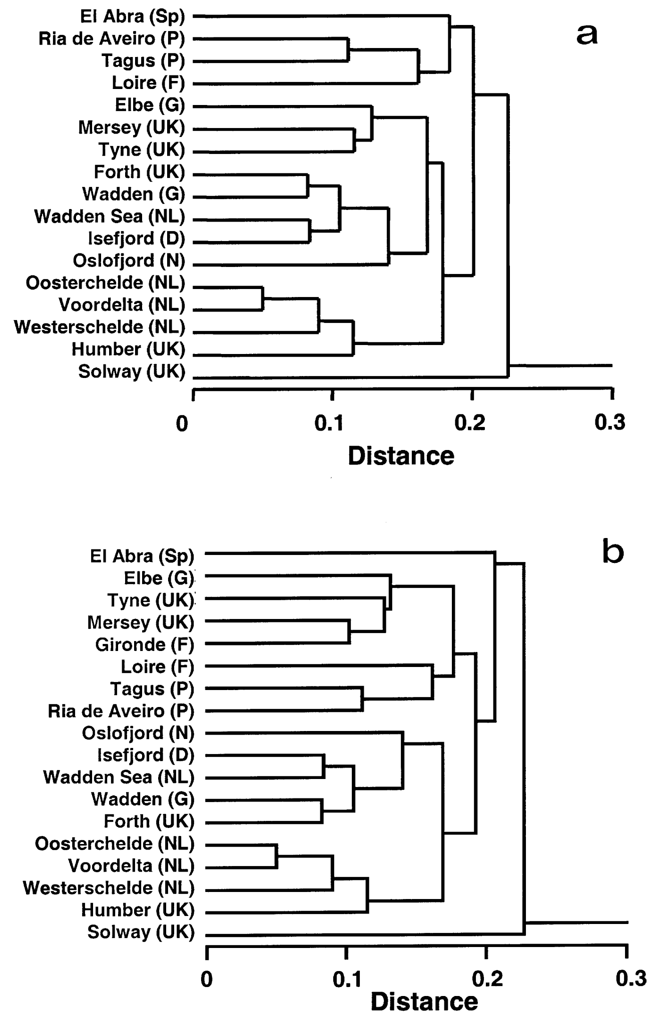

Fig. 5. Cluster analyses based on Bray-Curtis similarity index. (a) Without the Gironde estuary. (b) With the Gironde estuary.

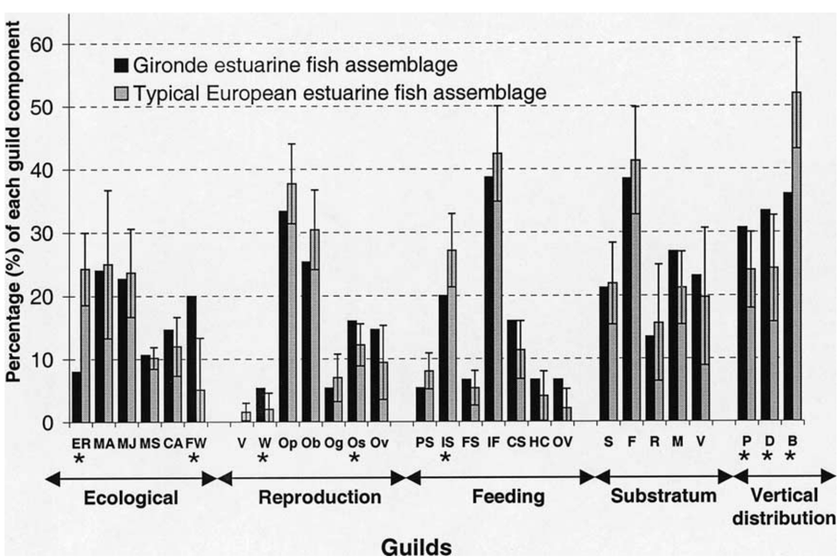

Fig. 4. Comparison of the structure of the Gironde estuarine fish assemblage to Elliot and Dewailly's typical european estuary. The mean percentage ± standard deviation of the guild components for the typical european estuary is represented. Abbreviations are listed in Table 1. Main differences are indicated by*.

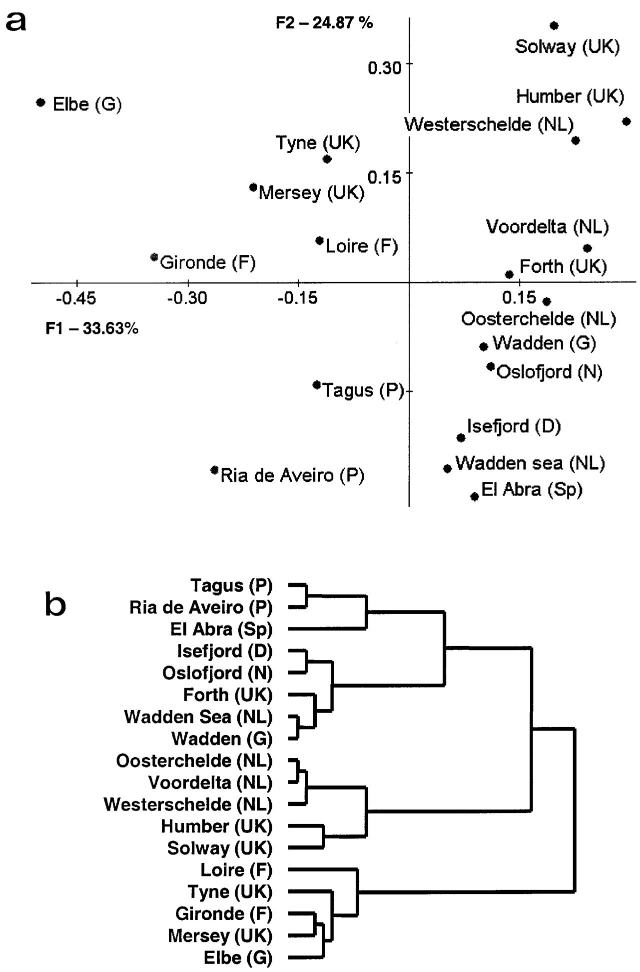

Fig. 6. Factor analyses and corresponding classifications based on Ward criterion.

The group that is composed of the Elbe, Tyne, Mersey, Loire and Gironde mainly differs from the other three groups on three criteria: the importance of freshwater species, a small proportion of species that spend their entire cycle in the estuary and a high proportion of pelagic species.

4. Discussion

4.1. Back to the guild concept

In a relatively large-scale comparison such as this one, the need to go beyond the strictly systematic level to investigate the functional dimension of species has led to the use of the guild concept (Ramade, 1993). The utility of the guild concept as a tool for understanding and simplifying the structure of complex ecosystems such as estuaries is well recognized (Garrison and Link, 2000; Link, 2002). It is widely used in estuarine fish assemblage studies (Pomfret et al., 1991; Rebelo, 1992; Hamerlynck and Hostens, 1994; Hostens and Hamerlynck, 1994; Thiel et al., 1995; Maes et al., 1998; Marshall and Elliott, 1998; Mathieson et al., 2000; Cabral et al., 2001; Thiel and Potter, 2001) even if the original meaning (Simberloff and Dayan, 1991) was much more restrictive than the definition we use in this study: a guild was defined as "a group of species that exploit the same class of environmental resources in a similar way" (Root, 1967 in Simberloff and Dayan, 1991). The term as used in this study incorporates the widest meaning of "functional group" and is similar to that used by Elliott and Dewailly (1995). It has the advantage of providing some indication of the extent to which a particular species uses an estuary. However, some reservations need to be mentioned. Assigning an ecophysiological characteristic to a species as in this study is highly subjective. Elliott and Dewailly have stressed in their article, that it means making the assumption that each species belongs to the same guilds in every environment in which it is found. The authors' classification may therefore be criticized, but it does have the great advantage of standardizing the task. Here, we have simply made a few additions regarding the ecological types of the species found in the Gironde without questioning the results given above (Table 4 and Fig. 7). Whether this classification will withstand the test of time is also debatable. A species may change guilds during its lifetime, growth cycle, year, and even during the day. Including the dimensions of space and time would be a valuable follow-up study to this piece of work. The concept of guild itself is, however, particularly useful in the estuarine context, but doubtless requires spatial and temporal reference in fluctuating transitional environments such as in estuaries.

Table 4
Ecological guilds encountered in the Gironde estuary. We display only the species in which ecological group is different from Table 2. M, marine fish; FW, freshwater fish; ER, estuarine resident fish; CA, diadromous migrant fish

Scientific name	Elliott and Dewailly ecological type	Ecological type in the Gironde estuary
Ammodytes tobianus	ER	M
Gasterosteus aculeatus	CA	FW
Nerophis ophidion	ER	M
Platichthys flesus	ER	CA
Syngnathus rostellatus	ER	M

This study can be considered to be an initial approach to the concept of the ecological niche in Odum's terms (1971). It makes it possible to examine two types of results: the use of the Gironde estuary by fish assemblages and the position of the Gironde among its European neighbours in terms of the specific composition of its fish fauna.

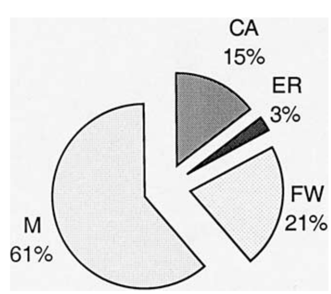

Fig. 7. Ecological guilds in the Gironde estuary with respect to Table 4.

4.2. The use of the Gironde estuary by fish

4.2.1. A rich and varied environment

The Gironde is a particularly unspoilt estuary (Mauvais and Guillaud, 1994) with a rich array of species. It also has the distinction of being the European estuary with the largest assemblage of migratory amphihaline fish (European eel, flounder, mullet, sea lamprey, river lamprey, European sturgeon, Atlantic salmon, sea trout, smelt, allis shad and twaite shad), making the Gironde a good reference estuary.

We shall simply compare the composition of the Gironde estuary's fish population to that of an average European estuary. While, overall the differences were minimal (the average estuary appears to be fairly representative), we would like to point out that the structure of the Gironde's fish assemblages differs from that of the average of the 17 European estuaries on several counts. We will discuss some points which, in our view, may be partly explained by the use of the estuary by those fish species that frequent it.

4.2.2. A temporary living environment

Relatively few species (8%) spend their entire life cycle in the Gironde. Among them, only the sand goby *Pomatoschistus minutus* is frequently found (Boigontier and Mounié, 1984). The Gironde estuary, therefore appears to be a temporary biotope for most species; 49% of the fish species found are present temporarily but regularly (juvenile migratory species, seasonal, catadromous or anadromous species). Marine adventitious species (MA) appear in the estuarine zone during spring and summer in the lower and middle parts of the estuary, when environmental conditions and salinity are particularly suitable. Marine seasonal species (MS) and most of marine juvenile species (MJ) occur in the Gironde estuary during summer and autumn, when salinity conditions are still favourable and when major predators are no longer present.

4.2.3. An environment that fulfils different types of ecological functions

The estuary seems to be a special environment that fulfils different types of ecological functions for different species. It is used as a corridor by amphihaline species –e.g., *Acipenser sturio* (Rochard et al., 2001), shad *Alosa fallax* and *Alosa alosa* (Rochard, 2001)–and enables them to gradually adapt to the change in salinity. It plays an important role in a trophic aspect for most seasonal or occasional migrants. Like other estuaries, it acts as a nursery ground (23% of juvenile migratory species). This is particularly true for the sole *Solea vulgaris* and *Solea senegalensis*. The high level of turbidity in the Gironde could also provide protection for the larval and juvenile stages against predation, as mentioned by Maes et al. (1998) for the Zeeschelde estuary. The above points indicate that this estuary is a place of transition and migratory route and can be regarded as a transitory key habitat as defined by Gili (2002).

4.2.4. Indicators of physical and environmental aspects

The Gironde's high turbidity is a major limiting factor in the development of phytoplankton in the estuary; thus, very few fish species with strict phytoplankton diets are found.

4.3. Importance of sampling

The two methods do not sample the same species in a similar manner (Table 2). Several differences in terms of presence and frequency of the different species are noticeable. The sampling methods used in the Gironde seem to be fairly complementary in the size range of fish sampled and in their sampling of the whole water body. This is not necessarily the case for the other estuaries, such as the Loire (Marchand and Elie, 1983). Compared to the Loire, our sample appears to be weighted more towards the pelagic part of the fish population. Owing to the use of the surface frames in the transect surveys and the wide-mouth trawl in the trawl surveys, our samples contained 31% pelagic species, while the data from other estuaries indicated an average of around 25%. Many estuary samples have been obtained using an otter trawl (Marchand and Elie, 1983; Hostens and Hamerlynck, 1994; Elliott and Dewailly, 1995) or beach seine (Thiel et al., 1995). Otter trawls, which are designed to target flatfish (Rogers et al., 1998; Riou et al., 2001), induce a significant underestimation of the pelagic component.

The space–time dimension of the sampling also plays an important role. Species richness as a function of sampling effort increases up to a theoretical threshold (Frontier, 1983; Dallot, 1998). The probability of capturing an additional species, therefore, increases with the surface area of the zone under exploration and the number of samples taken. So, spatially, while small estuarine fauna may not be picked up in the downstream area, the trawl surveys covered the entire area from the sea to the river, from the polyhaline to the oligohaline sectors. The salinity ranged from 30 to 0, and it is thus not surprising to find such a large proportion of freshwater species. The range of sampling, in the other estuaries under comparison, is not necessarily as extensive. This is particularly the case for the Loire (Marchand and Elie, 1983). Similarly, our data come from a relatively long time series (20 years for the small fish fauna, 5 years for the larger). The number of samples is therefore high (over 6700 frame samples and 1300 trawls). Consequently, it is not surprising that the number of species found in the Gironde (75) is the second highest of the 18 estuaries studied.

The issue of sampling is widely discussed in Elliott and Dewailly (1995). It would seem vital in comparative studies to take account of the bias introduced by different sampling methods. For instance, the book by Elliott and Hemingway (2002) discusses the validity and effectiveness of the different sampling techniques in more detail.

4.4. The Gironde compared to other European estuaries

As in most typological analyses, the choice of method and aggregation criteria is difficult and is obviously debatable.

The introduction of the Gironde does not to any extent affect the groups previously defined by Elliott and Dewailly (1995), whatever the method used. The clusters obtained appear relatively coherent and robust.

With the exception of the Solway, the BC classification obtained by Elliott and Dewailly (1995) featured three main groups: the first group containing the estuaries of the Dutch delta area (Oosterschelde, Westerschelde, Voordelta) and the Humber, a second comprising the French and Iberian estuaries, and a group described as representing North-Western Europe. Without mentioning gradients, the authors argued that fish assemblage structures reflected major differences in latitude. This is essentially a biogeographical interpretation and should be discussed. Initially, the classifications obtained with our two techniques give similar results insofar as they produce four groups, but the AHC does not produce the three groups found by Elliott and Dewailly. In particular, the Elbe, Tyne and Mersey form a separate group in the AHC, that is further supported when the Gironde is included in the analysis. Both techniques put the Gironde in the latter group of estuaries. A uniquely regional explanation for this would then seem unconvincing. Several hypotheses provide possible discriminating criteria that could explain the differences in assemblages. The criteria could be useful in comparisons between estuaries.

4.4.1. The physical dimension

Differences in size or morphology could partly explain ecological differences. Such criteria influence hydrology, salinity, the upstream saltwater penetration limit and the boundary of the external estuary. The latter concept is particularly interesting. It is not easy to quantify the influence (through freshening and turbidity) of an estuary on the coastal environment. Yet, several zones usually designated as estuaries may be "external estuaries". One example is the Voordelta, which is a coastal zone under the varying influence of the Rhine and Maas in the north and the Scheldt in the south (Hostens and Hamerlynck, 1994). It is therefore important to clearly demarcate and describe the system. Thus, for Roy et al. (2001), it is probably much more effective—if a comparative analysis is to be taken further—to include criteria, such as tidal range and upstream limit of saline intrusion, the surface area of the estuary, the substrate composition and turbidity. In this way, despite the fact that they are in the same geographical area, it is not surprising that the Dutch estuaries should be in the same group, as they have similar morphologies and are subject to the same level of marine influence.

Also, the Ria de Aveiro, which is here considered to be an estuary, is often described as a coastal lagoon (Rebelo, 1992). Similarly, it is debatable whether the mouth of the Rhine, which appears to have more of a delta morphology and located close to an amphidromic point of the North Sea can really qualify as an estuary, and thus be compared to conventional estuaries such as the Loire, Tyne or the Gironde. It is clear that the very definition of the concept of an estuary is important (Elliott and McLusky, 2002).

4.4.2. The history of the environment

Channel dredging, port facilities, gravel extraction, fishing, waste discharges, chemical and bacteriological contamination all have direct, or localized, impact to different extents and affect the distribution and dynamics of the biological assemblages they reach, even though the consequences of these activities are difficult to evaluate. The degree of anthropogenic influence on an estuary is an important criterion that is worthwhile associating with the history of Man's influence on the environment. This helps to characterize the change in the environment related to anthropogenic impact. One example is the spectacular change that has occurred on the banks of the Seine estuary, following the creation of navigation channels and artificial tidal flat (Bessineton, 1997). In contrast, there are now proposals to restore the environmental quality of estuaries such as the Elbe (Thiel et al., 1995). Examination of historical data also helps to identify species that may previously have been present in the environment. An often-quoted example in the Gironde region is the harbour porpoise (*Phocoena phocoena*), which was once frequently seen in the estuary (Laporte, 1853), particularly in the spring, but which has now totally disappeared (Wolff, 2000), although it is still found in the sea, albeit in smaller numbers. Also in the Gironde, the smelt *Osmerus eperlanus* has become much less abundant over the last 15 years (Pronier and Rochard, 1998). The disappearance of fish species from particular areas or the arrival of new ones may reveal changes in environmental quality in its widest sense.

5. Conclusion

Based on the structure of the Gironde estuarine fish assemblages, this study provides an initial indication of the ecological state of that environment. It has also made it possible to place the Gironde in relation to other major European estuaries and to make comparisons between them. In that, the study is part of the current trend in aquatic ecology research, which aims to use biocoenoses in general and ecological communities in particular (especially fish communities) as an indicator of environmental quality. The new European Water Framework Directive (EU, 2000) uses the same philosophy. A notable example of this type of approach is the work done to create a biotic index for estuarine environments on the western seaboard of the United States (Deegan et al., 1997).

Obviously, this view of estuarine populations, which takes account of neither time nor space, is still insufficient in an environment with high seasonal fluctuations, where the salinity gradient is an important factor in structuring communities (Rebelo, 1992; Hostens and Hamerlynck, 1994; Thiel et al., 1995; Maes et al., 1998; Maes, 2000).

Finally, this work raises a number of questions on the ecological diagnosis of estuaries. Important points include: the need for inter-calibration of sampling practices and definitions, the advantage of fairly extensive spatial and historical coverage and the inclusion of certain criteria for comparisons (tidal range, salinity and especially the upstream limit of saline intrusion, surface area, substrate and turbidity and change resulting from anthropogenic influence). The implementation of the typologies for estuaries (or transitional waters) is being carried out under the European Water Framework Directive (EU, 2000). If this type of comparative diagnostics is to be undertaken more widely, it seems important to classify European estuaries according to their physical and morphological criteria, before establishing ecological comparisons similar to those that exist on other continents (Roy et al., 2001).

Acknowledgements

We would like to thank Jean-François Bigot, Bernard Ballion, Christine Gazeau, Mario Lepage and all the other persons who took part in the different sampling campaigns. We wish to thank the support from EDF (The Blayais Nuclear Power Plant and Direction des études et des recherches, Département Environnement), the European Union LIFE programme and the Cemagref (Ecological State Programme, research grant "Estuaires: Typologie et évaluation de l'état écologique des milieux de transition de type estuarien à partir du cas de la Gironde") for supplying the data used in this study. The study is part of the ECOBAG programme. Finally, we thank Michael Elliott, Miran Aprahamian, and the anonymous referees who helped us to improve this article.

References

Albiges, C., Rochard, E., Elie, P., Boigontier, B., 1985. Etude de suivi halieutique de l'estuaire de la Gironde, 1984. Cemagref de Bordeaux, Div. ALA, EDF.

Allen, G.P., 1972. Etude des processus sédimentaires dans l'estuaire de la Gironde. Dr Thesis, Université de Bordeaux I.

Bachelet, G., Castel, J., Desprez, M., Marchand, J., 1997. Biocénose des milieux estuariens. In: Dauvin, J.C (Ed.), Les biocénoses marines et littorales françaises des côtes Atlantiques, Manche et mer du Nord : synthèse, menaces et perspectives. Laboratoire de Biologie des Invertébrés marins et Malacologie. Service du Patrimoine Naturel/IEGB/MNHN, Paris , pp. 130–140.

Bauchot, M.L., Pras, A., 1980. Guide des poissons marins d'Europe. Delachaux et Niestlé, Lausanne, Paris.

Bessineton, C., 1997. La création de vasières artificielles dans l'estuaire de la Seine. In: Auger, C., Verrel, J.L (Eds.), Les estuaires français : évolution naturelle et artificielle. IFREMER, Paris, pp. 111–121.

Boigontier, B., Mounié, D., 1984. Contribution à la connaissance de la dynamique de la macrofaune bentho-démersale et pélagique en Gironde. Tentatives et difficultés pour relativiser l'impact mécanique d'une centrale nucléaire: Le Blayais (Gironde). Dr Thesis, ENSA, Toulouse.

Cabral, H.N., Costa, M.J., Salgado, J.P., 2001. Does the Tagus estuary fish community reflect environmental changes? Clim. Res. 18, 119–126.

Castel, J., 1993. Long-term distribution of zooplankton in the Gironde estuary and its relation with river flow and suspended matter. Cah. Biol. Mar. 34, 145–163.

Dallot, S., 1998. Sampling properties of biodiversity indices. Océanis 24, 89–105.

Deegan, L.A., Finn, J.T., Buonaccorsi, J., 1997. Development and validation of an estuarine biotic integrity index. Estuaries 20, 601–617.

Dreux, P., 1986. Précis d'écologie. Presses universitaires de France, Paris.

Elie, P., 1997. Restauration de l'esturgeon européen *Acipenser sturio*. Contrat Life rapport final du programme d'exécution. Cemagref, Bordeaux, n °24.

Elie, P., Feunteun, E., Rigaud, C., 1990. The inshore brackish water domain of the French Atlantic coast: ecological functions for the exploited species-impact of physical development. Bull. Ecol. 21, 33–38.

Elie, P., Rochard, E., 1994. Migration des civelles d'anguilles (*Anguilla anguilla* L.) dans les estuaires, modalités du phénomène et caractéristiques des individus. Bull. Fr. Pêche Piscic. 335, 81–98.

Elliott, M., Dewailly, F., 1995. The structure and components of European estuarine fish assemblages. Neth. J. Aquat. Ecol. 29, 397–417.

Elliott, M., Hemingway, K., 2002. Fishes in Estuaries. Blackwell, London.

Elliott, M., McLusky, D.S., 2002. The need for definitions in understanding estuaries. Estuar. Coast. Shelf Sci 55, 815–827.

EU, 2000. Parliament and Council Directive 2000/60/EC of 23rd October 2000. Official Journal Establishing a Framework for Community Action in the field of Water Policy PE-CONS 3639/1/00 REV 1 .

Frontier, S., 1983. L'échantillonnage de la diversité spécifique. Stratégies d'échantillonnage en écologie. Masson, Les presses de l'université de Laval, Québec, pp. 416–436.

Garrison, L.P., Link, J.S., 2000. Dietary guild structure of the fish community in the Northeast United States continental shelf ecosystem. Mar. Ecol. Prog. Ser. 202, 231–240.

Gili, J.M., 2002. Towards a transitory or ephemeral key habitat concept. Trends Ecol. Evol. 17, 453.

Hamerlynck, O., Hostens, K., 1994. Changes in the Fish Fauna of the Oosterschelde estuary: a 10-year time-series of Fyke catches. Hydrobiologia 283, 497–507.

Hostens, K., Hamerlynck, O., 1994. The epimobile epifauna of the soft bottom in the subtidal Oosterschelde estuary: structure, function and impact of the storm surge barrier. Hydrobiologia 282/283, 479–496.

Keith, P., Allardi, J., 2001. Atlas des poissons d'eau douce de France. Muséum National d'Histoire Naturelle, Paris.

Laporte, E., 1853. Faune ichthyologique du département de la Gironde. Actes de la Société linnéenne de Bordeaux 19, 153–224.

Latouche, C., Jouanneau, J.M., 1994. Etude de la dynamique de l'eau et des sédiments. In: Mauvais, J.L., Guillaud, J.F (Eds.), Livre blanc de l'estuaire de la Gironde. IFREMER, Agence de l'eau Adour-Garonne, Bordeaux, pp. 8–21.

Legendre, L., Legendre, P., 1984. Ecologie numérique Tome 2 : La structure des données écologiques. Masson - Les presses de l'université de Laval, Québec.

Link, J., 2002. Does food web theory work for marine ecosystems? Mar. Ecol. Prog. Ser. 230, 1–9.

Maes, J., 2000. The structure of the fish community of the Zeeschelde estuary. Thesis, Leuven Katholeke Universiteit.

Maes, J., Taillieu, A., Van Damme, P.A., Cottenie, K., Ollevier, F., 1998. Seasonal patterns in the fish and crustacean community of a turbid temperate estuary. Estuar. Coast. Shelf Sci. 47, 143–151 (Zeeschelde Estuary, Belgium) .

Marchand, J., Elie, P., 1983. Contribution à l'étude des ressources bentho-démersales de l'estuaire de la Loire : biologie et écologie des principales espèces. 3. Comité Scientifique pour l'Environnement de l'Estuaire de la Loire.

Marshall, S., Elliott, M., 1998. Environmental influences on the fish assemblage of the Humber estuary, UK. Estuar. Coast. Shelf Sci. 46, 175–184.

Mathieson, S., Cattrijsse, A., Costa, M.J., Drake, P., Elliott, M., Gardner, J., Marchand, J., 2000. Fish assemblages of European tidal marshes: a comparison based on species, families and functional guilds. Mar. Ecol. Prog. Ser. 204, 225–242.

Maurice, L., 1994. La qualité des eaux de l'estuaire. In: Mauvais, J.L., Guillaud, J.F (Eds.), Livre blanc de l'estuaire de la Gironde, IFREMER, pp. 32–45 Agence de l'eau Adour-Garonne.

Mauvais, J.L., Guillaud, J.F., 1994. Etat des connaissances sur l'estuaire de la Gironde. Agence de l'eau Adour-Garonne, Toulouse.

Mc Dowall, R.M., 1988. Diadromy in Fishes, Migrations between Freshwater and Marine Environments. Croom Helm Publ., London.

Methven, D.A., Haedrich, R.L., Rose, G.A., 2001. The fish assemblage of a Newfoundland Estuary: diel, monthly and annual variation. Estuar. Coast. Shelf Sci. 52, 669–687.

Odum, E.P., 1971. Fundamentals of Ecology. W.B. Saunders Company, Philadelphia.

Pomfret, J.R., Elliott, M., O'Reilly, M.G., Phillips, S., 1991. Spatial and temporal patterns in the fish communities in two UK North Sea estuaries. In: Elliott, M., Ducrotoy, J.P (Eds.), Estuaries and Coasts: Spatial and Temporal Intrecomparisons. Olsen and Olsen, Fredensborg, Denmark, pp. 277–284.

Potter, I.C., Claridge, P.N., Warwick, R.M., 1986. Consistency of seasonal changes in an estuarine fish assemblage. Mar. Ecol. Prog. Ser. 32, 217–228.

Pronier, O., Rochard, E., 1998. Fonctionnement d'une population d'éperlan (*Osmerus eperlanus,* Osmériformes Osmeridae) située en limite méridionale de son aire de répartition, influence de la température. Bull. Fr. Pêche Piscic. 350/351, 479–497.

Ramade, F., 1993. Dictionnaire encyclopédique de l'écologie et des sciences de l'environnement. Ediscience International, Paris.

Rebelo, J.E., 1992. The ichthyofauna and abiotic hydrological environment of the Ria-De-Aveiro, Portugal. Estuaries 15, 403–413.

Riou, P., Le Pape, O., Rogers, S.I., 2001. Relative contributions of different sole and plaice nurseries to the adult population in the Eastern Channel: application of a combined method using generalized linear models and a geographic information system. Aquat. Living Resour. 14, 125–135.

Rochard, E., 2001. Migration anadrome estuarienne des géniteurs de grande alose *Alosa alosa,* allure du phénomène et influence du rythme des marées. Bull. Fr. Pêche Piscic. 362/363, 853–867.

Rochard, E., Lepage, M., Dumont, P., Tremblay, S., Gazeau, C., 2001. Downstream migration of juvenile European sturgeon *Acipenser sturio* L. in the Gironde estuary. Estuaries 24, 108–115.

Rogers, S.I., Rijnsdorp, A.D., Damm, U., Vanhee, W., 1998. Demersal fish populations in the coastal waters of the UK and continental NW Europe from beam trawl survey data collected from 1990 to 1995. J. Sea Res. 39, 79–102.

Roy, P.S., Williams, R.J., Jones, A.R., Yassini, I., Gibbs, P.J., Coates, B., West, R.J., Scanes, P.R., Hudson, J.P., Nichol, S., 2001. Structure and function of south-east Australian estuaries. Estuar. Coast. Shelf Sci. 53, 351–384.

Simberloff, D., Dayan, T., 1991. The Guild concept and the structure of ecological communities. Annu. Rev. Ecol. Syst. 22, 115–143.

Sorbe, J.C., 1980. La macrofaune vagile de l'estuaire de la Gironde : distribution et migration des espèces, modes de reproduction et régimes alimentaires. Océanis 6, 562–579.

Sottolichio, A., Castaing, P., 1999. A synthesis on seasonal dynamics of highly-concentrated structures in the Gironde estuary. C.R. Acad. Sci. Sér. II Fasc.A- Sci. Terre Planètes 329, 795–800.

Thiel, R., Potter, I.C., 2001. The ichthyofaunal composition of the Elbe Estuary: an analysis in space and time. Mar. Biol. 138, 603–616.

Thiel, R., Sepulveda, A., Kafemann, R., Nellen, W., 1995. Environmental-factors as forces structuring the fish community of the Elbe estuary. J. Fish Biol. 46, 47–69.

Williot, P., Rochard, E., Castelnaud, G., Rouault, T., Brun, R., Lepage, M., Elie, P., 1997. Biological characteristics of European Atlantic sturgeon, *Acipenser sturio*, as the basis for a restoration program in France. Environ. Biol. Fish 48, 359–372.

Wolff, W.J., 2000. The south-eastern North sea: losses of vertebrate fauna during the past 2000 years. Biol. Conserv. 95, 209–217.