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THE STRUCTURE AND COMPONENTS OF EUROPEAN ESTUARINE FISH ASSEMBLAGES

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KEYWORDS: European estuaries; fish community; guilds; feeding; reproduction.

ABSTRACT

This paper discusses the structure of fish assemblages using information from 17 European estuarine areas (in the British Isles, Portugal, Belgium, France, the Netherlands, Germany, Norway and Spain). Binary (presence/absence) and quantitative data for each assemblage have been used to assess the assemblage structure according to taxonomy (*i.e.* species identity). Following this, a total of 29 functional guilds were created in order to describe the use made of an estuarine area for each taxon encountered: feeding preferences, reproduction type, substratum preferences (for bottom dwelling fish) and position within the water column (vertical preference guild). The paper focuses on the designation and determination of the proportions of the guild members of the fish assemblage within each estuary. Ecological guilds within the assemblage include estuarine residents, marine juvenile migrants, catadromous and anadromous migrants, marine seasonal users, and freshwater and marine adventitious species. Feeding guilds include detritivores, planktonic feeders, infaunal croppers and sediment ingesters, piscivores, and active predators of mobile crustaceans. Reproduction guilds include planktonic and demersal spawners and those using brood-protection. The substratum preference indicates the proportions of sand, mud, rock and vegetation dwellers, and the vertical preference denotes benthic, demersal or pelagic species. The analysis has allowed both the estuaries to be grouped according to taxonomic and guild similarity and the characterisation of a typical European estuarine fish assemblage. Within the limits posed by differing sampling methods, times of sampling and survey rationale, there is a high similarity between estuaries. The data indicate common patterns of estuarine usage irrespective of the differences between the estuaries although such patterns cannot be interpreted fully given the incomplete knowledge of their physical and anthropogenic characteristics.

INTRODUCTION

Estuaries have long been regarded as important sites for fish, for long-term residence as well as nursery and overwintering, as migration routes and areas which naturally support large numbers of fish (McHUGH, 1967; HAEDRICH, 1983). Similarly, the impact of human activities on the fishes' habitat and the utility of fish study in estuarine management has received much attention (*e.g.* ELLIOTT *et al.*, 1988; COSTA and ELLIOTT, 1991; POMFRET *et al.*, 1991). Much previous information has been provided by studies on single estuaries (*e.g.* HAMERLYNCK 1993; ELLIOTT and TAYLOR, 1989) or at most on two or three estuaries (POMFRET *et al.*, 1991; COSTA and ELLIOTT, 1991; HOVENKAMP and VAN DER VEER, 1993). There have been studies of inshore fish assemblage structure within countries (*e.g.* HENDERSON, 1989) and the International Council for the Exploration of the Sea (ICES) is charged with co-ordinating international studies on commercial marine species. Within the southern hemisphere, there have been extensive studies of estuarine fish assemblages (BLABER, 1991; BLABER *et al.*, 1989) but it is of note that within Europe there have been no previous studies which compare estuarine fish assemblages over large

Fig. 1. Location of the estuarine and coastal areas included in the present study.

Table 1. Estuaries covered in this study and the source of the main data sets.

Site	Country	Latitude	Source of publication
Tagus	Portugal	38° 40´ N	COSTA and ELLIOTT, 1991
Ria de Aveiro	Portugal	40° 40´ N	REBELO, 1992
El Abra	Spain	43° 50´ N	Entec Ltd., unpubl.
Loire	France	47° 10´ N	MARCHAND, unpubl.
Westerschelde	The Netherlands	51° 20´ N	HAMERLYNCK, 1993; HOVENKAMP and VAN DER VEER, 1993
Oosterschelde	The Netherlands	51° 40´ N	HAMERLYNCK, 1993; HOVENKAMP and VAN DER VEER, 1993
Voordelta	The Netherlands	52° 00´ N	HAMERLYNCK, 1993; HOVENKAMP and VAN DER VEER, 1993
Wadden Sea	The Netherlands/Germany	53° 00´ N	DANKERS *et al.*, 1979
Elbe	Germany	53° 50´ N	THIEL, *et al.*, 1995
Mersey	England	53° 20´ N	HOLLAND, 1989; TAYLOR, 1983, 1985
Solway	England/Scotland	54° 50´ N	Unpubl. data
Humber	England	53° 40´ N	MARSHALL and ELLIOTT, unpublished and in press.
Tyne	England	55° 00´ N	POMFRET *et al.*, 1991
Forth	Scotland	56° 10´ N	POMFRET *et al.*, 1991; COSTA and ELLIOTT, 1991
Isefjord	Denmark	55° 50´ N	RASMUSSEN, 1973
Oslofjord	Norway	59° 10´ N	NASH, 1988

Table 2. Summary of the sampling programmes' methodology for each area; nk = not known.

Estuary	Period	Frequency	Stations	Methods	Species	Families
Tagus	1976-91	monthly	6	Beam trawl	45	23
Ria de Aveiro	1987-88	monthly	10	Purse seine-type net (`chincha')	55	27
El Abra	1989-93	annually	7	Beam trawl	23	16
Loire	1981-82	monthly	nk	Beam trawl	36	24
Westerschelde	1989	monthly	14	Beam trawl	33	21
Oosterschelde	1989	monthly	12	Beam trawl	39	23
Voordelta	1989	monthly	22	Beam trawl	40	24
Wadden Sea (NL)	1931-78	various	nk	Beam trawl, fyke net, etc.	94	51
Wadden Sea (G)	1931-78	various	nk	Beam trawl, fyke net, etc.	67	39
Elbe	1989-92	monthly	11	Framed gape stow net, Demersal otter trawl	62	28
Mersey	1981	nk	4	Beam trawl, Intake screens	51	31
Solway	1992-93	quarterly	nk	Beam/frame trawl, beach seine, Push net	22	15
Humber	1992-93	quarterly	14	Beam trawl	26	18
Tyne	1982-89	9/year	6	Beam trawl	32	21
Forth	1985-89	monthly	11	Beam/Agassiz trawl,	43	27
Isefjord	1940-70	nk	110	Commercial, angling, beam trawl	70	38
Oslofjord	1981-82	monthly	2	Bag beach seine	40	20

geographical areas. In contrast, the COST 647 initiative (KEEGAN, 1991a, b) attempted with some success to compare marine benthic invertebrate populations and communities throughout western Europe.

Most studies which describe and compare the structure of communities and assemblages do so through an analysis of the taxonomic attributes and components, *i.e.* the presence, abundance and/or biomass of species (or other taxonomic separation). However, it is increasingly accepted that an analysis of other attributes which describe ecological interactions and features also provides valuable information. There are two groups of such attributes which

Table 3. Summary of characteristics of estuarine areas studied.

Tagus	Large open basin with constricted entrance, high freshwater flows (300 m^3s^{-1}) and large area (320 km^2), extensive saltmarshes and industrialisation (U.N.E.S.C.O./C.N.A.(D.G.Q.A.) 1984; COSTA, 1988; GAUDENCIO *et al.*, 1991).
Ria de Aveiro	Lagoonal, 47 km^2, relatively shallow to 10m depth, with extensive industrialisation and fisheries (BARROSA, 1980; REBELO, 1992).
Abra	Narrow estuary, 29km^2, small amount of industrialisation, small amount of information (Entec Ltd., Newcastle, pers. comm.).
Loire	Estuary 285 km^2, rock banks and large mudflats, with some anthropogenic influences; water quality deterioration in upper reaches (MARCHAND, 1993; MARCHAND and ELIE, 1983).
Westerschelde	Deep channels and intertidal sandbanks, up to 4.6m tidal range, flow of 105 m^3s^{-1}, large amount of industrialisation (HEIP, 1989; HAMERLYNCK, 1993; PETERS and STIRLING, 1976; MEES *et al.*, 1993).
Oosterschelde	Storm surge barrier at mouth, flow reduced to 55 m^3s^{-1}, concomitant changes to characteristics, wider basin, little industry (NIENHUIS and SMAAL, 1994).
Voordelta	Shallow coastal ebb-tidal deltaic area, extensive sandbanks and channels; Dutch-Belgian delta area (LOUTERS *et al.*, 1991; HAMERLYNCK *et al.*, 1992; HAMERLYNCK, 1993).
Wadden Sea	German and Dutch area, shallow coastal area, extensive (8000 km^2), predominantly sandy bed, up to 4m tidal range (DANKERS *et al.*, 1979).
Elbe	Narrow estuary, heavily industrialised from Hamburg, tidal range of >3m (KÜHL, 1972; ARGE ELBE, 1984, THIEL *et al.*, 1995).
Mersey	Extensively industrialised, only recently regained fish community; bed of soft and hard clay, mud and some rock areas; 8m tidal range, mean flow 66 m^3s^{-1} (N.E.R.C., 1975).
Solway	Shallow area, large intertidal sandbanks with little industrialisation or urbanisation; extensive saltmarsh areas (PERKINS and WILLIAMS, 1966).
Humber	Shallow, well-mixed and highly turbid, up to 20m depth, 7m tidal range, 220 m^3s^{-1} maximum flow, muddy and mixed sand-mud substratum; moderately industrialised (MARSHALL and ELLIOTT, in press, NRA 1993).
Tyne	Canalised and heavily industrialised; sand, silt and rock bottom, relatively narrow (POMFRET *et al.*, 1991; JAMES, 1978).
Forth	Mixed bed of mud and muddy-coarse; moderate saltmarsh areas; depth to 70m at mouth, 6m tidal range, moderately industrialised (McLUSKY, 1987).
Isefjord	extensive, up to 280 km^2, mean depth 7m; sand-mud, fine sand and rocky areas; shallow with 0.2 m tidal range; very little industrialisation (RASMUSSEN, 1973).
Oslofjord	Deep, typically fjordic structure, muddy basin, very high organic pollution loadings; fish data from shallow area (NASH, 1988; BEYER, 1968).

may be used irrespective of taxonomic identity - the individual size and/or biomass of the community members, *i.e.* to give the importance of an individual dependent on size (*e.g.* see SCHWINGHAMER, 1988), and the use of functional groups or guilds which denote the biological characteristics of organisms (*e.g.* nature of reproduction, feeding, spatial and temporal use of an area) (*e.g.* FAUCHALD and JUMARS, 1979; WORD, 1990). Such ecotrophic guilds have been proposed for fish by McHUGH (1967) and developed by other workers (*e.g.* HAEDRICH, 1983; ELLIOTT and TAYLOR, 1989; HENDERSON, 1989; ELLIOTT *et al.*, 1990). However, the increasing availability of data for estuarine fish communities gives an oppórtunity for their use in greater detail such that the present paper aims to further develop the number and type of guilds and to give the proportions of taxa in each guild in each estuary.

The present study is part of a programme which attempts to present and summarise the taxonomic characteristics of estuarine fish assemblages of the European Atlantic seaboard; to assess the resemblances and dissimilarities between the areas, according to the different biological characteristics observed (taxonomic and biological characteristics); to make comparisons at family level (presence-/absence analysis) and species level (presence-/absence and semi-quantitative analysis); to define ecotrophic guilds based on several parameters; to define different categories of fish species which inhabit the European estuaries; to provide the background for determining biology-environment links and biology-biology links; and to provide further fish-related information for estuarine management.

Data included here have been derived from the European Atlantic seaboard covering the area from Norway to Portugal and they have been selected for their quality and quantity and, to a lesser extent, comparability of methods. It is of note that most of the methods used are biased towards demersal and benthic species although the shallow nature of the estuaries dictates that pelagic forms are also taken (see below). Data are from published or unpublished sources or provided by workers from studies in progress.

SOURCES OF DATA AND DATA MANIPLULATION

The estuaries under study and data sources are given in Fig. 1 and Table 1 and the studies' main features are given in Table 2. These illustrate some of the similarities between the surveys but also indicates that there exists a large spatial and temporal database for estuarine fish assemblages. The assessment here largely ignores the temporal data provided by the studies and also the spatial information within any single estuary. The characteristics of the estuaries are given in brief in Table 3 and more fully in the references cited. The term estuary has been used in its broadest sense, as the transition zone between freshwater areas and the open coast, and is as used by the authors of the data sources, thus its definition may differ with area.

Many techniques are available for interpreting community data (ELLIOTT, 1994) but the analysis here has been restricted to the most simple multivariate technique, cluster analysis (SOUTHWARD, 1978; LUDWIG and REYNOLDS, 1988). The available data were used to create an inventory of fish species for all estuaries and the taxonomy was standardised by removing synonyms; WHEELER (1969) and WHITEHEAD *et al.* (1984) were used as the main taxonomic authorities. The use of common names in some studies and the merging by authors of taxa to family (*e.g.* Mugilidae) or group (*e.g.* 'gobies') provided some difficulty in merging data sets and resulted in statistical analyses being carried out before and after these difficulties were resolved. A binary matrix (of presence/absence of taxa per estuary) was created and the similarity of estuaries assessed by producing a Q-mode cluster analysis (dendrogram) based on the Jaccard similarity coefficient. The binary analyses were carried out for taxonomic attributes on both a species and family basis. Similarly, a semi-quantitative data matrix was created by taking from the studies some measure of abundance or relative presence of species and then defining each species according to the semi-quantitative scale: abundant (5), frequent (4), common (3), occasional (2), rare (1), absent (0). Thus species which occurred often in an area were given the same score as species which were in high abundance or biomass. The similarity between estuaries was determined by computing the Bray-Curtis similarity coefficient followed by production of a dendrogram using group average sorting. The semi-quantitative analyses were carried out for taxonomic attributes only on a species basis.

The biological characteristics of each species were then determined using literature and information form the studies and each species was assigned to guilds in each of several categories. A quantitative cluster analysis, again using the Bray-Curtis similarity coefficient and dendrogram production, was then used on the data showing the percentages of taxa within each category (guild) in each estuary.

This treatment was designed to reveal affinities between estuaries according to the functional groups present.

Development of ecotrophic guilds

This was based on several parameters: (i) ecological type, indicating the use and importance of an estuary made for fish; (ii) place occupied by a species within the water/sediment column, or vertical distribution; (iii) bottom-type (substratum) preference for benthic and demersal fishes, thus those designated as pelagic fishes were not included in this guild; (iv) food preference of each species; (v) mode of reproduction used by each species. This approach produced a total of 29 guild components from 5 guild categories. The designated guilds were:

Ecological guilds

ER - Truly estuarine resident species, which spend their entire lives in the estuary; MA - Marine adventitious visitors, which appear irregularly in the estuary but have no apparent estuarine requirements; CA - Diadromous (catadromous or anadromous) migrant species, which use the estuary to pass between salt and fresh waters for spawning and feeding; MS - Marine seasonal migrants species, which have regular seasonal visits to the estuary, usually as adults; MJ - Marine juvenile migrant species, which use the estuary primarily as a nursery ground, usually spawning and spending much of their adult life at sea but often returning seasonally to the estuary; FW - Freshwater adventitious species, which occasionally enter brackish waters from fresh waters but have no apparent estuarine requirements.

Vertical distribution guilds

These guilds give information on the degree of dependence of the fishes on the bottom substratum: P - Pelagic fishes, living in the main water column; D - Demersal fishes, living in the water layer just above the bed; B - Benthic fishes, living on or in the substratum.

Substratum (preference) guilds

This category has been used for the benthic and demersal fishes to assess the ability of a bed to support a particular species; it has been simplified with few categories: S - Sandy bottom, for species living solely on sand; F - Soft bottom, for species living on sand, mud and/or fine gravel; R - Rough bottom, for species living on rocks, stones and/or pebbles; M - Mixed or various bottom, for species living indiscriminately on any kind of bottom; V - For species living above or amongst the vegetation or seaweeds. The latter category has been added concurrently to S, F, R, M for species living among the vegetation on a certain bottom type.

Feeding guilds

As fish feed on plankton (P), invertebrates (I) such as molluscs, crustaceans or insects, other fishes (F), plants (V) and/or detritus (D) either singly or in combination, it has been necessary to generate guilds which allow for the combinations: PS - fishes feeding strictly on plankton; IS - fishes feeding strictly on invertebrates (crustaceans, molluscs); FS - fishes feeding strictly on other fish species; IF - fishes feeding on invertebrates and fishes; CS - carnivorous fishes, but other than PS, IS, FS or IF; HC - fishes partly herbivorous, partly carnivorous, but not omnivorous; OV - omnivorous fishes.

Reproductive guilds

Three main reproduction types exist within fishes: V - Viviparous, giving birth to a 'free' living progeny; W - Ovoviviparous, giving birth to living organisms first enclosed in eggs; O - Oviparous, producing a certain quantity of eggs evolving into larvae and then adults. However, as most fish are oviparous, this category has been subdivided: Op - Species producing pelagic eggs; Ob - Species producing benthic/bottom deposited eggs; Og - eggs guarded by one or both parents; Os - eggs shed/protected in a nest or case or pouch; Ov - eggs deposited in/stuck to vegetation.

RESULTS

Taxonomic assemblage structure

Table 4 lists the species taken; the complete species per estuary matrices can be obtained from the authors. The estuaries each held between 22 and 94 species from 15 to 51 families (Table 2). There was no significant trend with increasing latitude and the areas with the greatest taxonomic richness were the Dutch Wadden Sea and the Isefjord in Denmark (Fig. 2). It is of note that these areas have been extensively studied, the studies may cover the greatest time period and that the fish records are from many different surveys. The data indicate a large variability in the middle latitudes covered, the area with greatest data.

The similarity assessment based on binary data for species separated the Iberian and French estuaries from the remainder and then one cluster

Table 4. Species encountered and guild characteristics. See text for explanation of abbreviations.

Nb	Scientific name	Type	Habitat	Bottom	Food	Reproduction
1	*Abramis ballerus*	FW	P	/	P,I	Ov
2	*Abramis brama*	FW	D	M,V	P,I	Ov
3	*Acipenser sturio*	CA	D	S	I,F	Ob
4	*Agonus cataphractus*	ER	B	F	I	Ov
5	*Alburnus alburnus*	FW	P	/	I,J,F	Ov
6	*Alopias vulpinus*	MA	P	/	I,F	W
7	*Alosa alosa*	CA	P	/	P	Ob
8	*Alosa fallax*	CA	P	/	P,F	Ob
9	*Ammodytes lanceolatus* (= *Hyperoplus lanceolatus*)	MA	B	S	P,F	Ob
10	*Ammodytes marinus*	MA	B	S	P,I,F	Ob
11	*Ammodytes tobianus* (= *Ammodytes lancea*)	ER	B	S	P	Ob
12	*Anarhichas lupus*	MA	D	R	I	Ob
13	*Anguilla anguilla*	CA	B	F	P,I,J,F	Op
14	*Aphia minuta* (=*Aphya pellucida*)	ER	P	/	P	Os
15	*Argyrosomus regius* (= *A. regium*; *Sciaena aquila*)	MA	P	/	I,F	Op
16	*Arius latiscutatus* (= *Arius gambensis*)	?	?	?	?	?
17	*Arnoglossus laterna*	MA	B	F	I,F	Ob
18	*Arnoglossus thori*	MA	B	R	I,F	Ob
19	*Aspitrigla cuculus*	MA	B	F	I,F	Ob
20	*Aspius aspius*	FW	P	/	I,J,F	Ob
21	*Atherina boyeri* (= *Hepsetia boyeri*)	ER	P	/	P,I	Ov
22	*Atherina presbyter* (= *Hepsetia presbyter*)	MJ	P	/	I,F	Ov
23	*Balistes carolensis*	MA	D	R,V	I	Og
24	*Barbus barbus*	FW	D	S	I,J	Ob
25	*Belone belone*	MS	P	/	I,F	Ov
26	*Blennius gattorugine* (= *Parablennius gattorugine*	MA	B	R,V	I,V	Og
27	*Blennius pholis*	MA	B	R	I,V	Og
28	*Blicca bjoerkna*	FW	P	/	P,I,V	Ov
29	*Boops boops*	MA	D	M	O	Op
30	*Brama brama (Brama raji)*	MA	P	/	I,F	Op
31	*Buglossidium luteum*	MA	B	S	I	Op
32	*Callionymus lyra*	MA	B	F	I	Op
33	*Callionymus reticulatus*	MA	B	S	I	Op
34	*Carassius auratus*	FW	P	/	O	Ov
35	*Carassius carassius*	FW	P	/	O	Ov
36	*Centrolabrus exoletus*	MA	D	R,V	I	Ob
37	*Centrolophus niger*	MA	P	/	P,I,F	Op
38	*Cetorhinus maximus*	MA	P	/	P	V
39	*Chelon labrosus* (= *Mugil chelo, Crenimugil labrosus*)	MS	D	R,V	P,I,D	Op
40	*Chondrostoma nasus*	FW	D	R I,	V	Ob
41	*Ciliata mustela* (= *Onos mustelus*)	MS	B	M I,	F	Op
42	*Ciliata septentrionalis*	MA	P	/	I	Op
43	*Clupea harengus*	MJ	P	/	- I,F	Ob
44	*Cobitis taenia*	FW	B	F	I,V	Ov
45	*Conger conger*	MA	B	R	I,F	Op
46	*Coregonus oxyrinchus*	ER	P	/	P,I	Ob
47	*Cottus gobio*	FW	B	R	I,F	Og
48	*Crystallogobius linearis*	MA	P	/	P	Og
49	*Ctenolabrus rupestris*	MA	D	R,V	I	Og
50	*Cyclopterus lumpus*	MS	B	R	I,F	Og
51	*Cyprinus carpio*	FW	D	M,V O		Ov
52	*Dasyatis pastinaca*	MS	B	F	I,F	W
53	*Deltentosteus quadrimaculatus*	MA	D	F	?	Ob
54	*Dicentrarchus labrax* (= *Morone labrax*)	MJ	D	M	I,F	Op
55	*Dicologoglossa cuneata*	MJ	D	S	I	Ob
56	*Diplodus annularis*	MJ	D	S,V	I	Ob
57	*Diplodus sargus*	MJ	D	M,V	O	Ob
58	*Diplodus vulgaris*	MJ	D	M,V	I	Ob
59	*Engraulis encrasicolus*	MS	P	/	P	Op
60	*Entelurus aequoreus*	MA	D	M,V	?	W
61	*Esox lucius*	FW	D	M,V	I,F	Ov
62	*Euthynnus pelamis*	MA	P	/	I,F	Op
63	*Eutrigla gurnardus*	MS	B	S	I,F	Op
64	*Gadus morhua*	MJ	D	F	I,F	Op
65	*Gaidropsarus mediterraneus*	MA	B	R	I,F,V	Op
66	*Gaidropsarus vulgaris*	MA	B	R	I,F	Op
67	*Galeorhinus galeus*	MA	D	S	I,F	W
68	*Gambusia affinis*	FW	D	R	I	W
69	*Gasterosteus aculeatus*	CA	P	/	I,F	Og
70	*Gobio gobio*	FW	D	S	I,J	Ov
71	*Gobius ater*	ER	D	M,V	?	?
72	*Gobius niger*	ER	B	F,V	I,J,F	Ob
73	*Gobius paganellus*	ER	B	R,V	I	Ob
74	*Gobius strictus*	ER	D	R	?	?
75	*Gobiusculus flavescens* (= *Coryphopterus flavescens*)	MA	P	/	I	Ov
76	*Gymnocephalus cernua*	FW	P	/	I,J,V	Ov
77	*Hippocampus hippocampus*	MA	D	M,V	I	W
78	*Hippocampus ramulosus*	ER	D	M,V	I	W
79	*Hippoglossoides platessoides*	MA	B	F	I,F	Op
80	*Hippoglossus hippoglossus*	MA	B	F	I,F	Op
81	*Hypophthalmichthys molitrix*	FW	?	?	?	?
82	*Labrus bergylta*	MA	D	R,V	I	Os
83	*Labrus viridis*	MA	D	R,V	I,F	Ob
84	*Lagocephalus lagocephalus*	MA	P	/	I	?
85	*Lamna nasus*	MA	P	/	F	W
86	*Lampetra fluviatilis* (= *Petromyzon fluviatilis*)	CA	B	F	F(paras.)	Os
87	*Lampetra planeri*	FW	B	F	/	Ob
88	*Lampris luna*	MA	P	/	I,F	Op
89	*Leuciscus cephalus*	FW	P	/	O	Ov
90	*Leuciscus idus*	FW	P	/	I	Ov
91	*Leuciscus leuciscus*	FW	P	/	I,J,V	Ob
92	*Limanda limanda*	MJ	B	S	I,F	Ob
93	*Liparis liparis*	ER	B	M	I,F	Ov
94	*Liparis montagui*	MA	B	R,V	I	Ov
95	*Liza aurata* (= *Mugil auratus*)	MS	P	/	P,I,J,V	Op
96	*Liza ramada* (= *Mugil capito*)	CA	P	/	P,I,D,V	Op
97	*Liza saliens*	CA	P	/	P,I	Os
98	*Lophius piscatorius*	MA	B	M	F	Os
99	*Maurolicus muelleri*	MA	P	/	I	Op

Table 4. Contd.

Nb	Scientific name	Type	Habitat	Bottom	Food	Repro-duction
100	*Melanogrammus aeglefinus*	MA	D	M	I,F	Ob
101	*Merlangius merlangus*	MJ	D	F	I,F	Ob
102	*Merluccius merluccius*	MA	D	M	F	Op
103	*Micromesistius poutassou*	MA	P	/	I	Op
104	*Microstomus kitt*	MA	B	R	I	Op
105	*Mola mola*	MA	P	/	I,V	Op
106	*Molva molva*	MA	D	R	I,F	Ob
107	*Mugil cephalus*	ER	P	/	P,I,D,V	Op
108	*Mullus surmuletus*	MA	B	R	I	Op
109	*Mustelus asterias*	MA	D	M	I,F	W
110	*Mustelus mustelus*	MA	D	M	I	V
111	*Myoxocephalus scorpius* (=*Acanthocottus scorpius)*	ER	B	F,V	I,F	Og
112	*Nerophis lumbriciformis*	ER	B	R,V	I,F	Og
113	*Nerophis ophidion*	ER	D	M,V	I	Og
114	*Noemacheilus barbatulus*	FW	B	M,V	I	Ob
115	*Oedalechilus labeo* (= *Mugil labeo, Liza labeo)*	MA	P	/	?	?
116	*Onchorhynchus mykiss* (=*Salmo gairdneri)*	FW	P	/	O	Ob
117	*Osmerus eperlanus*	CA	P	/	I,F	Ob
118	*Pagellus bogaraveo* (= *Pagellus centrodontus)*	MJ	D	M	O	Op
119	*Parablennius sanguinolentus*	MA	D	R,V	V	Ob
120	*Perca fluviatilis*	FW	P	/	P,I,F	Ov
121	*Petromyzon marinus*	CA	B	F	F(paras.)	Os
122	*Pholis gunnellus*	ER	B	M,V	I	Og
123	*Phoxinus phoxinus*	FW	P	R	P,J,V	Ob
124	*Platichthys flesus* (= *Pleuronectes flesus)*	ER	B	F	I,F	Op
125	*Pleuronectes platessa*	MJ	B	F	I	Op
126	*Pollachius pollachius*	MJ	D	R	F	Op
127	*Pollachius virens*	MA	D	R	I,F	Op
128	*Polyprion americanus*	MA	P	/	I,F	Op
129	*Pomatoschistus lozanoi*	MA	B	S	I	Ob
130	*Pomatoschistus microps*	ER	B	S	I	Ob
131	*Pomatoschistus minutus*	ER	B	S	I	Ob
132	*Pomatoschistus pictus*	MA	B	S	I	Ob
133	*Pungitius pungitius*	FW	P	/	I	Og
134	*Raja batis*	MA	B	S	I,F	Os
135	*Raja brachyura*	MA	B	S	I	Os
136	*Raja clavata*	MA	B	S	I	Os
137	*Raniceps raninus*	ER	B	M	I,F	Ob
138	*Rhinonemus cimbrius* (= *Onos cimbrius)*	MA	B	F	I	Op
139	*Rhodeus sericeus*	FW	B	F	P,I,J,V	Os
140	*Roccus labrax*	MA	?	?	?	?
141	*Rutilus rutilus*	FW	P	/	P,I,J,V	Ov
142	*Salmo salar*	CA	P	/	I,J,F	Os
143	*Salmo trutta*	CA	P	/	I,J,F	Os
144	*Sardina pilchardus*	MS	P	/	P,I	Op
145	*Scardinius erythrophthalmus*	FW	P	/	I,J	Ov
146	*Scomber scombrus*	MA	P	/	I,F	Op
147	*Scomberesox saurus*	MA	P	/	P,I,F	Op
148	*Scophthalmus maximus* (= *Psetta maxima)*	MJ	B	F	F	Op
149	*Scophthalmus rhombus*	MJ	B	F	I,F	Ob
150	*Scorpaena spp*	MA	D	M,V	I,F	Os
151	*Scyliorhinus canicula*	MA	D	F	I,F	Os
152	*Scyliorhinus stellaris*	MA	D	R	I,F	Os
153	*Sebastes marinus*	MJ	P	/	I,F	W
154	*Sebastes viviparus*	MA	B	R	I,F	W
155	*Serranus cabrilla*	MA	B	M,V	I,F	Ob
156	*Solea lascaris*	MA	D	F	I	Op
157	*Solea senegalensis*	MJ	D	F	I	Ob
158	*Solea solea (= Solea vulgaris)*	MJ	B	F	I	Op
159	*Sparus aurata*	MA	B	F,V	O	Ob
160	*Spinachia spinachia*	ER	D	R	I	Os
161	*Spondyliosoma cantharus*	MJ	B	M,V	O	Og
162	*Sprattus sprattus*	MS	P	/	P	Op
163	*Squalus acanthias*	MA	B	F	I,F	W
164	*Squatina squatina*	MA	B	F	I,F	W
165	*Stizostedion lucioperca*	FW	D	R	I,F	Ob
166	*Symphodus bailloni* (= *Crenilabrus bailloni)*	MA	D	R,V	I	Ob
167	*Symphodus melops* (= *Crenilabrus melops)*	ER	D	R,V	I	Ob
168	*Syngnathus abaster*	ER	D	F	I	Ob
169	*Syngnathus acus*	ER	B	M	I,F	Os
170	*Syngnathus rostellatus*	ER	B	S,V	I	Os
171	*Syngnathus typhle* (=*Siphonostomus typhle)*	ER	D	F,V	I,F	Os
172	*Taurulus bubalis* (= *Acanthocottus bubalis)*	MA	B	R,V	I,F	Ov
173	*Thunnus thynnus*	MA	P	/	I,F	Op
174	*Tinca tinca*	FW	P	/	I,J	Ov
175	*Trachinotus ovatus*	MA	P	/	I,F	Op
176	*Trachinus draco*	MA	B	F	I,F	Op
177	*Trachinus vipera* (= *Echiichthys vipera)*	MA	B	F	I,F	Op
178	*Trachurus trachurus*	MA	D	S	I,F	Op
178	*Trigla lucerna*	MJ	D	F	I,F	Ob
180	*Trisopterus luscus*	MJ	D	M	I,F	Ob
181	*Trisopterus minutus*	MA	D	R	I,F	Ob
182	*Umbrina canariensis*	MA	D	F	I	Op
183	*Xiphias gladius*	MA	P	/	F	Op
184	*Zeugopterus punctatus*	MA	B	R	I,F	Ob
185	*Zeus faber*	MA	P	R,V	I,F	Op
186	*Zoarces viviparus*	ER	B	M,V	I	V

of the Delta area (Oosterschelde, Voordelta and Westerschelde) with the UK estuaries (Forth, Tyne, Humber, Solway) (Fig. 3a). The Elbe and Mersey showed similarity then the Dutch and German Wadden Sea areas together with the Scandinavian Isefjord and Oslofjord. The analysis based on family data at a binary level and the semi-quantitative species level produced similar clusters but at a greater degree of similarity (Figs. 3b and c). In general the estuaries were linked with a similarity ranging from 25 to 65%.

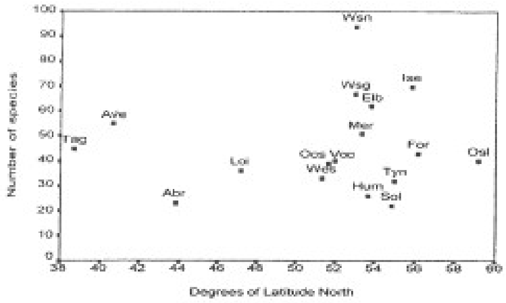


Fig. 2. The change in species richness with latitude; Key: Abr, Abra; Ave, Ria de Aveiro; Elb, Elbe; For, Forth; Hum, Humber; Ise, Isefjord; Loi, Loire; Mer, Mersey; Oos, Oosterschelde; Osl, Oslofjord; Sol; Solway; Tag, Tagus; Tyn, Tyne; Voo, Voordelta; Wsn, Wadden (NL); Wsg, Wadden (G); Wes, Westerschelde.

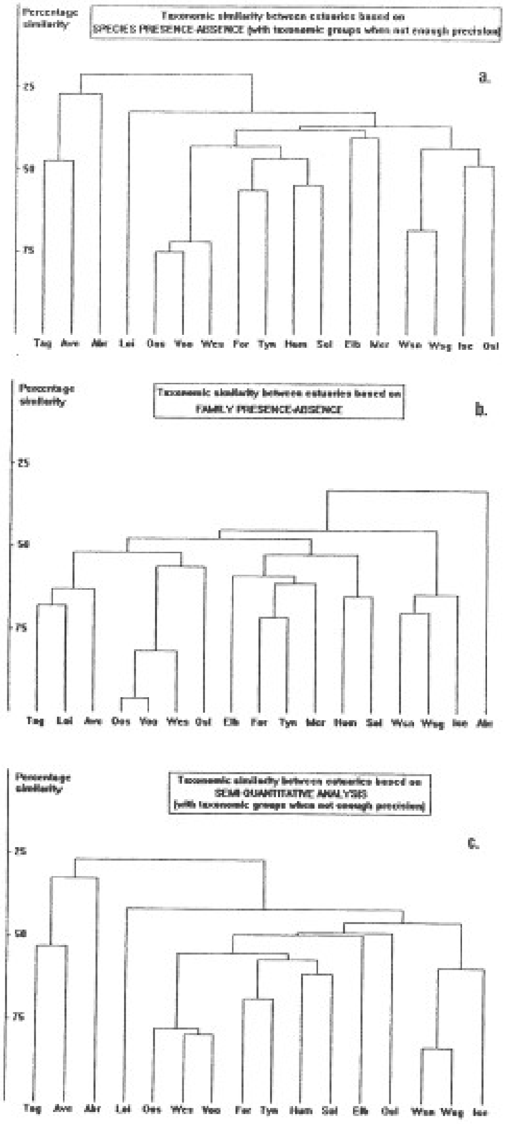


Fig. 3. Similarity analysis (a) for species binary data, (b) for family binary data; (c) for species semi-quantitative data (Mersey not included through insufficient data); (a) and (b) based on Jaccard coefficient whereas (c) based on Bray-Curtis coefficient. Area codes as in Fig. 2.

similarity analysis produced 3 clusters - I (the Iberian and French estuaries), II (the Dutch Delta areas and the UK areas Forth, Tyne and Humber), and III (the Wadden and Scandinavian areas and the Mersey and Solway). The areas were clustered with a high degree of similarity at >75%.

Structure of assemblages based on guilds

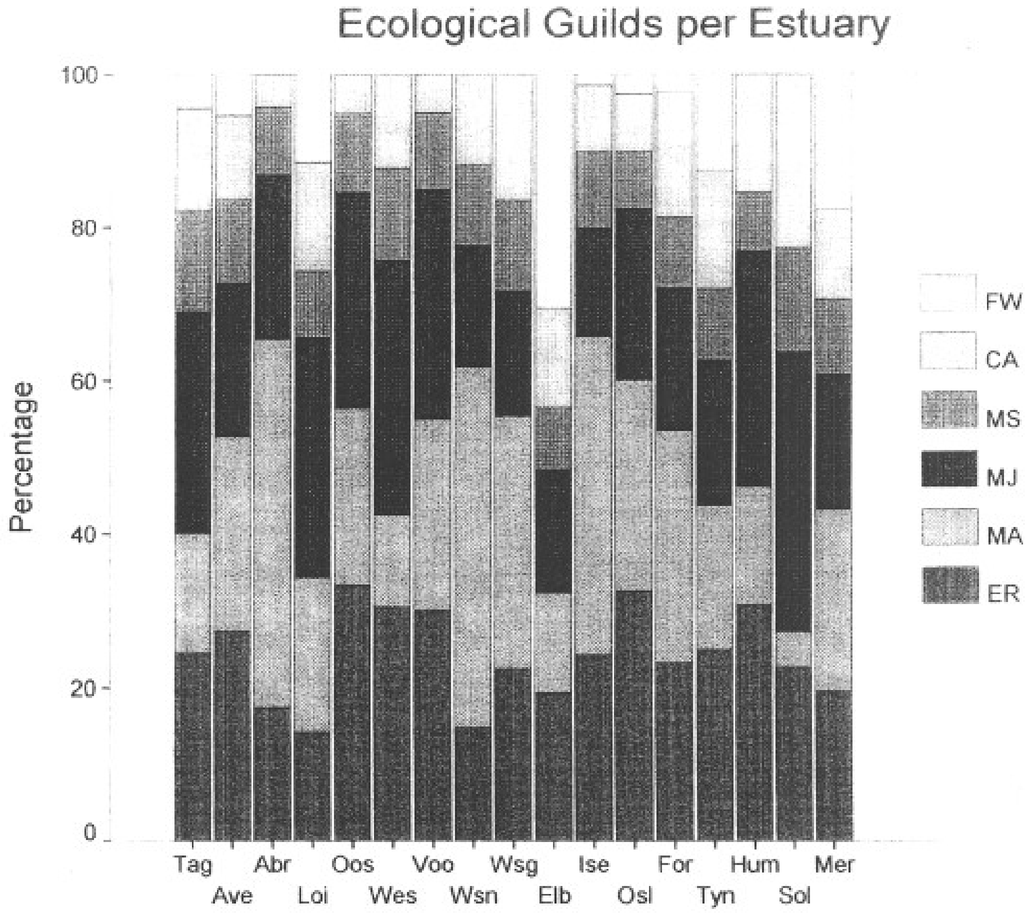
The species taken in all surveys and the guilds assigned to them are given in Table 4; the incidence of species in each of the guild components per estuary is given in Table 5.

Ecological guilds per estuary

The relative proportions of each guild varied between estuaries although there were few major differences between estuaries (Fig. 4a). Most had either none or only small proportions of freshwater species (FW) although the Elbe had 31%. The greatest variability appeared to be in the proportion of marine adventitious species (MA). The close similarity between the assemblages is shown by the dendrogram (Fig. 4b) in which the most dissimilar linkages are still at 70% similarity. The Elbe is separated through its high freshwater component and the Solway through its low marine adventitious group. The remaining groups are I (Tagus, Westerschelde, Humber, Oosterschelde, Voordelta and Oslofjord), II (Aveiro, German Wadden, Forth, Tyne, Mersey and Loire), and III (Abra, Dutch Wadden and Isefjord). The separation of the Wadden areas across 2 groups indicates the similarity of the groups.

Vertical distribution guilds per estuary

As there were only 3 guilds then major differences are unlikely (Figs. 5a and b). The majority of estuaries had more than 50% of the taxa with a benthic (B) preference and then similar proportions of demersal (D) and pelagic (P) species (Fig. 5a). The more southern estuaries, the Tagus, Aveiro, Abra and Loire had the lowest proportion of benthic species and the Abra had few pelagic species. The



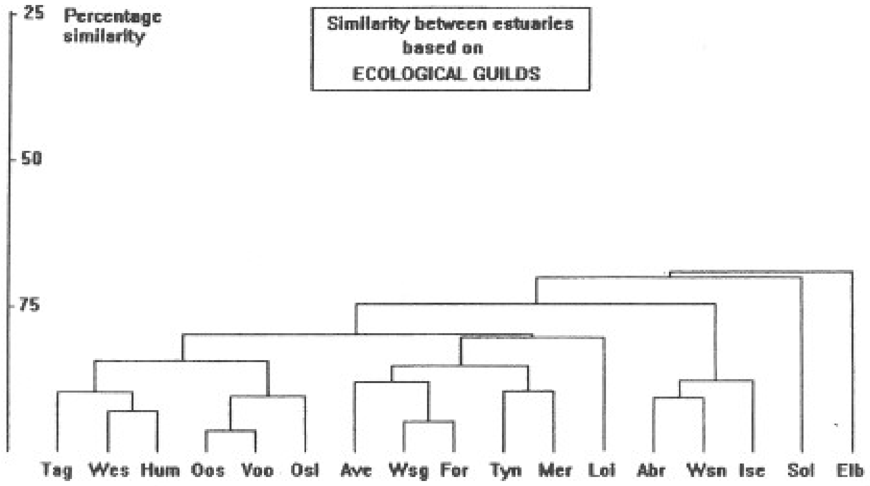


Fig. 4. The relative presence of ecological guilds per estuary - top: percentage block diagram; bottom: similarity dendrogram (see text for guild definitions and abbreviations; Area codes as in Fig. 2).

Table 5. Percentage guild components for each estuary. See text for abbreviations.

	Ecological Guild						Reproduction Guild							
Estuary	ER	MA	MJ	MS	CA	FW	V	W	Op	Ob	Og	Os	Ov	PS
Tagus	25	16	29	13	13	4	0	2	42	36	4	11	4	11
Ria de Aveiro	27	26	20	11	11	5	0	4	31	37	6	10	12	6
El Abra	18	48	22	9	4	0	0	4	44	44	0	9	0	9
Loire	14	20	31	9	14	11	0	0	51	31	0	9	9	6
Oosterschelde	33	23	28	10	5	0	3	3	36	33	8	8	10	11
Westerschelde	30	12	33	12	12	0	3	0	33	39	6	9	9	9
Voordelta	30	25	30	10	5	0	3	3	40	33	8	8	8	10
Wadden (NL)	15	47	16	11	12	0	3	9	39	22	10	12	5	7
Wadden (G)	23	33	16	12	16	0	2	6	37	27	8	15	6	8
Elbe	19	13	16	8	13	31	2	0	23	30	8	12	25	3
Isefjord	24	41	14	10	9	1	3	3	45	20	13	9	7	9
Oslofjord	33	28	23	8	8	3	3	0	33	30	15	15	5	13
Forth	23	30	19	9	16	2	2	0	42	26	9	14	7	5
Tyne	25	19	19	9	16	12	3	0	34	22	9	16	16	3
Humber	31	15	31	8	15	0	0	0	42	31	4	15	8	12
Solway	23	5	37	14	23	0	0	0	36	32	5	18	9	9
Mersey	20	24	18	10	12	18	0	0	33	24	6	18	20	6
Average	24	25	24	10	12	5	2	2	38	30	7	12	9	8
%CV	24	49	30	18	40	163	91	132	17	21	56	30	64	36
Std. Dev.	6	12	7	2	5	8	1	3	7	7	4	4	6	3
Maximum	33	48	37	14	23	31	3	9	51	44	15	18	25	13
Minimum	14	5	14	8	4	0	0	0	23	20	0	8	.0	3

	Feeding Guild						Substratum Guild					Vertical Guild		
Estuary	IS	FS	IF	CS	HC	OV	S	F	R	M	V	P	D	B
Tagus	22	7	29	13	9	9	15	38	18	29	32	24	38	38
Ria de Aveiro	28	2	26	16	14	10	10	40	28	23	43	27	36	36
El Abra	35	4	35	13	0	4	19	38	14	29	29	9	44	48
Loire	17	11	43	14	6	3	15	37	22	26	7	23	34	43
Oosterschelde	34	0	47	5	3	0	25	38	13	25	22	18	21	62
Westerschelde	27	3	49	9	3	0	35	42	0	23	12	21	18	61
Voordelta	33	3	46	5	3	0	30	42	3	24	15	18	18	65
Wadden (NL)	26	9	43	9	5	2	21	31	25	22	19	29	23	48
Wadden (G)	23	8	49	11	3	0	20	41	20	18	18	27	22	51
Elbe	20	5	36	22	9	5	18	44	15	23	23	35	18	47
Isefjord	30	6	44	9	1	1	20	35	27	18	31	30	20	50
Oslofjord	38	5	35	10	0	0	27	37	27	10	30	25	25	50
Forth	26	7	51	9	2	0	23	34	23	20	9	19	19	63
Tyne	25	6	44	13	9	0	17	48	9	26	22	28	13	59
Humber	31	8	46	4	0	0	33	52	5	10	5	19	15	65
Solway	18	5	55	14	0	0	19	69	0	12	0	27	24	50
Mersey	28	2	43	18	2	2	25	36	17	22	19	29	24	47
Average	27	5	42	11	4	2	22	41	16	21	20	24	24	52
%CV	22	54	19	41	99	147	30	21	61	28	56	26	36	18
Std. Dev.	6	3	8	5	4	3	7	9	9	6	43	6	9	9
Maximum	38	11	55	22	14	10	35	69	28	29	43	35	44	65
Minimum	17	0	26	4	0	0	10	31	0	10	0	9	13	36

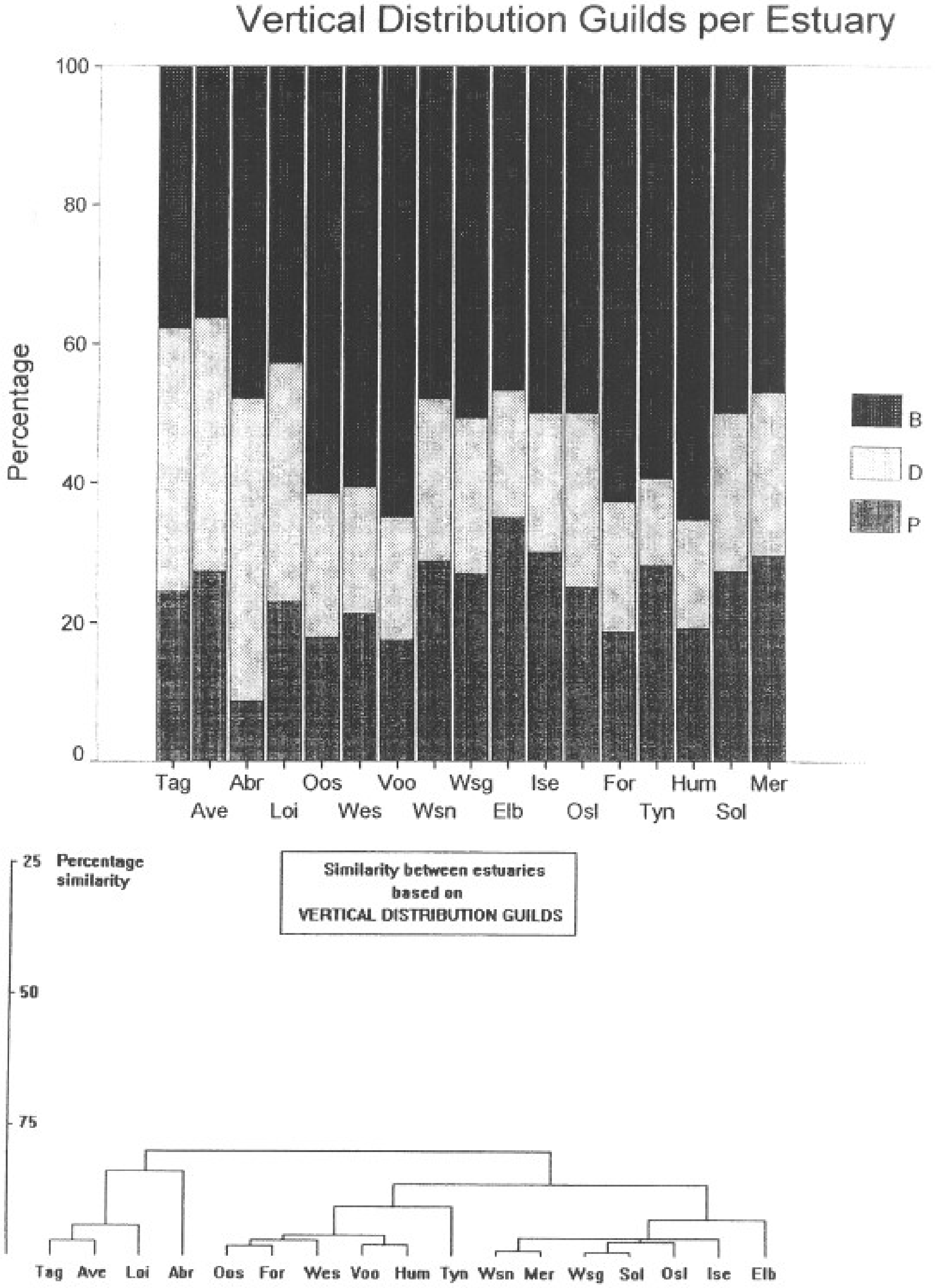


Fig. 5. The relative presence of vertical distribution guilds per estuary - top: percentage block diagram; bottom: similarity dendrogram (see text for guild definitions and abbreviations; Area codes as in Fig. 2).

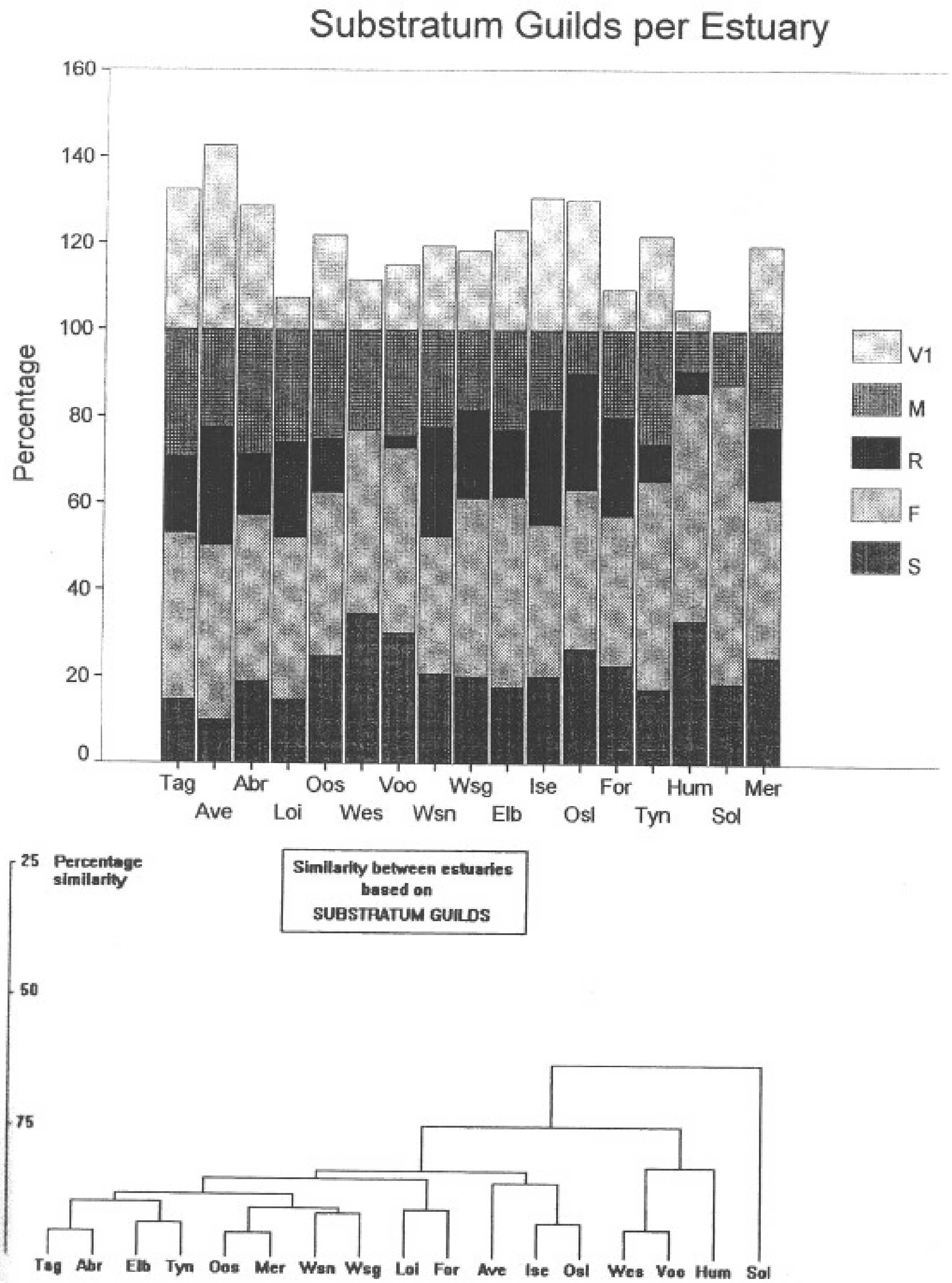


Fig. 6. The relative presence of substratum preference guilds per estuary - top: percentage block diagram; bottom: similarity dendrogram (see text for guild definitions and abbreviations; Area codes as in Fig. 2).

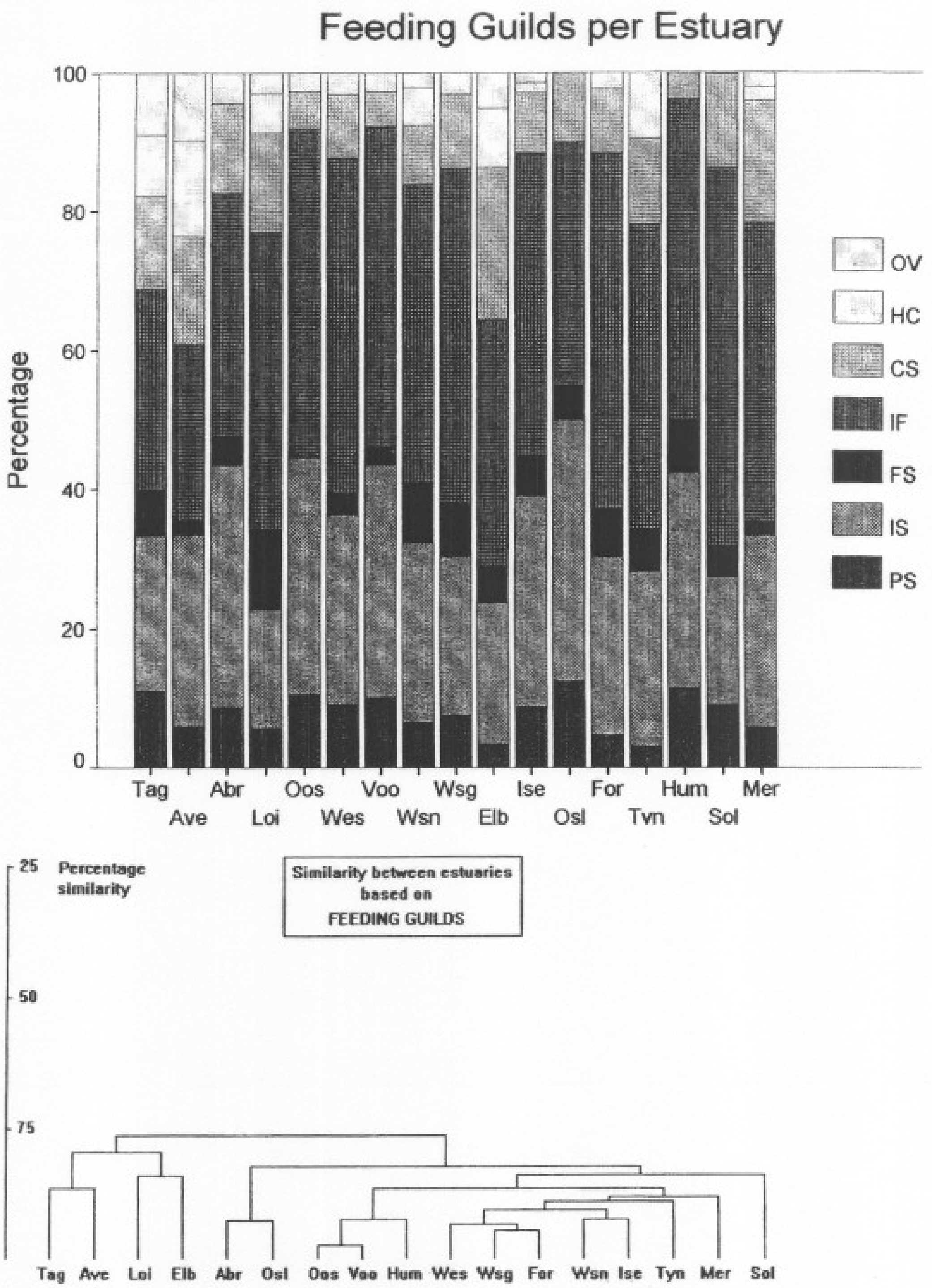


Fig. 7. The relative presence of feeding guilds per estuary - top: percentage block diagram; bottom: similarity dendrogram (see text for guild definitions and abbreviations; Area codes as in Fig. 2).

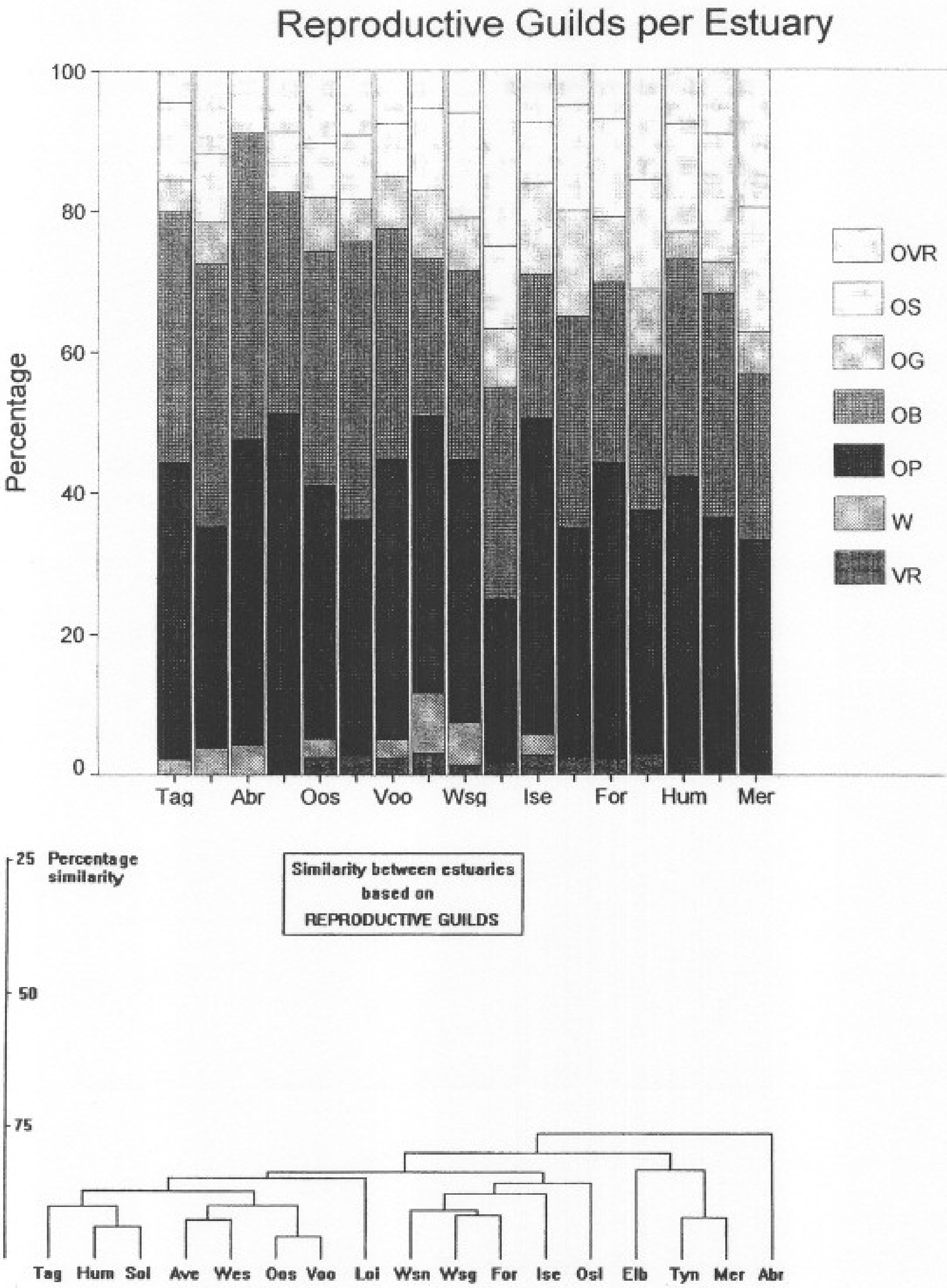


Fig. 8. The relative presence of reproductive guilds per estuary - top: percentage block diagram; bottom: similarity dendrogram (see text for guild definitions and abbreviations; Area codes as in Fig. 2).

Fig. 9. Similarity dendrogram based on total guild components (Area codes as in Fig. 2).

Substratum preference guilds per estuary

The predominant guild was for soft bottom, including sand and mud, or sandy bottom, which were found in all areas (Fig. 6a) although the presence of these guilds is especially dependent on the sampling methodology employed. Fish with a preference for rough bottom were absent in the Westerschelde and Solway and low in the Humber, Tyne and Voordelta. The proportion of taxa with a preference for vegetation varied from 0% in the Solway to >30% in the Iberian and Scandinavian areas. The similarity analysis reveals few differences between areas; the areas were clustered at >80% similarity apart from the small group Westerschelde, Voordelta and Humber, while the Solway was separated because of the absence of one guild (V) and the dominance of a few others (Fig. 6b). The absence of a guild preferring vegetation is unusual given the nature of the Solway which has extensive saltmarsh areas (see Table 3). Again it should be emphasised that few of the surveys included especially studied estuarine vegetated areas such as saltmarsh.

Feeding guilds per estuary

Most of the estuaries were dominated by invertebrate and invertebrate/fish predators with omnivores, herbivores and piscivores being in a minority or even absent from certain areas (Fig. 7a). Each area has some planktivores although the proportion was always small. The catholic preferences of many species dictated that there was overlap in the guild definitions (see Table 4). The overall similarity as shown by the percentage block diagram is well-indicated by the cluster analysis (Fig. 7b). Although all areas are similar at a level >75%, there are only 2 main groupings - the Tagus, Aveiro, Loire and Elbe are separated from the remaining areas.

Reproductive guilds per estuary

Although all estuaries had a large number of species producing pelagic eggs (Op), there was a large or larger number with benthic or bottom deposited eggs (Ob) (Fig. 8a). The assemblage of certain areas, *e.g.* the Loire and Abra, was composed almost entirely of representatives of these two guilds. Most of the areas had a few viviparous (V) and/or ovoviviparous (W) types and all had species dependent on vegetation for egg deposition. The dendrogram for these guilds indicated that the Abra differed from all other areas, possibly because of the paucity of guild components, while the group containing the Elbe, Tyne and Mersey, which all had a lower proportion of pelagic and benthic spawners, was separated from the remainder (Fig. 8b).

All guilds

In addition to each guild being analysed separately, all were combined in a single similarity analysis. The dendrogram produced after combining all guilds again indicate an overall similarity of >75% although the estuaries are in 3 groups with the Solway exhibiting slightly different characteristics from all other areas (Fig. 9). Group I, at the highest similarity, contains the Dutch Delta areas (Oosterschelde, Westerschelde, Voordelta) and the Humber; Group II contains the Wadden Sea (Dutch and German), UK estuaries (Forth, Tyne, Mersey), and Scandinavian areas (Isefjord, Oslofjord), while group III contains the Iberian and French estuaries.

DISCUSSION

This study has shown, firstly, the value of the guild approach and, secondly, the overall structure of the European estuarine fish assemblages. The guild approach is considered informative but has a fundamental difficulty in the amount of information available to assign individual species to a category. In some cases a species designation is uncertain or it could be assigned to two categories; if the latter then here the species has been assigned to the more frequent designation encountered. This subjectivity may have produced possible differences from original authors' designations where used. It is likely that many species may each have a combination of guilds within any single guild type; however, the number of guilds has been kept to a minimum thus making further assumptions about the species' characteristics. Furthermore, it has been assumed that a species will have the same guilds in all areas in which it is encountered. These assumptions cannot be tested fully without further spatial and temporal data. However, the assumptions hold in previous comparisons of estuaries (*e.g.* COSTA and ELLIOTT, 1991; HOVENKAMP and VAN DER VEER, 1993).

A further source of bias here, during the similarity analysis for all guilds, is the equal weighting given to all guilds. It is considered that some of the guilds, especially the ecological guild components, should be regarded as being of greater importance as they integrate other guilds and describe the overall usage made of an estuary and the time spent in the estuary. The use of the ecological guilds includes information on seasonal and spatial distribution where this is available although the absence of further quantitative information dictates that no weighting can yet be given to different guilds.

The dominance of certain characteristics of the estuarine assemblage as shown here will reflect any bias introduced by the sampling methods. For example, the estuaries were sampled predominantly by bed trawling or netting over the bed and although the methods differed with area, it is considered that the data are still comparable. The differing methods used in the various studies do not explain the differences in community structure, either at the taxonomic or functional level, although the predominance of bed trawling and other sampling will have imposed part of the similarity between surveys. The methods are likely to bias the samples towards certain guilds, *e.g.* benthic/demersal in preference to pelagic, epibenthic/infaunal feeders in preference to planktonic feeders, and soft/sand substratum in preference to vegetative and rocky/mixed bed species. However, as shown elsewhere (ELLIOTT *et al.*, 1990), the use of bed trawling methods in shallow estuarine areas takes a representative pelagic population, especially at the qualitative level but to a large extent also at the quantitative level.

The analysis here has allowed comparison both between the estuaries based on each of the taxonomic and guild approaches and between the patterns produced by the two approaches. The degree of similarity between the estuaries was higher for the guilds approach than for the taxonomic basis although this partly is the result of the fewer attributes being included. Based on different treatments (of taxonomic resolution and semi-quantitative/qualitative), the taxonomic approach produced 3 groups: group I contains the Iberian estuaries (Tagus, Ria de Aveiro, Abra) and the Loire which have similar taxonomic assemblages; group II contains the Dutch Delta areas (Oosterschelde, Westerschelde, Voordelta), and the UK estuaries (Forth, Tyne, Humber, Mersey and Solway) together with the Elbe; and group III links the Isefjord with the Dutch and German Wadden sea areas; the Oslofjord was not consistent across the treatments. The guild component approach, using information for all guilds taken together, also produced 3 groups with the Solway exhibiting slightly different characteristics from all other areas. Group I, at the highest similarity, contains the Dutch Delta areas (Oosterschelde, Westerschelde, Voordelta) and the Humber; Group II contains the Wadden Sea (Dutch and German), UK estuaries (Forth, Tyne, Mersey), and Scandinavian areas (Isefjord, Oslofjord), while group III contains the Iberian and French estuaries. The largest group in both treatments, of Dutch and British estuaries, are considered to illustrate a usual NW European boreal assemblage.

The diversity of fish species within an area is partly a function of the number of available niches and partly the area size (WOOTTON, 1990). Thus, as found here, it is not unexpected that the large Wadden Sea and Isefjord areas had greatest species richness. Diversity also increases through biogeographical considerations, for example, the greater diversity at biogeographical boundaries. Some of the groupings produced are the combined result of similarities in estuary characteristics and sampling methods. For example, the Dutch delta studies were carried out by the same group (HOVENKAMP and VAN DER VEER, 1993; HAMERLYNCK, 1993), and the Wadden studies were an extension of the same areas. Finally, although there was no consistent latitudinal gradient, contrary to suggestions by FISCHER (1960) and HENDERSON (1989), the separation of the Iberian and French estuaries with both treatments indicate a strong latitudinal difference and possibly the separation of Lusitanian and Boreal faunas.

The analysis here gives differences and similarities between the estuarine fish assemblages but the physico-chemical characteristics of those estuaries is not known in sufficient detail to allow explanation of the differences. For example, there are differences in types of area - from the deep, muddy and typically fjordic Oslofjord, to the shallow, sandy and gradually tapering form of the Solway; the Ria-type Aveiro lagoon and the lagoonal Isefjord differ from the major drainage estuaries of the Humber and Tagus; the coastal Voordelta and Wadden areas would be expected to have similarities; the Tyne, Elbe and Loire have been canalised to a greater or lesser extent. The Wadden, Isefjord, Voordelta and Tagus are the largest areas which are thus expected, with even a moderate diversity of habitats, to have a high diversity as shown especially in the case of the first two areas. The Humber and Solway have large uniform sand-mud areas whereas the Loire and Forth, for example, have muddy and mixed bottoms although if the latter have more niches available this is not reflected in species richness. It is of importance that the findings are complicated by the length of period of study - the Wadden and Isefjord have extensive time series, and the Forth and Tyne to a lesser extent.

Fish studies have importance in estuarine water quality evaluation and assessments of human impacts (ELLIOTT *et al.*, 1988); there is the high need to determine what is a normal assemblage and to assess what deviation there has been from that normality due to human impacts. As most studies of estuarine fish communities carried out to date refer to anthropogenic impact detection, it is thus difficult to define a normal (natural) community. The estuaries studied cover the range of anthropogenically influenced estuaries: the Westerschelde, Oslofjord and Mersey are the most industrialised/urbanised, the Humber, Forth and Tagus are moderately industrialised, and the Solway, Isefjord and Loire have a small amount of industry and urban area. The analysis used here does not indicate that this subjective indication of industrialisation/urbanisation explains the differences in the estuarine fish assemblages.

The above illustrates the need for further detailed and quantitative study with respect to the features, especially anthropogenic ones, of the estuaries. All estuaries are subjected to diffuse and direct inputs of natural and anthropogenic materials such that the relevance and fate and effects of these with respect to the fish communities requires especial study. It is of note that the importance of the functional role of the various fish assemblages with regard to evaluations of large and small estuaries has not been fully quantified (*e.g.* BAIRD and ULANOWICZ, 1989; ELLIOTT and TAYLOR, 1989; BOYNTON *et al.*, 1995). In particular, the estuarine cycling of nutrient and carbon and their transport to adjacent coasts requires an indication of the importance of the different guilds within the fish assemblages.

The groupings produced by both treatments and thus the fish assemblage status do not easily reflect the putative and subjective similarities of the estuaries' environmental characteristics. There appears to be an overall similarity in assemblage between the estuaries despite large differences in their physical and anthropogenic characteristics. Ideally, the use of further multivariate techniques would be valuable to link the biotic and environmental variables (as for the benthos, see ELLIOTT, 1994). However, in the case of fish studies, a lack of consistent and complete information of the characteristics of the estuaries makes it difficult to use such techniques and to explain fully the differences between estuaries with respect to their fish assemblages. It is axiomatic that a true comparison of the estuaries requires study effort to be rigorously standardised.

The taxonomic analysis based on family data at a binary level and the semi-quantitative species level produced similar clusters but at a greater degree of similarity than that using presence/absence data at the highest taxonomic separation (species). Studies of benthic invertebrate communities have indicated that taxonomic discrimination at lower levels of taxonomic separation, *i.e.* family, are suitable for identifying similar community assemblages and the effects of human impacts (WARWICK, 1988). This feature is shown here for the fish assemblages where a greater similarity is shown between estuaries. The latter agrees with the suggestion by COSTA and ELLIOTT (1991) in an earlier and less extensive comparison that although particular species differ between estuaries, the assemblages based on families are of greater similarity. Thus the analysis at the lower level of taxonomic resolution is considered to have value when assessing overall assemblage structure.

Similarly, and again following the initial indications given by COSTA and ELLIOTT (1991), the similarity between estuaries based on functional guilds which incorporate biological characteristics rather than taxonomic identities, is relatively high. This is considered to represent the availability of ecological niches and the overall physico-chemical functioning of estuaries, *i.e.* estuaries are inhabited by similar functional types irrespective of the taxonomic identities. Thus the groupings of fish usage of estuaries, initially proposed by McHUGH (1967) and developed further by HAEDRICH (1983) and the present and previous studies (ELLIOTT and TAYLOR, 1989) appear to hold for most estuarine areas.

Based on the present analysis, and the available quality and quantity of data, it is possible to define what may be termed a typical European (Atlantic seaboard) estuarine fish assemblage. The guild approach indicates that on a qualitative basis, such an assemblage has the following characteristics:

– *Ecological Guild:* a majority equally of taxa of estuarine resident (ER), marine adventitious (MA) and marine juveniles (MJ) (each 25%); a small number of marine seasonal migrant (MS) and diadromous (CA) taxa (each 10%), with few (5%) freshwater adventitious (FW) taxa.

– *Reproduction Type:* the taxa encountered were mostly oviparous with pelagic eggs (Op, 40%) but many oviparous taxa with benthic eggs (Ob, 30%); a lesser number (7-12% for each) of oviparous taxa with eggs guarded (Og), eggs protected (Os) or eggs deposited on vegetation (Ov); with few (<2% for each) viviparous (V) or ovoviviparous (W) taxa. This indicates that most of the taxa (>60%) use sessile eggs, brooding or other egg protection which is considered as a mechanism for retaining the eggs and young within the estuary (HAEDRICH, 1983).

– *Feeding Type:* most taxa feed on both invertebrates and fish (IF, >40%) or only invertebrates (IS, 27%); there are some other carnivores (11%) with a few (<8% for each) other categories (plankton, (PS), herbivores (HC), omnivores (OV)); there are very few (<5%) true piscivorous taxa (FS). These features reflect the presence of small and young fish present in the estuaries, but that the taxa are still high in the estuarine food chain. This supports the predominance of detritus-based food webs for estuarine nekton (DA SYLVA, 1975) and the central role of small epibenthic crustaceans and infaunal invertebrates (COSTA and ELLIOTT, 1991; MARSHALL and ELLIOTT, in press).

– *Substratum Preference:* the fish mostly prefer soft bottom (F, 40%) but many also prefer sand (S) and mixed bed (M) and/or living in vegetation (V) (20% for each) with slightly less taxa (15%) prefer rough bottom (R). This indicates the preference for and predominance of soft-sedimentary dominated areas in the estuaries studied.

– *Vertical Distribution:* over half of the taxa prefer intimate contact with benthos (B, 52%) with half of remainder remaining close to the bed (D, 25%), and only 25% were pelagic (P). This reflects the dependence on benthic food but may also reflect the dependence on sheltered areas, the use of estuaries for protection (by turbidity) against visual predators, and hydrodynamically quieter areas near the bed.

It is again emphasised that the above characteristics are based on a qualitative (binary data approach) and there is likely to be some notable differences on a quantitative basis. Within the ecological guilds, marine juvenile (*e.g.* gadoids) and marine seasonal (*e.g.* clupeoids) migrants will be more important through high abundance (*e.g.* see ELLIOTT, *et al.*, 1990) than, for example the low abundance of freshwater or marine adventitious taxa. The reproductive guilds derived on a qualitative basis are not expected to change markedly on a quantitative basis. Within the feeding types, quantitatively the pelagic feeders may be more represented owing to the large numbers of, *e.g.* clupeoids, which inhabit estuaries for part of the year. Similarly, the proportion of pelagic organisms within the vertical distribution guild is likely to be greater (ELLIOTT, *et al.*, 1990).

It is not possible to indicate whether the typical assemblage defined here differs from other areas, *e.g.* temperate North American or southern (Australian and South African) estuaries. However, data for the latter areas exist and are suitable for assessing with the North-west European data. McHUGH (1967) and HAEDRICH (1983) gave the basic ecological categories but they did not give the proportions of each. Furthermore, although there are descriptions of guilds available in open coastal areas (*e.g.* WOOTTON, 1990), there are few quantitative estimations of the number of taxa in each guild. It is likely that there would be greater numbers of pelagic and, for rocky coasts and seabed, vegetation dwelling species. Thus it is not possible to quantify here the major differences between estuarine and coastal areas.

Finally, it is emphasised that a greater analysis is required for all estuaries in order to determine and quantify the functional role of fish assemblages in ecosystem evaluations. This requires a quantitative analysis of the guilds, an analysis of the spatial and seasonal differences within an estuary, and the change of structure and predominance of guilds with distance downstream (along the salinity gradient, as shown in the Forth by ELLIOTT *et al.* (1990)). In summary, the input of quantitative fish-based information to the evaluation of estuarine functioning, including nutrient cycling and transport, is particularly required (see also BOYNTON *et al.*, 1995).

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