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Factors affecting the annual abundance and regional distribution of English inshore demersal fish populations: 1973 to 1995

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The 2 m beam trawl and 1.5 m push net were used to sample the small epibenthic fish assemblage during September on the east and south coasts of England. Fishing stations were distributed along the entire coast within four depth bands to 20 m. A total of 104 species were caught between 1973 and 1995, and these included infrequent Lusitanean species such as the big-scale sand-smelt (*Atherina boyeri*), and the undulate ray (*Raja undulata*), and infrequent boreal species such as the Norway haddock (*Sebastes viviparus*). Fifty-four taxa were selected as representative of the small, demersal inshore fish community that would be most vulnerable to capture by the two sampling gears, and were used in subsequent analyses of community structure. The north-east coast assemblage was the least diverse (H′=1.58) and least even (J′=0.47). It also supported the least number of species (55), and the variation in catch of the only dominant genus, *Pomatoschistus* spp., was partly responsible for large year-to-year variations in diversity and in the total population abundance of selected demersal species. On the east and south-east coasts, both diversity (H′=1.78 and 1.93) and evenness (J′=0.50 and 0.51) were greater than in the north, as a result of larger numbers of species available to the gears, and several species with relatively high catch density, such as *Pomatoschistus* spp., dab (*Limanda limanda*), solenette (*Buglossidium luteum*), and dragonet (Callionymidae). As a result, the fish assemblages of these coasts showed lower inter-annual variation in evenness and diversity. Trends in mean catch density of some species were correlated with the mean surface water temperature and salinity, especially for species which were near the edge of their normal geographic distribution in the southern North Sea. In addition, mean surface water temperatures were positively correlated with the total number of Lusitanean species on the south coast. These data provide evidence that during a period of more than 20 years, hydrographic factors have not only affected species abundance, but, at low density, also their presence or absence in catches.

Key words: boreal, diversity, evenness, Lusitanean, *Pomatoschistus*, salinity, temperature.

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Introduction

The extensive shallow areas of the North-west European continental shelf support large juvenile populations of commercially important fish species, as part of a varied and largely demersal assemblage of small fish and crustacea (Boddeke *et al.*, 1971; Creutzberg and Fonds, 1971; Riley *et al.*, 1981; Reina-Hervas and Serrano, 1987; Gibson *et al.*, 1993). Descriptions of fish assemblages such as these are frequent in the literature, and cover a wide range of fauna types (Iglesias, 1981; Brown and McLachlan, 1991; Magurran, 1991), yet the majority of studies have been relatively short-term, and analyses of entire assemblages over a number of years are uncommon (but see Henderson and Seaby, 1994; van Leeuwen *et al.*, 1994).

In the late 1960s, no quantitative information existed on the distribution and abundance of fish species in the coastal waters of England and Wales. In order to provide these data, preliminary surveys were undertaken in the inshore waters of England between 1970 and 1972 (Riley *et al.*, 1981). These surveys were used to establish a grid of depth-stratified sampling stations that have since been fished regularly, and have provided indices of abundance for juvenile sole (*Solea solea*) and plaice (*Pleuronectes platessa*) to use in the management of these stocks (Whiting, 1983). Samples were collected using the 2 m beam trawl and 1.5 m push net. These gears have been widely used during surveys of juvenile fish populations in inshore waters up to low tide mark (Riley and Corlett, 1965; Edwards and Steele, 1968; van der Veer, 1986; Riley, 1971; Ansell and Gibson, 1990).

The British Isles lie at a point of transition between the cold-temperate Atlantic (boreal) fauna extending southwards from the North Cape, and the warm-temperate Lusitanean fauna extending northwards from the Portuguese coast (Ekman, 1953). As there are no effective physical boundaries to hinder the free passage of species across this faunal boundary, there is considerable mixing of species in the intermediate zone, normally considered to be in the region of the Celtic Sea and eastern Channel. The annual variation in the northerly extent of the isotherm in winter is thought to be one of the more important factors which regulate the number of Lusitanean species occupying this intermediate zone (Briggs, 1974).

The purpose of this article is to describe the geographic distribution of inshore demersal species on the east and south coasts of England, and the annual trends in species evenness and diversity. The distribution of the total number of fish species belonging to the boreal and Lusitanean fauna is also used to monitor long-term changes in the contribution of the different faunal elements to the total assemblage. Trends in abundance of some species that are representative of the major faunal types are compared with annual changes in surface water temperature and salinity.

Materials and methods

Survey design

Preliminary surveys of the east and south coasts of England were undertaken in 1970 and 1971, and these were used as a basis for more thorough surveys in 1973 (east coast), 1974 (south coast), and 1979 (east coast). From 1981 to 1995, stations on both coasts were sampled annually, during September. The coast was divided into sectors on the basis of major geographical features such as bays and estuaries (Fig. 1), and, within these, fishing stations were distributed within each of four depth bands, 0–1.9 m, 2–5.9 m, 6–11.9 m, and 12–20 m. Stations occurred most frequently in depth bands where common species were caught in largest numbers. For the analyses presented in this article, 15 sectors have been grouped into major coastal regions: 1 – the north-east coast of England between Flamborough Head and Winterton and including the Humber estuary, 2 – the east coast including the estuarine area of the rivers Thames, Orwell and Stour between Winterton and North Foreland; and 3 – the south coast of England between North Foreland and Portland Bill, including the Hampshire harbours and the Solent (Fig. 1).

Sampling

The two fishing gears used during the survey, the 2 m beam trawl and 1.5 m push net, were designed to have similar efficiency and selectivity, so that the catches of fish per unit area from each gear could be directly compared (Riley, 1971; Riley and Corlett, 1965; Riley *et al.*, 1981, 1986). Both gears used a fine mesh net with a codend liner of 4 mm knotless mesh, a light chain footrope and three tickler chains stretched loosely between the shoes. The push net was operated at low water mark in water of 0–1 m depth, while the beam trawl was deployed from a small boat in water depths of up to 20 m. Both gears passed over the ground at a speed of approximately 1 knot, or 35 m min^{-1}. The distance covered was recorded with an odometer attached to the beam trawl shoe, or estimated for the push net using a measured distance on the beach (Riley *et al.*, 1986).

At each station, all fish caught were identified to species wherever possible and measured to the half centimetre below. The catch numbers of each species and age group were then converted to catch densities (numbers per 1000 m^2) based on the swept area of each gear. The length frequency distributions of sole and plaice were used to estimate the age composition as 0-group, 1-group, and 2+-group. In surveys undertaken between 1973 and 1979, the estimated age of both sole and plaice was recorded only as 0 group and 1+-group. The efficiency of the gears is not known, and probably varies with both species and body size. The temperature and salinity of the surface water were also recorded.

Catch densities for some species have been combined where there was a risk of incorrect identification of species of similar appearance in the field, or where an identification was incomplete. For example, the dragonets (*Callionymus reticulatus* and *C. lyra*) were combined into the Callionymidae, herring (*Clupea harengus*) and sprat (*Sprattus sprattus*) were combined into the Clupeidae, the sandeel (*Ammodytes tobianus*), Raitt's sandeel (*A. marinus*), and the greater sandeel (*Hyperoplus lanceolatus*) were combined into the Ammodytidae, and sand goby (*Pomatoschistus minutus*), common goby (*P. microps*), Norway goby (*P. norvegicus*), and painted goby (*P. pictus*) were combined into the *Pomatoschistus* spp.

Data analysis

The mean catch densities of all species caught for each region, for 1973 to 1995, were ranked and compared using Spearman's rank correlation coefficient (r_s, Krebs, 1989). A value of +1 indicated that the two rankings were the same, and a value of −1 indicated that they disagreed entirely.

Fifty-four taxa were identified as representative of the small, demersal inshore fish community that would be

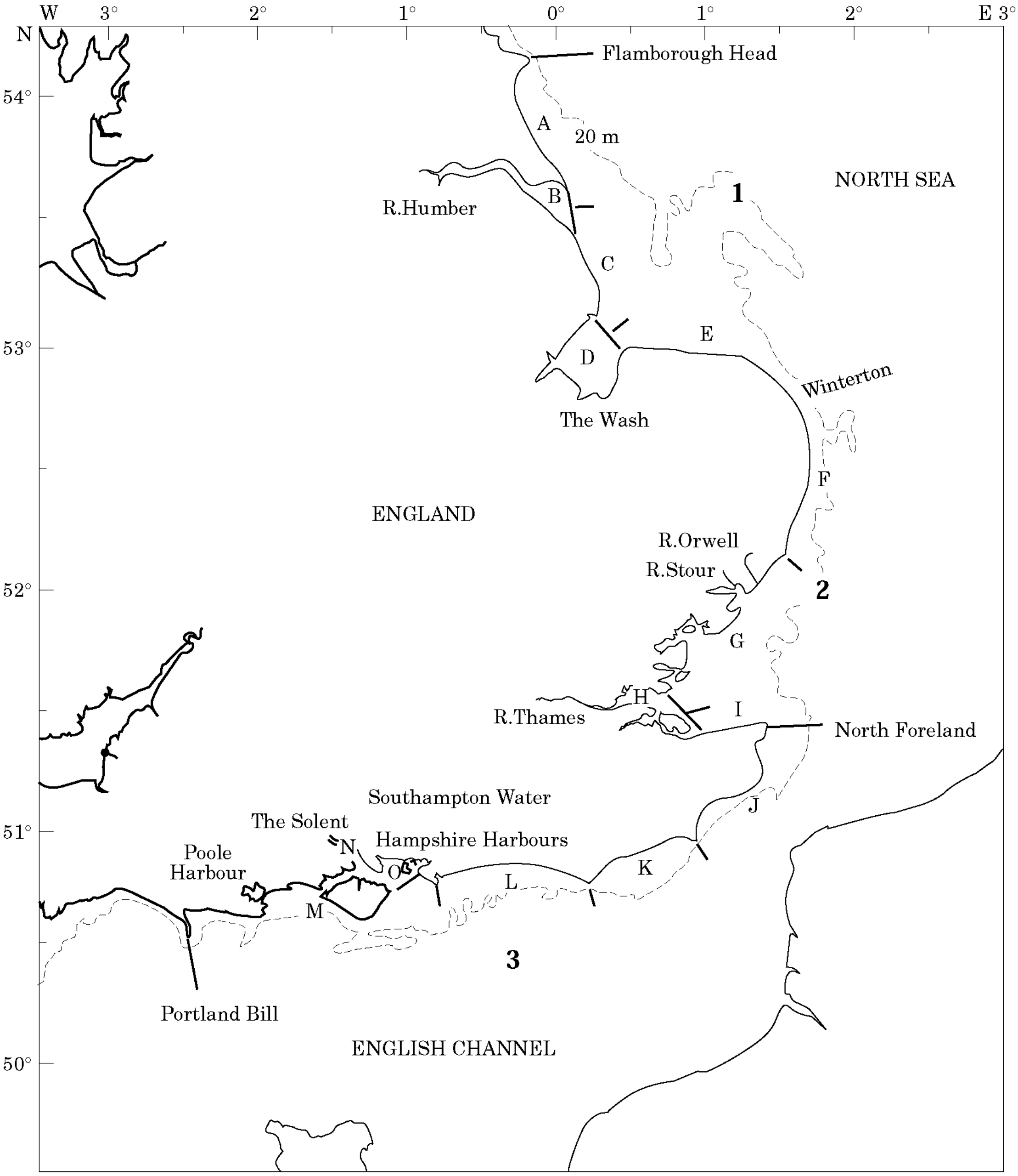


Figure 1. Map of the study area showing three numbered regions delimited by long bold lines, lettered sectors delimited by shorter lines, and place names referred to in the text. The 20 m depth contour is shown.

most vulnerable to capture by the two sampling gears. The purpose of this selection was primarily to exclude the occasional large catches of pelagic species which would not normally be considered as typical of the demersal small fish community, and for which catch efficiency is presumed to be low. Species which were rare (fewer than three individuals) were also excluded.

Shannon's diversity index (H′) is a measure of the average degree of uncertainty in predicting what species an individual chosen at random from a sample will belong to. This index reaches its maximum value when all species are represented by the same number of individuals (Krebs, 1989). Shannon's diversity index and Pielou's evenness index (J′) were calculated for the selected demersal species according to Ludwig and Reynolds (1988).

Mean catch densities (numbers/1000 m^2) of selected taxa were calculated for each depth band within each region. The nominal population abundances of these taxa were then estimated as the product of the mean density and the total surface area of the depth band, determined by planimetry. The population abundances in all depth bands were added to provide an estimate of the total population in each region. Year classes of sole and plaice were combined for these estimates. To obtain the total population abundance, the estimates of population abundance for the 54 demersal taxa were added.

A number of species with distributions which ranged from north, such as the pogge (*Agonus cataphractus*), butterfish (*Pholis gunellus*), and sea snail (*Liparis liparis*), to south, such as balan wrasse (*Labrus bergylta*) and spotted ray (*Raja montagui*), were chosen to illustrate variation in catch during the period of the survey, and the influence on abundance of mean surface water temperature and salinity.

All statistical analyses were performed using the SAS System (SAS Institute Inc., Cary, NC, USA).

Results

Sampling intensity

A total of 6019 stations were fished on the east and south coasts of England between 1973 and 1995 (Table 1a). The mean number of stations fished per year was greater on the south coast (149) than on the north-east coast (94), and within each region the annual sampling effort was also variable. For example, on the south coast the total number of stations fished per year ranged from 80 to 173, while on the north-east coast they ranged from 58 to 114. There were also differences in the sampling effort by depth band. On the east and north-east coasts there were more stations fished between 2 and 11.9 m than in other depth bands, while on the south coast the 0–1.9 m depth band was sampled most intensively (Table 1b).

Table 1a. Total number of beam trawl and push net stations fished in each region and each year (1973–1995). N/A=data not available.

	Region		
	1	2	3
1973	99	82	N/A
1974	N/A	N/A	154
1979	114	86	N/A
1981	84	105	154
1982	98	107	158
1983	97	98	80
1984	102	109	139
1985	58	132	121
1986	58	124	148
1987	58	125	143
1988	99	127	142
1989	97	114	154
1990	109	131	170
1991	111	139	168
1992	106	143	154
1993	110	145	173
1994	97	146	168
1995	95	130	158
Mean	94	120	149
Total	1592	2043	2384

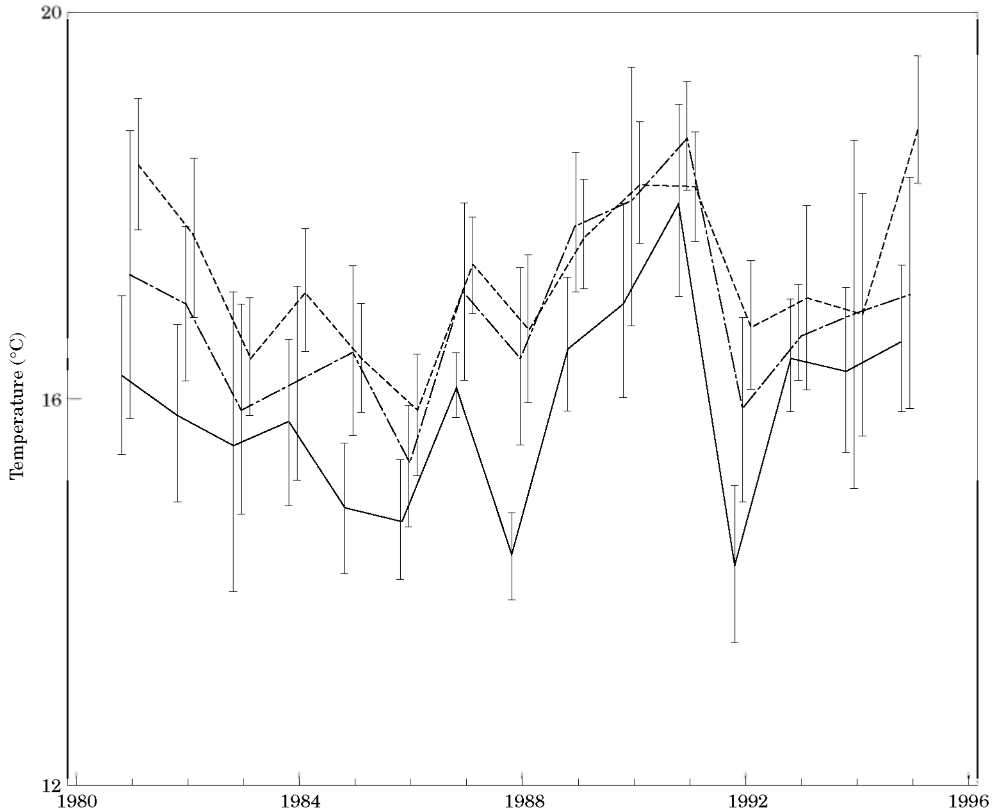
Table 1b. Mean, minimum, and maximum number of beam trawl and push net stations fished in each depth band during 1973 to 1995, with the geographical area of each depth band (million m^2).

Region		Depth band			
		0–1.9 m	2–5.9 m	6–11.9 m	12–20 m
1	Mean	20	31	34	9
	Min	7	9	17	4
	Max	28	48	47	13
	Area	166.5	478.9	1178.1	2423.8
2	Mean	22	40	39	19
	Min	8	16	28	11
	Max	35	56	58	24
	Area	306.0	617.4	774.2	1050.2
3	Mean	44	44	37	24
	Min	9	21	22	8
	Max	65	63	48	38
	Area	19.4	41.6	96.1	193.3

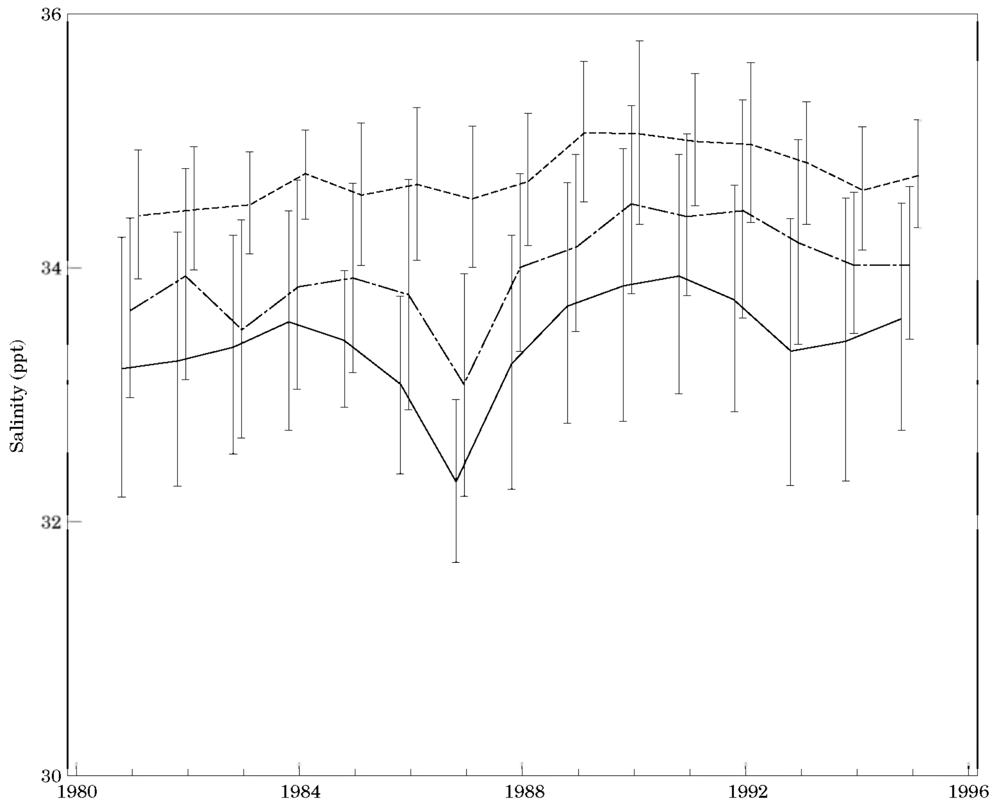
Regional variation in temperature, salinity and fish catches

Mean surface water temperatures ranged from 14 to 19°C and mean salinity was consistently above 32 ppt in all regions, and both were consistently higher in the south than in the north-east. There was a general pattern of a decrease in temperature and salinity during the mid-1980s and an increase in 1990 and 1991 (Fig. 2).

A total of 104 species were collected between 1973 and 1995 (Table 2). Species caught most frequently included gobies, dragonets, pogge, pipefish (*Syngnathus* spp.) and lesser weever (*Echiichthys vipera*), and also the juveniles of larger flatfish species of commercial importance, particularly plaice and sole. The most frequently occurring taxon, *Pomatoschistus* spp., was found in 77–99% of the catches within each sector, and 12 taxa occurred at a frequency of >50% in at least one sector. Of the 54 selected taxa, 18 (33%) were found in all sectors of the survey (Table 3).



20
16
12
Temperature (°C)
1980
1984
1988
1992
1996



36
34
32
30
Salinity (ppt)
1980
1984
1988
1992
1996

Some of the differences in occurrence of species between sectors and regions were directly related to the extent of their normal geographic distribution. For example, solenette (*Buglossidium luteum*), greater pipefish (*S. acus*), and bib (*Trisopterus luscus*) occurred in almost every sector, yet were more frequent in stations on the south coast than on the north-east coast. Some, such as the gobies of the genus *Gobius* and some members of the wrasse family (Labridae) occurred only on the south coast. Conversely, boreal species (Ekman, 1953) such as the butterfish and the sea snail, were rare on the south coast, but were caught more frequently on the north-east coast (Table 2). Only approximately 25% of the fish fauna was comprised of species with either a Lusitanean or a boreal origin (Table 4).

Ranked abundances of taxa in each region showed a significant similarity between populations on the east and north-east coasts ($r_s=0.490$), and a tendency to dissimilarity between those on the east and south coasts ($r_s=-0.219$), which was not significant. This confirmed that fish communities bordering the southern North Sea (region 2) were more influenced by the presence of northern populations than those of southern origin, and confirms that the zoogeographic boundary between the regions may be close to the eastern entrance to the English Channel (Fig. 1).

Annual variation

Number of taxa

The total number of taxa caught in each region, during each year, varied both in time and in space (Fig. 3). The general trend of decreasing numbers of taxa from south to north is typical of fish distributions in the north-east Atlantic (Ekman, 1953). Variation with time, however, is more complex, and involves both annual variations in sampling effort (number of tows, Table 1) and genuine changes in fish distribution between years. Analysis of variance on square-root transformed data showed that the number of taxa caught per year was significantly affected by the region of origin and also by the number of stations fished ($p<0.0001$; Table 5). A significant year effect was caused by within-region variability in catches during the sampling period, but the slope of the regression for combined data was not significant ($p=0.78$), indicating that there was no trend with time. Neither was there any significant interaction between the number of stations and year, and the number of stations and region (Table 5; Fig. 3). Thus, low sampling effort, as seen for example on the north-east coast during 1985–1987, and on the east coast before 1990, is only partly responsible for the lower number of taxa recorded from those areas during these years (Table 2a; Fig. 3).

The effect of sampling effort on the number of taxa caught is shown by the approximately asymptotic relationship between sampling effort and the cumulative number found (Fig. 4). In all surveys, the cumulative catch initially increased rapidly, so that after only 20 stations between 19 and 30 taxa had been recorded, and after 50 stations this number had increased to approximately 25–40 (Fig. 4). So, at the observed levels of sampling, most of the small demersal species that were available for capture by these gears had probably been sampled, even though new species would continue to be caught with continued sampling effort.

The numbers of fish in each of the three faunal categories did not vary significantly with time, although there was some year-to-year variation (Table 4). A comparison between the number of species of each faunal type, in each region, and the mean annual water temperature for that region showed that only the number of Lusitanean species on the south coast were significantly positively correlated ($p=0.026$). The same comparison with the regional mean water salinity showed no significant correlation (Table 4).

Catch density and population abundance

During the period of the survey, annual catch densities varied substantially both within and between species (Table 2). The highest mean catch densities were of dab (<28 per 1000 m^2) and *Pomatoschistus* spp. (<74 per 1000 m^2), although several families such as the pipefish, Syngnathidae, and the dragonets were often found at catch densities greater than 2 fish per 1000 m^2. Mean catch densities of the boreal species pogge, eelpout, and butterfish, tended to be relatively high during the mid-1980s, when water temperature and salinity were low, and then declined in 1989 and 1990, when temperature and salinity reached peak values (Fig. 2a,b; Fig. 5a,b). The negative correlations between surface water temperature and catch were significant for both pogge ($p=0.038$) and butterfish ($p=0.014$) on the south coast, and the negative correlation between salinity and the catch density of eelpout was significant on the north-east coast ($p=0.045$) (Fig. 2a; Fig. 5d). The catch density of another boreal species, the sea snail, has remained relatively stable, and trends were not correlated with changes in mean annual temperature or salinity (Fig. 5c).

Patterns in catch density of the Lusitanean species, balan wrasse and spotted ray, were not associated with changes in temperature or salinity in any of the regions (Fig. 5e,f). The catch density of the continental shelf

Figure 2. Mean surface water temperature (above) and mean surface salinity (below) on the north-east coast (continuous line), east coast (dot-dashed line), and south coast (dashed line) from all fishing stations. The standard deviation of the mean for each year, in each region, is indicated.

Table 2. Latin and common names of all fish species caught between 1973 and 1995 on the north-east (region 1), east (region 2), and south (region 3) coasts of England, with their mean catch (numbers per 1000 m^2). Those taxa which occur mainly in the Lusitanean (L) or boreal (B) fauna, or a combination of both (S), are marked accordingly. Species for which there is no catch in a region are marked by (–).

			Mean catch		
			Region 1	Region 2	Region 3
S	*Scyliorhinus canicula*	Lesser spotted dogfish	–	0.016	0.002
S	*Galeorhinus galeus*	Tope shark	0.001	–	–
S	*Mustelus asterias*	Starry smooth hound	–	0.001	–
L	*Mustelus mustelus*	Smooth hound	0.001	0.001	–
S	*Squalus acanthias*	Spurdog	–	0.002	–
L	*Raja brachyura*	Blonde ray	–	–	0.019
S	*Raja naevus*	Cuckoo ray	0.001	–	–
L	*Raja microocellata*	Small-eyed ray	–	0.001	0.018
L	*Raja montagui*	Spotted ray	0.023	0.003	0.022
B	*Raja radiata*	Starry ray	–	0.001	–
S	*Raja clavata*	Thornback ray	0.086	0.167	0.321
L	*Raja undulata*	Undulate ray	–	–	0.003
S	*Anguilla anguilla*	Eel	0.012	0.114	0.024
S	Congridae	Conger family	–	–	<0.001
S	Clupeidae	Herring family	4.204	0.518	0.156
	Sprattus sprattus	Sprat			
	Clupea harengus	Herring			
B	*Osmerus eperlanus*	Smelt	0.008	0.141	0.045
S	*Ciliata mustela*	Five-bearded rockling	0.106	0.246	0.129
B	*Enchelyopus cimbrius*	Four-bearded rockling	0.001	0.010	0.005
S	*Gaidropsarus vulgaris*	Three-bearded rockling	0.002	–	0.001
B	*Gadus morhua*	Cod	0.077	0.021	0.003
S	*Merlangius merlangus*	Whiting	5.868	3.059	0.158
S	*Pollachius pollachius*	Pollack	–	–	0.044
B	*Pollachius virens*	Saithe	0.004	–	–
B	*Trisopterus esmarkii*	Norway pout	0.002	–	–
S	*Trisopterus luscus*	Bib	0.082	4.154	3.626
S	*Trisopterus minutus*	Poor cod	0.006	0.264	0.591
S	*Lophius piscatorius*	Angler	0.001	–	–
L	*Apletodon microcephalus*	Small-headed clingfish	–	–	0.046
L	*Diplecogaster bimaculata*	Two-spotted clingfish	–	–	0.008
S	*Belone belone*	Garfish	0.002	0.003	–
S	*Atherina presbyter*	Sand-smelt	0.004	0.016	0.044
L	*Atherina boyeri*	Big-scale sand-smelt	–	–	<0.001
S	*Zeus faber*	John dory	–	–	0.002
S	*Spinachia spinachia*	Fifteen-spined stickleback	–	–	0.197
B	*Pungitius pungitius*	Nine-spined stickleback	–	–	0.002
S	*Gasterosteus aculeatus*	Three-spined stickleback	0.009	0.006	0.005
S	*Syngnathus typhle*	Deep-snouted pipefish	–	0.002	0.009
S	*Syngnathus acus*	Greater pipefish	0.061	0.358	0.565
S	*Syngnathus rostellatus*	Nilsson's pipefish	14.950	1.667	0.987
S	*Entelurus aequoreus*	Snake pipefish	0.002	0.013	0.017
S	*Nerophis ophidion*	Straight-nosed pipefish	–	–	0.001
L	*Nerophis lumbriciformis*	Worm pipefish	–	–	0.030
B	*Sebastes viviparus*	Norway haddock	–	0.001	–
S	*Trigla lucerna*	Tub gurnard	0.050	0.035	0.123
L	*Aspitrigla cuculus*	Red gurnard	–	0.001	–
S	*Eutrigla gurnardus*	Grey gurnard	0.337	0.047	0.036
B	*Myoxocephalus scorpius*	Bull-rout	0.076	0.076	0.002
S	*Taurulus bubalis*	Sea scorpion	0.087	0.020	0.214
B	*Agonus cataphractus*	Pogge	3.366	4.887	1.197
B	*Cyclopterus lumpus*	Lump sucker	0.002	–	<0.001
B	*Liparis montagui*	Montagu's sea-snail	0.002	–	0.003
B	*Liparis liparis*	Sea-snail	1.255	0.845	0.011
S	*Dicentrarchus labrax*	Bass	0.002	0.098	0.143
S	*Trachurus trachurus*	Scad	0.011	0.016	0.016
S	*Spondyliosoma cantharus*	Black sea-bream	–	–	0.357
S	*Mullus surmuletus*	Red mullet	0.075	0.005	0.021

Table 2. *Continued.*

			Mean catch		
			Region 1	Region 2	Region 3
L	*Liza aurata*	Golden grey mullet	–	0.006	0.004
S	*Chelon labrosus*	Thick lipped mullet	0.001	–	0.001
L	*Centrolabrus exoletus*	Rock cook	–	–	0.002
L	*Ctenolabrus rupestris*	Goldsinny	–	–	0.023
L	*Labrus bergylta*	Balan wrasse	–	–	0.295
S	*Crenilabrus melops*	Corkwing wrasse	0.001	0.001	2.002
L	*Labrus mixtus*	Cuckoo wrasse	–	–	0.171
L	*Coris julis*	Rainbow wrasse	–	–	0.009
B	*Zoarces viviparus*	Eelpout	0.255	0.353	–
B	*Pholis gunellus*	Butterfish	1.001	0.079	0.062
S	*Echiichthys vipera*	Lesser weever	1.607	0.314	1.948
L	*Blennius ocellaris*	Butterfly blenny	–	–	0.001
B	*Lumpenus lampretaeformis*	Snake blenny	–	0.001	–
S	*Lipophris pholis*	Shanny	–	–	0.003
S	Ammodytidae	Sand eel family	2.796	0.150	0.097
	Ammodytes marinus	Raitt's sandeel			
	Hyperoplus lanceolatus	Greater sandeel			
S	Callionymidae	Dragonet family	2.035	0.920	15.390
	Callionymus lyra	Dragonet			
	C. reticulatus	Reticulated dragonet			
S	*Gobius niger*	Black goby	–	0.026	1.416
L	*Crystallogbius linearis*	Crystal goby	–	0.001	0.001
L	*Gobius cobitis*	Giant goby	–	0.107	–
L	*Thorogobius ephippiatus*	Leopard-spotted goby	–	–	0.002
S	*Pomatoschistus* spp.	Sand goby family	74.320	41.060	43.480
	P. minutus	Sand goby			
	P. microps	Common goby			
	P. pictus	Painted goby			
	P. norvegicus	Norway goby			
L	*Gobius paganellus*	Rock goby	–	0.003	0.214
S	*Aphia minuta*	Transparent goby	–	–	0.027
S	*Gobiusculus flavescens*	Two-spotted goby	–	0.005	0.276
S	*Scomber scombrus*	Mackerel	0.001	–	–
S	*Scophthalmus maximus*	Turbot	0.432	0.210	0.100
S	*Scophthalmus rhombus*	Brill	0.225	0.111	0.158
S	*Zeugopterus punctatus*	Topknot	0.001	–	<0.001
S	*Arnoglossus laterna*	Scaldfish	0.029	0.003	0.205
B	*Hippoglossoides platessoides*	Long rough dab	–	0.002	–
S	*Limanda limanda*	Dab	12.060	12.720	27.710
S	*Microstomus kitt*	Lemon sole	0.042	0.076	0.008
S	*Platichthys flesus*	Flounder	0.085	0.383	0.291
S	*Pleuronectes platessa*	Plaice (0-group)	16.460	7.195	5.065
	Pleuronectes platessa	Plaice (1-group)	2.046	1.775	0.548
	Pleuronectes platessa	Plaice (2+-group)	0.070	0.324	0.293
S	*Buglossidium luteum*	Solenette	0.010	0.070	21.890
L	*Microchirus variegatus*	Thickback sole	–	–	0.016
L	*Pegusa lascaris*	Sand sole	0.001	–	0.009
S	*Solea solea*	Sole (0-group)	3.264	13.960	4.002
	Solea solea	Sole (1-group)	0.576	2.236	1.166
	Solea solea	Sole (2+-group)	0.257	0.706	0.463

species, the lesser weever, peaked in 1990 and 1991, and on both the east and south coasts the trend was positively correlated with temperature ($p=0.014$, 0.023); on the east coast the trend was positively correlated with salinity ($p=0.023$; Fig. 5g).

The total population abundance of selected taxa on the north-east coast peaked during 1982 and 1993 as a result of large catches of *Pomatoschistus* spp. (930–835 million; Table 6a), while on the south coast during 1987 high abundances were caused by large catches of dab (*Pomatoschistus* spp.) and dragonet (Table 6c). Although the south coast had a much smaller mean total population abundance than the north-east coast (41 million compared to 567 million), it also had a

Table 3. Percentage occurrence of selected taxa by sector within each region (number of stations in which the species occurred/total number of stations in the sector).

Region	1					2				3					
Sector	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
Pollachius virens	2	–	1	<1	–	–	–	–	–	–	–	–	–	–	–
Enchelyopus cimbrius	–	–	1	–	–	–	<1	–	1	–	–	<1	<1	1	1
Zoarces viviparus	3	3	9	13	1	7	1	4	7	–	–	–	–	–	–
Scyliorhinus canicula	–	–	–	–	–	1	1	1	–	1	<1	–	–	–	–
Microstomus kitt	–	–	1	1	<1	<1	2	8	2	2	<1	–	–	–	–
Gadus morhua	2	5	5	5	1	1	2	1	4	<1	1	–	–	–	–
Liparis liparis	1	24	44	27	10	19	10	10	5	–	1	<1	<1	1	–
Eutrigla gurnardus	24	2	11	14	13	2	2	5	3	2	2	3	3	1	–
Trisopterus minutus	1	–	1	<1	<1	3	7	10	6	12	11	10	3	2	–
Arnoglossus laterna	11	<1	1	1	<1	<1	–	–	–	3	12	11	7	3	–
Raja montagui	2	1	6	1	<1	<1	<1	–	–	1	1	1	3	2	–
Scophthalmus maximus	17	6	10	2	15	8	2	<1	–	7	3	5	8	1	1
Myoxocephalus scorpius	2	<1	8	4	1	2	3	3	7	<1	–	–	–	<1	1
Pomatoschistus spp.	78	79	93	99	93	77	94	95	96	87	94	93	80	80	92
Limanda limanda	76	27	61	75	68	57	70	81	57	76	84	44	28	22	24
Callionymidae	51	8	43	35	35	13	16	50	21	63	86	70	59	66	49
Syngnathus rostellatus	25	13	47	80	66	14	24	26	41	32	18	25	37	22	28
Pleuronectes platessa 0-grp	63	43	49	76	58	31	45	52	61	68	42	25	28	28	41
Pleuronectes platessa 1-grp	46	29	49	58	43	25	38	43	32	31	25	13	12	14	13
Pleuronectes platessa 2+-grp	10	6	6	1	1	7	12	18	6	21	17	12	5	6	6
Solea solea 0-grp	3	28	43	53	45	71	83	69	57	72	48	23	12	29	49
Solea solea 1-grp	7	31	30	12	15	37	43	39	35	40	34	19	22	15	30
Solea solea 2+-grp	3	26	23	2	4	21	32	27	22	26	21	14	11	9	11
Ciliata mustela	3	3	6	5	4	12	6	8	12	11	3	3	4	5	11
Echiichthys vipera	77	17	39	15	37	17	6	4	2	37	45	18	31	13	2
Merlangius merlangus	20	59	56	62	37	41	51	35	48	18	9	4	2	<1	1
Pholis gunellus	6	2	21	20	10	2	4	7	4	<1	2	1	2	6	7
Agonus cataphractus	24	10	46	52	33	51	38	48	21	41	34	10	7	10	7
Raja clavata	7	1	13	5	2	3	16	15	1	12	12	20	11	9	1
Platichthys flesus	2	12	3	6	1	7	3	2	33	<1	3	6	2	1	25

Table 3. *Continued.*

Region	1					2				3					
Sector	a	b	c	d	e	f	g	h	i	j	k	l	m	n	o
Syngnathus acus	1	–	1	2	4	4	10	7	7	15	16	13	22	31	47
Taurulus bubalis	5	–	4	4	4	2	–	1	1	<1	2	10	4	17	12
Buglossidium luteum	1	<1	1	1	1	<1	3	8	1	54	83	76	44	17	4
Anguilla anguilla	–	1	1	1	<1	2	5	6	20	2	2	2	<1	1	5
Trisopterus luscus	1	1	3	3	11	49	56	61	35	53	53	32	14	21	14
Scophthalmus rhombus	1	4	6	3	21	4	7	6	8	6	7	8	12	11	9
Gasterosteus aculeatus	–	<1	3	<1	<1	<1	<1	1	2	1	<1	–	<1	–	–
Trigla lucerna	–	–	1	2	6	1	3	2	4	8	10	9	7	4	3
Crenilabrus melops	1	–	–	–	–	–	–	1	–	3	3	22	29	42	32
Pegusa lascaris	1	–	–	–	–	–	–	–	–	1	<1	1	1	<1	–
Mullus surmuletus	–	–	1	2	5	<1	<1	1	<1	–	<1	1	2	2	1
Dicentrarchus labrax	1	–	–	<1	<1	–	1	8	6	8	3	7	1	4	5
Gaidropsarus vulgaris	–	–	–	–	1	–	–	–	–	–	–	–	<1	<1	–
Gobius niger	–	–	–	–	–	<1	1	1	2	1	2	5	7	32	57
Raja microocellata	–	–	–	–	–	–	<1	–	–	–	1	1	2	–	–
Gobiusculus flavescens	–	–	–	–	–	–	1	1	<1	<1	1	4	5	5	6
Gobius paganellus	–	–	–	–	–	–	<1	<1	<1	–	<1	1	4	6	4
Gobius cobitis	–	–	–	–	–	–	2	5	8	–	–	–	–	–	–
Liza aurata	–	–	–	–	–	–	–	–	1	–	–	<1	–	–	–
Syngnathus typhle	–	–	–	–	–	–	–	1	–	–	–	–	1	<1	1
Ctenolabrus rupestris	–	–	–	–	–	–	–	–	–	–	<1	4	1	2	1
Spondyliosoma cantharus	–	–	–	–	–	–	–	–	–	1	2	4	12	28	17
Pollachius pollachius	–	–	–	–	–	–	–	–	–	1	<1	–	4	3	3
Labrus mixtus	–	–	–	–	–	–	–	–	–	–	<1	5	6	8	5
Spinachia spinachia	–	–	–	–	–	–	–	–	–	1	<1	6	9	11	16
Labrus bergylta	–	–	–	–	–	–	–	–	–	–	–	3	7	17	17
Nerophis lumbriciformis	–	–	–	–	–	–	–	–	–	–	–	<1	3	4	4
Coris julis	–	–	–	–	–	–	–	–	–	–	–	–	<1	–	–

Table 4. The number of species in regions 1, 2, and 3, which form part of the Boreal, Lusitanean, and Shelf fauna, as defined by Wheeler (1978), and the mean number for the period 1973 to 1995. N/A=data not available. The significance of the correlation coefficient (r) between number of species in each region and the mean annual water temperature and salinity of that region is shown. Insufficient data marked by (–).

	Boreal			Lusitanean			Shelf		
	1	2	3	1	2	3	1	2	3
1973	8	6	N/A	1	1	N/A	27	25	N/A
1974	N/A	N/A	4	N/A	N/A	6	N/A	N/A	39
1979	5	6	N/A	0	1	N/A	22	25	N/A
1981	5	7	2	1	1	9	22	21	36
1982	5	6	2	1	0	10	22	24	38
1983	6	6	2	1	0	6	22	26	35
1984	8	6	3	1	1	11	24	27	36
1985	3	7	2	0	2	7	21	27	30
1986	3	7	6	1	1	4	19	28	32
1987	4	7	3	0	1	7	21	28	35
1988	6	8	3	0	1	5	24	28	36
1989	4	4	3	1	3	8	26	28	37
1990	6	7	2	1	1	6	23	27	36
1991	6	6	3	1	2	8	23	27	37
1992	6	6	6	0	3	7	21	27	35
1993	5	9	2	1	1	7	26	28	34
1994	5	6	3	1	1	7	29	30	34
1995	6	6	4	1	1	9	27	26	32
Mean	5	6	3	1	1	7	23	27	35
Temperature									
r	0.174	−0.250	−0.311	–	0.134	0.573	0.426	−0.095	0.383
Pr>F	(0.536)	(0.368)	(0.259)		(0.662)	(0.026)	(0.113)	(0.726)	(0.159)
Salinity									
r	0.180	−0.007	0.235	–	0.396	−0.112	0.176	0.149	0.223
Pr>F	(0.519)	(0.980)	(0.399)		(0.181)	(0.690)	(0.528)	(0.595)	(0.423)

correspondingly smaller geographic area between 0 and 20 m depth. As a result, the population densities on the south coast (0.11 fish m^{-2}) and the north-east coast (0.13 fish m^{-2}) were comparable. The population density on the east coast was relatively low (0.07 fish m^{-2}), and the mean total population abundance here was least variable of the three regions (C.V.=28%; Table 6b), suggesting that fish were relatively less dense in this predominantly estuarine environment, and that changes in abundance of individual species had less effect on the size of the total population than in other regions.

Evenness and diversity of fish assemblages

The mean indices of evenness and diversity for the 54 selected taxa decreased from the south coast to the north-east coast, although these differences were not statistically significant. There was some evidence of a significant variation in diversity with time, although the slope of the regression of diversity against year was not significantly different from zero (Pr=0.94; Fig. 6a,b; Table 7). The total number of species also decreased in the same direction (Table 8). The more diverse regions in the south tended not to be dominated by a single species, but by several which occurred frequently and at generally high abundance (Table 6). Thus, on the south coast, *Pomatoschistus* spp., solenette, dragonet, and dab occurred frequently and were relatively abundant members of the community, while on the east coast, *Pomatoschistus* spp. and dab occurred at high abundance in more than half of the years sampled, and on the north-east coast only *Pomatoschistus* spp. were dominant (Table 6). This gradual change in community structure along the coast, involving changes in dominance and population size, was evident from the ranked population indices (Fig. 7). The larger number of species in the south, and the greater diversity, resulted in slopes of ranked indices which were less steeply inclined for the more southerly populations (Fig. 7a–c). Also, the evenness and diversity indices were more variable for populations on the north-east coast than on the east and south coast (Table 8), and this was evident from the variability in the ranked indices, at least in the lower rank range (Fig. 7a–c).

Discussion

The ability of these catch data to accurately describe the inshore fish assemblage is based on the assumption that

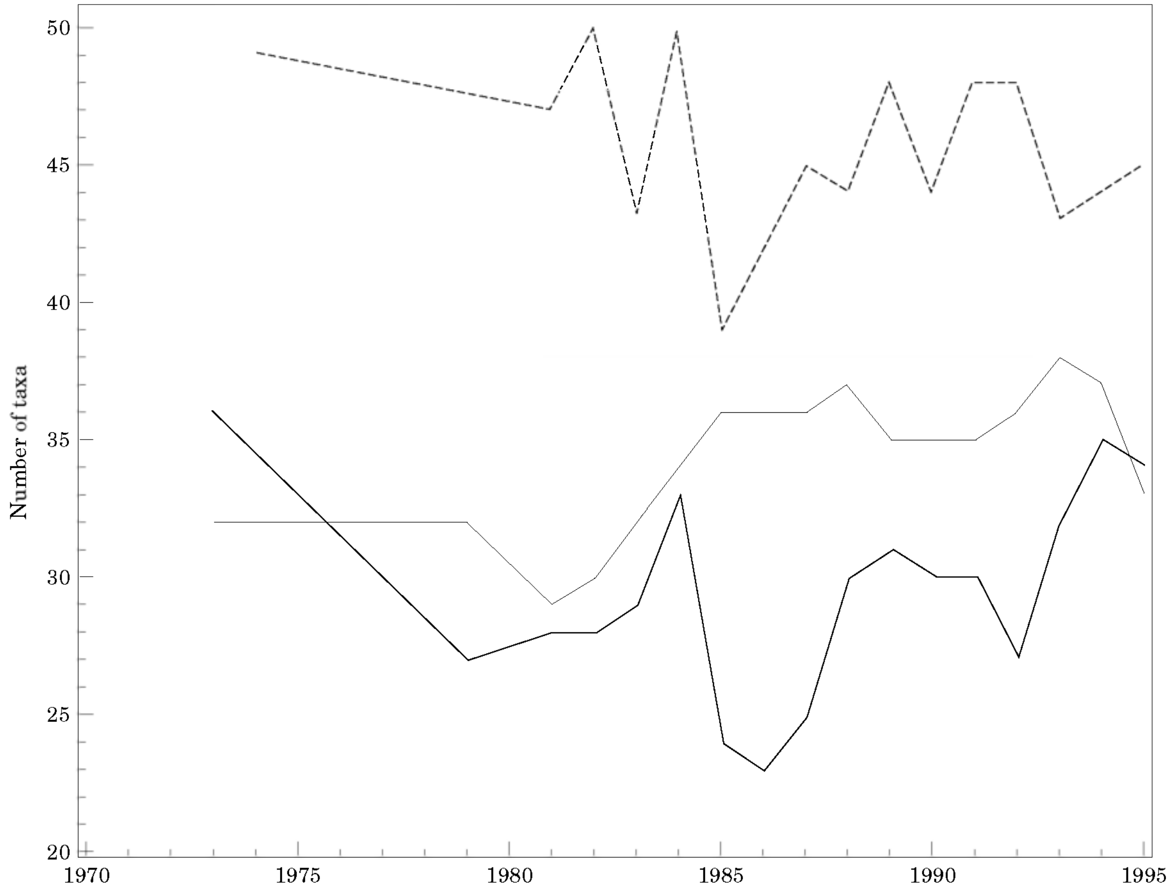


Figure 3. The total number of taxa caught (by region 1, 2 and 3) from all stations fished between 1973 and 1995. (1=—, 2=—, 3=– – – –).

Table 5. Analysis of variance table for total number of species caught. Effect of numbers of stations, region, year, and interactions.

Source	DF	Type I SS	Mean square	F value	Pr>F
No. of stations	1	11.96	11.96	29.5	0.0001
Region	2	2.86	1.43	51.3	0.0001
Year	17	2.05	0.12	4.3	0.0086
No. of stations*Year	16	1.25	0.08	0.8	0.0442
No. of stations*Region	2	0.01	0.01	0.2	0.8434

the 2 m beam trawl and the 1.5 m push net are efficient at sampling the small, demersal species that are found most frequently in the coastal zone. The catch density of the species recorded will be a function of their distribution with depth and substratum type, their ability to avoid the gear, the size selectivity of the meshes, and many other local conditions such as water temperature and turbidity (Kuipers *et al.*, 1992). The catch efficiency for most species is unknown, but data available for 0-group flatfish suggest that under optimal conditions the small beam trawl is the most suitable gear for these species, and may also be appropriate for others (Edwards and Steele, 1968; Kuipers, 1975; Kuipers *et al.*, 1992). Since the early 1960s, the 2 m beam trawl has been used extensively in the shallow coastal waters of North-west Europe (Riley and Corlett, 1965; Lockwood, 1974; de Vlas, 1979; Zijlstra *et al.*, 1982; Doornbos and Twisk, 1984; Berghahn, 1986), and on the east coast of England the gear has remained unaltered for 25 years (Riley *et al.*, 1981). The 1.5 m push net has

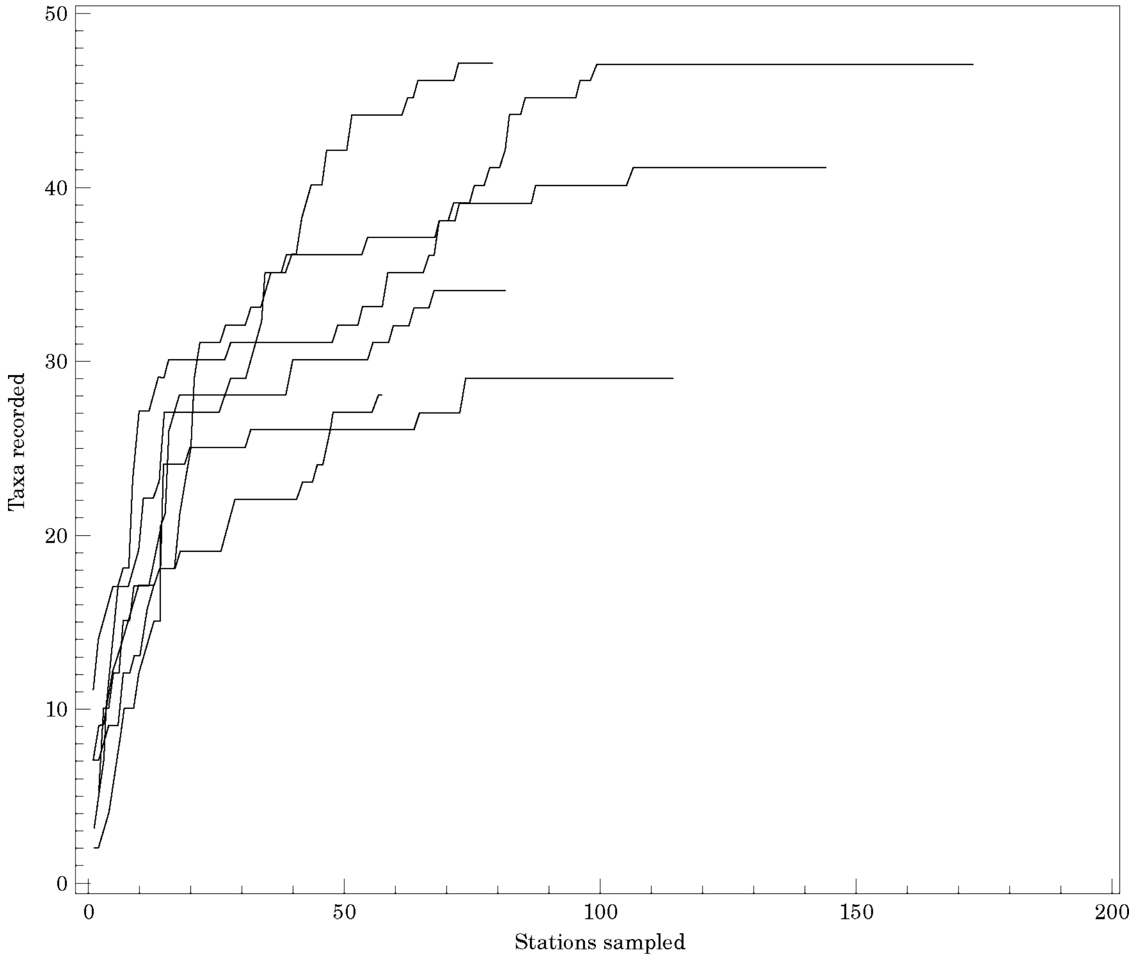


Figure 4. The cumulative number of taxa caught with increasing number of stations fished, for six surveys with the minimum and maximum number of stations fished per year, in each of the three regions.

also been widely used in UK coastal surveys, and was specifically designed to have similar efficiency and selectivity to the 2 m beam trawl so that the catches could be directly compared (Riley, 1971). At the very least, therefore, the relative annual catch rates by this survey of the most common species can be compared with some confidence, providing that sufficient tows are made to sample adequately the species within the community. Interspecific comparison of catch rates, however, should be treated with caution.

A total of approximately 122 species have been found at some stage in their life cycle in the inshore waters of the British Isles, and a further 100 species occur in the offshore waters of the North Sea (Wheeler, 1978; Jiming, 1982; Henderson, 1989). Evidence from a number of surveys in the North Sea suggested that inshore areas generally supported approximately 70 species (Henderson, 1989; van Leeuwen *et al.*, 1994), and data presented in this article showed total catches on the north-east and east coasts of 71 taxa since 1973 (Table 8). Complete descriptions of fish assemblages in the literature are relatively rare (Lasiak, 1984; Reina-Hervas and Serrano, 1987; Gibson *et al.*, 1993), and usually depend on the deployment of both demersal and pelagic gears, or the use of catches from power station intake screens (Henderson, 1989), in order to sample the entire water column. The English surveys reported here did not use gears designed to sample pelagic species, or even some demersal species such as sandeels, Ammodytidae, which easily escape capture by the beam trawl. Thus, the proportion of pelagic species taken on these surveys is relatively small (0.09), while evidence from the catch of power station intake screens suggests that the proportion of pelagic species is higher and can range up to 0.19 (Henderson, 1989).

The inshore fish fauna of the north-east coast of England was dominated by *Pomatoschistus* spp., and the total number of taxa found in the region (55) was

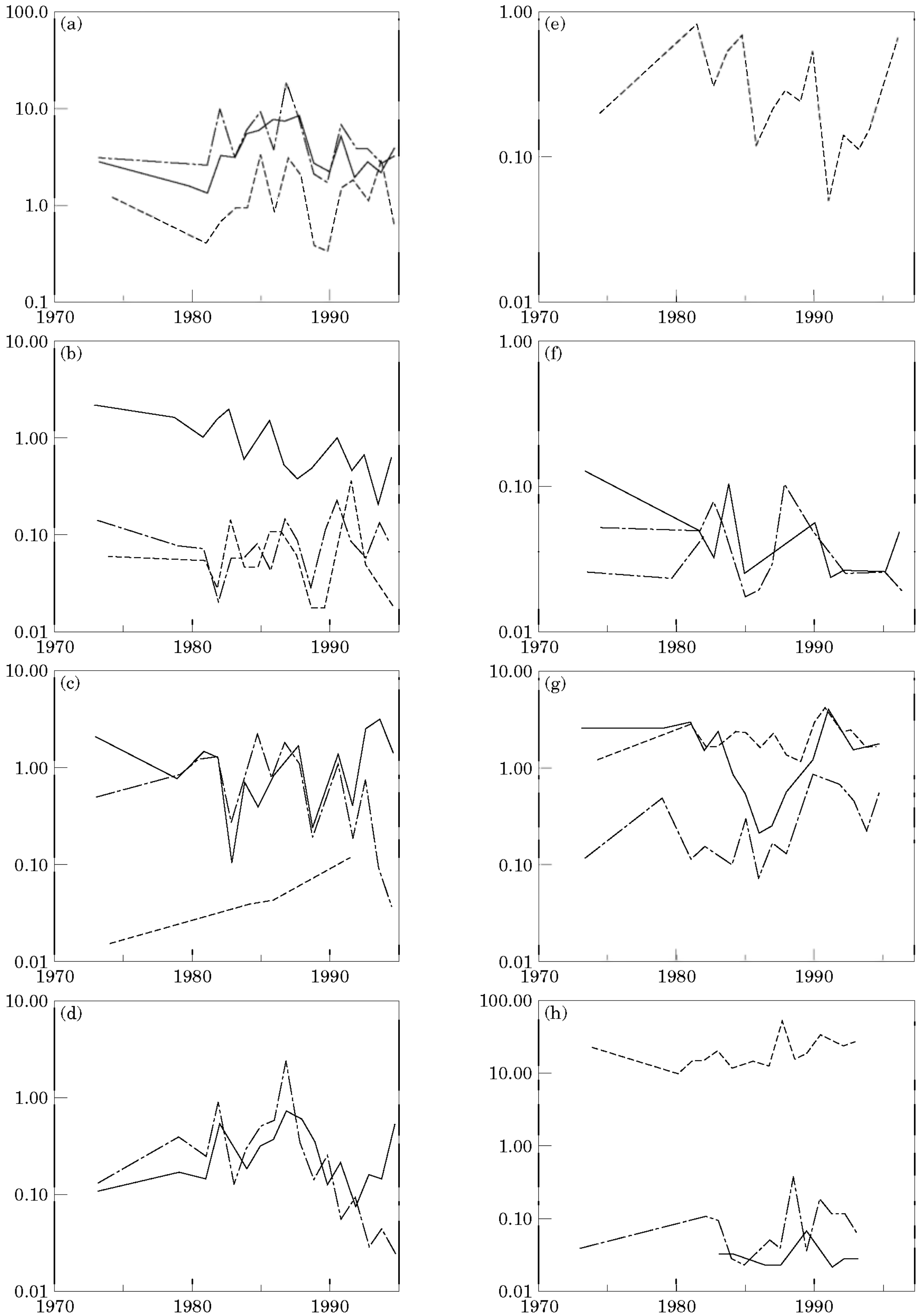


Figure 5. The mean catch (numbers/1000 m^2) of pogge (a), butterfish (b), sea snail (c), eelpout (d), balan wrasse (e), spotted ray (f), lesser weever (g), and solenette (h) in the period 1973–1995, for region 1 (continuous line), 2 (dot and dash line), and 3 (dashed line).

Table 6. Population size for selected abundant species (>10% of the total fish population) in region 1(a), region 2(b), and region 3(c), and the total population size. All numbers represent population indices in millions. Those species for which the population size was less than 10% of the total in any year are marked by (–). N/A=data not available.

	1973	1974	1979	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	Mean (C.V. %)
(a)																			
Pomatoschistus spp.	142	N/A	461	425	562	210	161	250	578	399	204	362	98	510	171	533	603	345	
Dab	–		–	–	–	–	–	58	–	–	92	146	62	–	–	86	–	80	
Nilsson's pipefish	–		–	73	176	–	–	–	–	–	–	–	75	–	72	–	–	–	
Pogge	–		–	–	–	–	–	–	–	–	58	–	–	–	–	–	–	–	
Whiting	–		–	–	85	–	–	–	–	–	–	–	–	–	125	–	–	–	
Dragonet	–		–	–	–	–	–	–	–	–	–	–	56	–	–	–	–	–	
Total	271		544	599	930	356	316	423	725	578	474	666	363	745	438	835	749	640	567 (35)
(b)																			
Pomatoschistus spp.	197	N/A	147	40	56	108	97	68	75	95	86	73	92	85	36	133	144	78	
Dab	20		25	–	83	32	52	38	39	41	72	18	–	36	–	–	–	–	
Pogge	–		–	–	49	–	25	31	–	61	25	–	–	30	–	–	–	–	
Bib	–		27	–	–	21	–	–	20	–	–	–	–	–	–	–	–	–	
Whiting	–		–	–	–	–	–	–	–	21	–	–	–	–	–	–	–	–	
Sole	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	
Plaice	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	32	
Total	257		236	96	222	195	203	177	163	256	212	120	156	177	82	192	184	229	185 (28)
(c)																			
Pomatoschistus spp.	N/A	10	N/A	27	–	8	11	4	10	21	7	13	5	15	15	12	11	17	
Solenette		9		8	7	6	12	5	6	7	6	24	8	12	11	13	10	11	
Dab		–		–	–	7	7	4	10	35	5	4	–	–	–	–	5	22	
Dragonet		7		–	–	5	11	–	–	12	4	13	–	10	4	–	9	17	
Poor cod		4		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	
Bib		–		–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	
Total		39		45	18	33	47	19	32	81	26	57	24	46	39	33	41	77	41 (44)

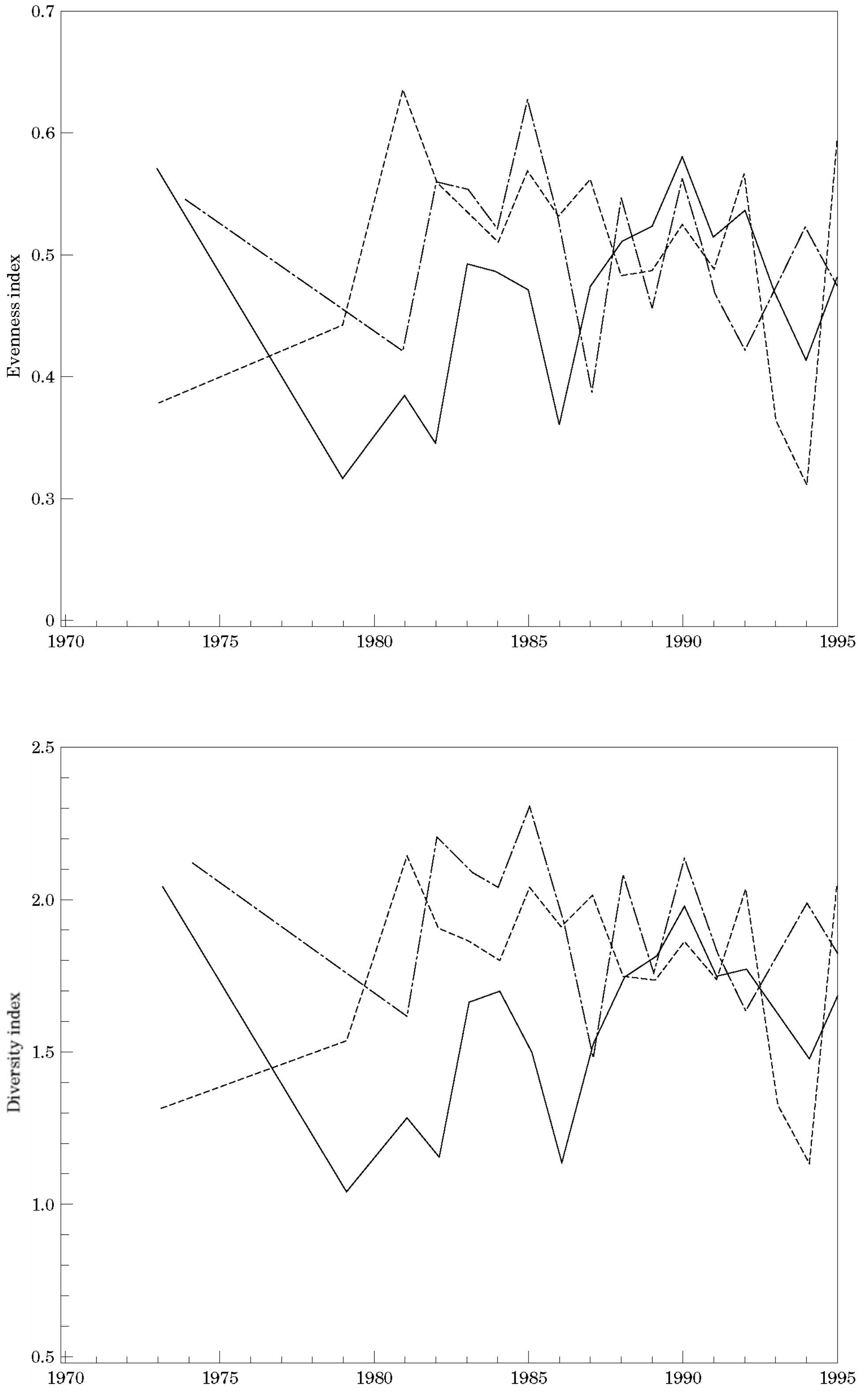


Figure 6. Pielou's evenness index (J′) (a), and Shannon's diversity index (H′) (b) for selected demersal species by regions (1=——, 2=– – – and 3=– . – . –).

Table 7. Analysis of variance tables for estimating the effect of region and year (1973–1995).

Source	DF	Type I SS	Mean square	F value	Pr>F
(a) Pielou's evenness index (J′)					
Region	2	0.006	0.003	0.9	0.4202
Year	17	0.05	0.003	0.9	0.6108
(b) Shannon's diversity index (H′)					
Region	2	0.11	0.05	4.5	0.5227
Year	17	0.21	0.01	0.9	0.0201

Table 8. Mean diversity (H′) and evenness (J′) indices, with coefficient of variation (C.V.), and total number of species, for each coastal region.

Region	Mean H′	C.V. (%)	Mean J′	C.V. (%)	N
1	1.58	18	0.47	16	55
2	1.78	16	0.50	17	59
3	1.93	12	0.51	13	77
1 and 2					71

relatively small (Table 8). The combination of these two factors resulted in a fish assemblage of low diversity (mean H′=1.58), and because the abundance of the dominant species varied substantially, this index also showed high annual variability (Table 8; Fig. 6a,b). In the predominantly estuarine region on the east coast, the total number of taxa (59) was higher, partly because the populations of typically estuarine species such as smelt (*Osmerus eperlanus*), eel (*Anguilla anguilla*), and flounder (*Platichthys flesus*) were augmented by stenohaline and stenothermal species from offshore. Unlike the north-east coast, the large populations of *Pomatoschistus* spp. in the assemblage occurred together with large populations of dab and pogge. These species are very abundant in the shallow and productive inshore areas of North-west Europe, and density can be high in peak season, up to 0.85 fish m^{-2} for dabs and 3.9 fish m^{-2} for *P. minutus* (Doornbos and Twisk, 1987; Bolle *et al.*, 1994). The combination of a generally larger number of species, with more than one occurring in substantial numbers, generated a more diverse and more even assemblage on the east coast, with lower annual variability. Large parts of the shallow coastal zone are brackish areas of the rivers Thames, Orwell and Stour, and these have increased the geographical area of the region without increasing the available substrate for abundant marine species. This partly explains the relatively low population density (0.07 fish m^{-2}) of the east coast.

Descriptions of the fish communities of the Continental coast between Belgium and the German Bight show broad similarities with those of the English east and north-east coast, even though a number of larger beam trawls up to 8 m width were used during sampling (van Leeuwen *et al.*, 1994). In the coastal regions of Continental Europe at corresponding latitudes, between the Westerschelde (51°30′N) and the northern German Bight (55°30′N), the range in both diversity indices (H′=1.46–2.21) and evenness indices (J′=0.38–0.62) was similar to that on the English coast. The total number of species and taxa found on the Continental coast (79) was also similar to that on the English coast (71). Although the shallow inshore areas of both coasts supported similar communities, generally dominated by *Pomatoschistus* spp., sole, plaice, dab, whiting (*Merlangius merlangus*), and clupeids, the annual variations in abundance of these species did not necessarily correspond on each coast. For example, on the English coast, the consistent decline in catch density of eelpout since the mid-1980s and the increase in catch of the lesser weever to peaks in 1990 and 1991 were also evident on the Continental coast (van Leeuwen *et al.*, 1994; ICES, 1995), while the increased catch of pogge and butterfish in the mid-1980s, and subsequent decline in 1989 and 1990, was not.

Some of these trends in abundance were correlated with the mean surface water temperature and salinity in the same region, especially for pogge, butterfish and eelpout which are near the edge of their normal geographic distribution in the southern North Sea (Wheeler, 1978). Warm summers, for example during 1976, 1979, 1982/83, and 1989, also resulted in particularly good recruitment of species such as bass (*Dicentrarchus labrax*), twaite shad (*Alosa fallax*), and red mullet (*Mullus surmuletus*) on the English coast (Holmes and Hederson, 1990). In addition to this influence on species abundance, mean water temperatures were also positively correlated with the total number of Lusitanean species on the south coast. There are more southern migrants found on the south coast than in the North Sea, for example the worm pipefish (*Nerophis lumbriciformis*), big-scale sand-smelt (*Atherina boyeri*), and undulate ray (*Raja undulata*), and it is clear that not only could the abundance of these species be affected, but when they are at low density also their presence or absence in catches. Although changes in seasonal water temperature and salinity have helped to explain some of the observed changes in species abundance, there are some trends that are consistent between the east and west margins of the southern North Sea, such as those shown by the eelpout, that cannot be explained by a common hydrographic regime. In future analyses of changes in inshore fish communities, it will be necessary to include a wider range of environmental factors, such as changes in productivity, or the direct and indirect effects of eutrophication, in order to explain more precisely the observed changes in population structure.

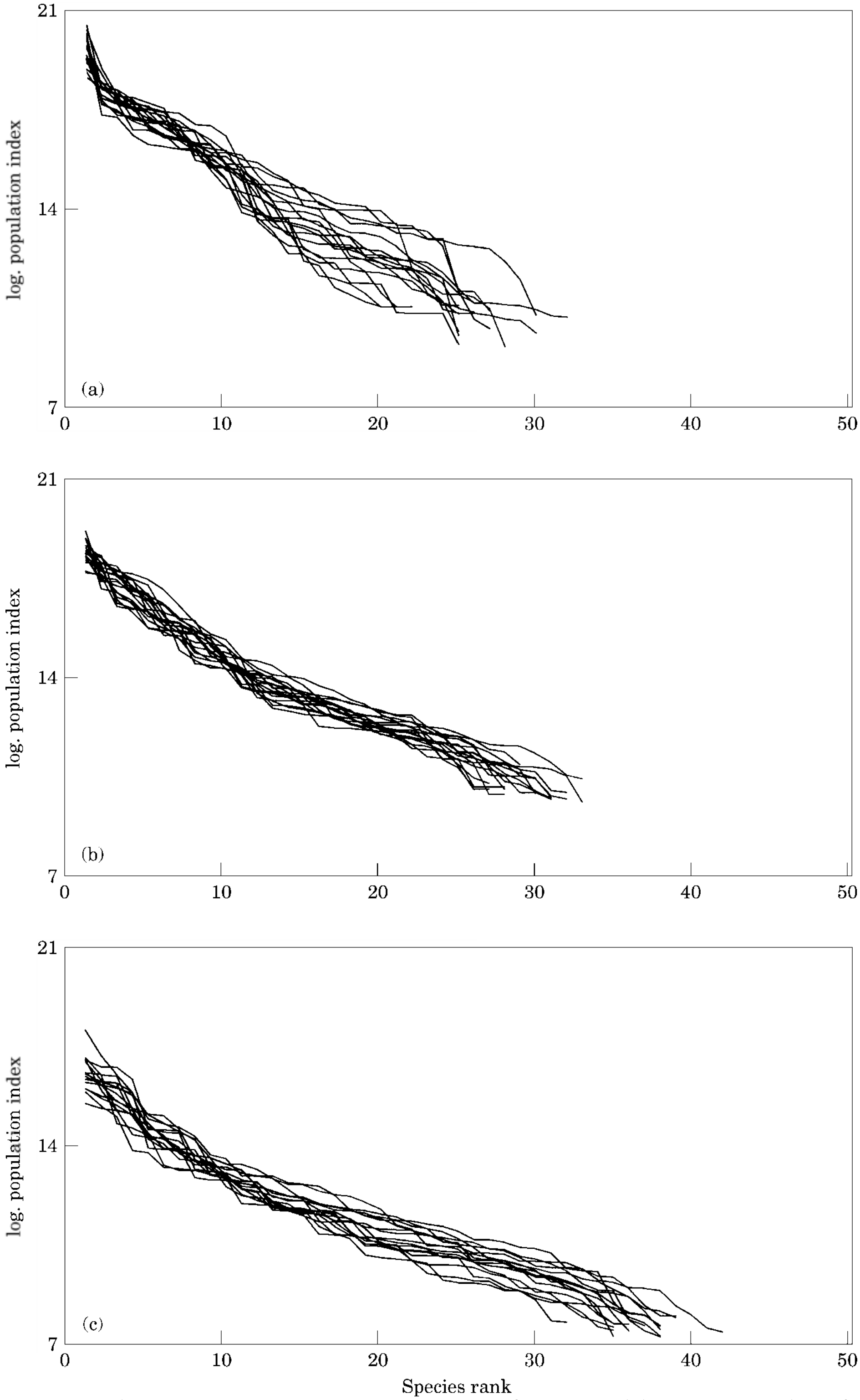


Figure 7. Population abundance estimates (Log_e population size; Table 6) for 54 selected demersal species, shown for each year in decreasing order of abundance for the north-east coast (a), the east coast (b), and the south-east coast (c). The top ranked species each year is that with the greatest population abundance estimate, and those species which were not found in a region (i.e. population abundance=zero) are ranked last.

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