

## Spatial patterns of groundfish assemblages on the continental shelf of Portugal

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The analysis of catch data from groundfish surveys (1985–1988) conducted on the Portuguese shelf and upper slope (20–500 m) revealed five major geographic areas, each characterized by the presence of a typical fish assemblage. These areas of distinct fish assemblages were found to be closely aligned with depth, in a way that resembles spatial patterns previously described for other continental shelves in the North Atlantic. The sharpest biological transition on the Portuguese shelf takes place as one moves from areas shallower than 120 m (“Shallow Groups”) towards deeper locations offshore (“Deep Groups”). Beyond the 150 m isobath, the biomass was dominated by blue whiting, whereas inshore variability in assemblage composition was much greater. Species such as sardine, horse mackerel, mackerel (to the north of Lisbon) and sparids (to the south) comprised significant and highly variable proportions of the population abundance inshore. There are similarities between the trophic and spatial organization of the marine community on the Portuguese shelf and that of other coastal upwelling ecosystems that are briefly reviewed here.

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### Introduction

In the past 15 years marine ecologists have identified and described areas on the continental margins of the Atlantic Ocean that are inhabited by relatively homogeneous fish assemblages. In short-term studies, fish assemblages have been defined merely on the basis that their component species tend to co-occur in catches taken over continuous geographic areas (Tyler *et al.*, 1982). Long-term studies have shown that the co-occurrence of a given set of fish species over broad geographic areas is usually not an incidental phenomenon. Fish assemblages are persistent, they appear to retain their species composition for periods of time that are at least comparable to the life span of most species in the assemblage. Examples of long-term studies (>ten years) in the north Atlantic are the ones conducted for the Georges Bank (Overholtz and Tyler, 1985), the

Middle Atlantic Bight (Colvocoresses and Musick 1984; Gabriel, 1992), the Nova Scotia Shelf (Mahon *et al.*, 1984; Duplisea *et al.*, 1997), the Grand Bank of Newfoundland (Gomes *et al.*, 1992), and the NE Newfoundland/Labrador Shelf (Gomes *et al.*, 1995). In the south Atlantic, short-term studies (usually one year) have been the norm. Amongst the areas studied are the Gulf of Guinea (Fager and Longhurst, 1968), the west coast of South Africa (Roel, 1987), the continental shelf of Angola (Bianchi, 1992a), and the shelf off Congo and Gabon (Bianchi, 1992b).

Identification of fish assemblages was made possible by the growing availability of data from very broad continental margins. However, another reason for the growing interest in this type of study has been the concern with the traditional single-species approach to fish stock management in areas like the Portuguese shelf. This shelf has been subjected to an intense fisheries

exploitation whose effects on the marine community as a whole are poorly understood. In such areas, it is especially important to monitor community composition and spatial distribution over time in order to evaluate resistance (*sensu* Pimm, 1984) to perturbation. Various authors and workshops have called for holistic alternatives to the dominant single-species approach. Populations should be recognized embedded in complex communities where biotic interactions are usually poorly understood but most likely not null (Mercer, 1982; May, 1984; Mahon *et al.*, 1984; Sinclair, 1985; Ulanowicz and Platt, 1985; Caddy and Sharp, 1986; Sherman, 1991, 1993; Gomes, 1993). A reasonable initial approach to the biological community on the continental shelf, and to any community in general (Underwood, 1986), is the definition of an appropriate spatial scale for whatever community studies are to be envisioned. Spatial scale is defined on the basis of the significant variation of some quantity of interest (Powell, 1989). If we are interested in the biotic component of the continental shelf, then the identification of zoogeographic areas that are characterized by a relatively homogeneous and persistent species composition, appears to be particularly relevant for the spatial framing of whatever multispecific approaches are to be conducted in the future.

Our study was intended to identify, describe, and map groundfish assemblages on the Portuguese continental shelf and upper slope (ICES Division Ixa, see Figure 1) in the fall. We used multivariate techniques to analyze catch data from four fall groundfish surveys conducted between 1985 and 1988 off the Portuguese coast. An additional fifth survey, conducted in the spring of 1986, was also analyzed for comparison. Our results are discussed in light of the general picture of spatial patterns of groundfish assemblages emerging from previous studies of continental shelves in the Atlantic.

## Materials and methods

### Study area

#### *Bottom topography*

Figure 1(b) presents the major bathymetric features of the Portuguese continental margin, including the continental shelf and upper slope where most sampling stations were located. The margin is oriented along the local meridian and is cut at some places by sharp submarine canyons that separate regions of relative topographic continuity. The northern half of the Portuguese shelf, from the Minho river (42°N) to the Nazaré Canyon (39°30'N) is relatively wide and flat. Between the Nazaré Canyon and the canyons of Lisbon and Setubal, the coastline is more irregular than to the north. To the north, the shelf is wide (40–70 km) then narrows considerably to the south of Lisbon, remaining

rather slim (15–20 km) down to the southern tip at Cape S. Vicente and all along the southern coast (15–30 km).

#### *General oceanography*

The upper layers of the ocean on the Portuguese shelf are under the influence of a summer upwelling that brings to the surface relatively cold water (Fiúza *et al.*, 1982; Fiúza, 1983) which then flows toward the equator near the shelf break, extending down to depths of 100–200 m. At subsurface layers (~200–1300 m) there is evidence for a mean northward circulation along the western slope of the Iberian Peninsula, transporting water of subtropical origin (~200–500 m) and saline Mediterranean water in the deeper layers (~500–1300 m) (Fiúza, 1982; Ambar, 1983). It is along the southern half of the west coast that the summer upwelling has greater intensity, being particularly strong in the area off Sines (38°N). As the upwelling response develops, cold water may extend as far as 30–50 km offshore, or even reach 100–200 km following stronger pulses of favorable wind (Fiúza, 1982, 1983). The transition from the period of minimum or lack of upwelling (March–May) into the upwelling season appears to take place simultaneously (at a month time-scale) all along the west coast. The end of the season, however, is less well known, taking place around September–October. On the northern half of the Portuguese shelf, from 42°N to the Nazaré Canyon (39°30'N), the upper layers of the ocean exhibit a seasonal alternation between vertical homogenization in the winter and the stratification of upwelled water that characterizes the summer, with isotherms roughly paralleling the isobaths. In the winter, Frouin *et al.* (1990) reported the presence of a more or less continuous strip of relatively cold water between the coastline and the 50 m isobath on account of the general cooling that follows the end of the autumn. To the west of this strip, the authors found evidence for the presence of a warm, salty surface current flowing northwards along the outer shelf and upper slope off northwest Portugal. This shelf-edge current appears to be a characteristic feature of the winter circulation in the area, reaching northern Spain, southwestern France and even the western of Ireland (Frouin *et al.*, 1990).

### Data and methods

#### *The groundfish surveys and the data*

We have analyzed data collected during five groundfish surveys (four in the autumn and one in the spring) conducted off Portugal between 1985 and 1988 by the research vessel “Noruega”, a 47.5-m long stern trawler, operating with a Norwegian Campell trawl (14 m horizontal opening, 4 m vertical opening, groundrope with rollers, 40-mm mesh size in the codend) of the National Institute for Fisheries Research (INIP). The fall surveys took place in October–November, lasted for about one

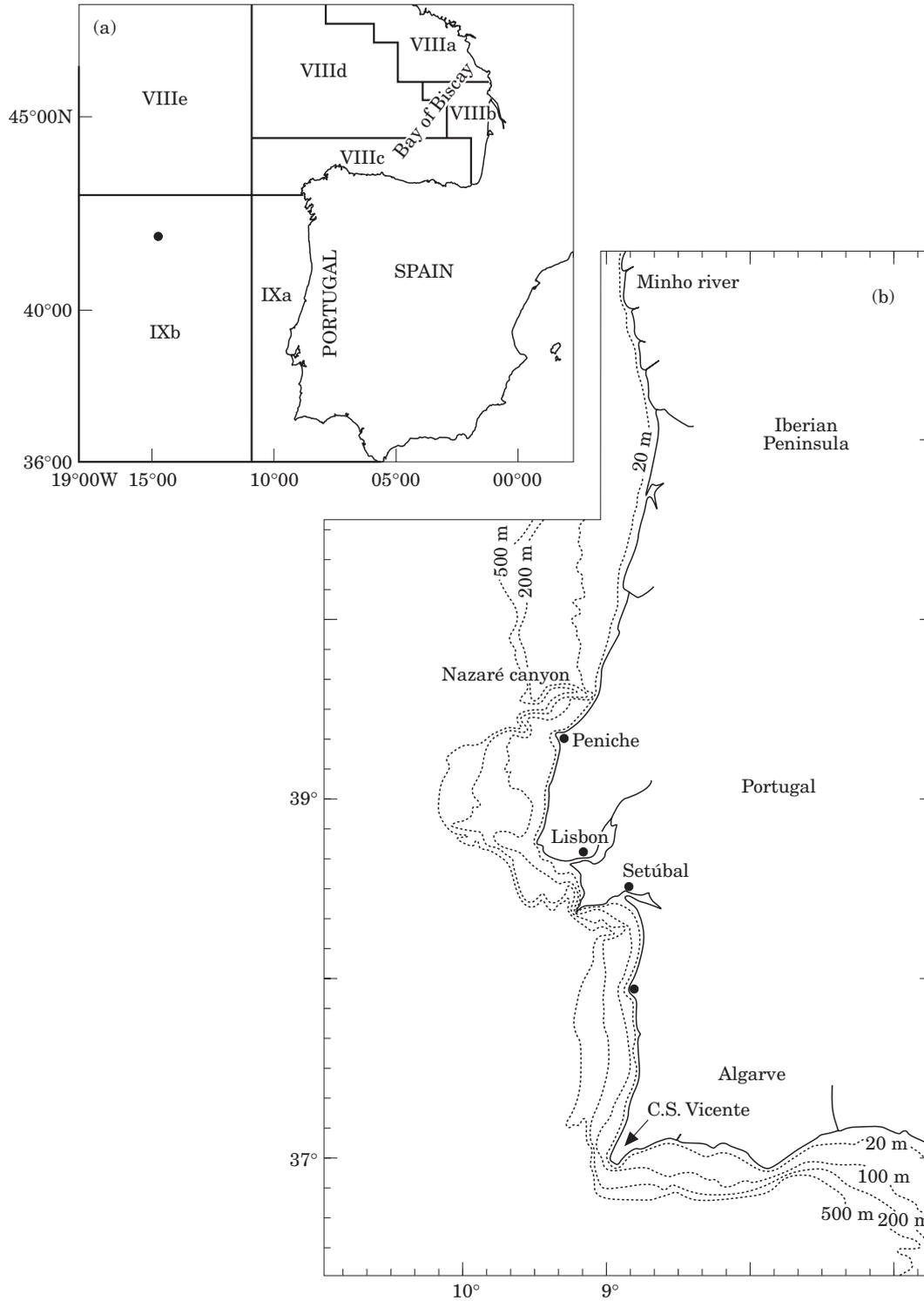


Figure 1. (a) ICES Divisions around Portugal and Spain. (b) Major topographic features of the Portuguese continental margin.

month, and the number of sampling stations per survey were 152 (in 1985), 117 (in 1986), 81 (in 1987), and 102 (in 1988). The spring survey took place in June 1986 and sampled 128 sites. Unlike groundfish surveys in the 1990s, which followed a plan of fixed stations, the 1985–1988 surveys employed a stratified random method, with stratification by depth, latitude and longitude. The Portuguese continental shelf and upper slope are divided into three major depth strata (20–100 m, 100–200 m, 200–500 m) and, superimposed on these, there are 12 major strata oriented by latitude along the west coast and by longitude along the south coast (Cardador, 1983; Borges, 1986). Within each of the resulting 36 strata, the position of every bottom-trawl station was randomly set, with all strata containing at least two stations. Tows were for 30 minutes, at about 3 knots, from sunrise to sunset. The sampling gear was the same for every survey in order to render results comparable across the years.

The individuals caught at each sampling station were identified, almost always to the species level, measured (length), weighed, and counted. Surface and bottom measurements of temperature were also made at selected stations. Every survey yields a two-way data matrix (stations  $\times$  species) whose entry (i, j) is the catch in weight of species j at station i. Not all species caught were included in the matrices. A selection of 31 species (Table 1) was made based on the total biomass and frequency of occurrence of each species in all surveys. Any species that comprised at least 1% of total biomass in at least one of the surveys was included in the analysis. The selection includes all the most important commercial species caught by the bottom trawl, as well as many of the most abundant pelagic species. For each of the five surveys the catch data in the corresponding stations-by-species matrix were log-transformed ( $\ln(x+1)$ ) before the analysis. The transformation is aimed to balance the exponential nature of differences in population biomass. The variance of the most abundant species could easily dominate the results of multivariate analysis, concealing the effect of smaller but relatively important changes in the least abundant species. Previous experience (Gomes *et al.*, 1992, 1995; see also Gauch, 1982) indicated that the reduction of information to one-digit values (after the log transform) achieves a reasonable balance among the biomass variances of groundfishes.

#### Cluster analysis

Cluster analysis was applied to group the sampling stations based on the species composition of their catches, thereby identifying broad areas on the shelf characterized by a relatively homogeneous faunistic composition. Stations were compared by pairs, using the dissimilarity index of Bray-Curtis (Clifford and Stephenson, 1975), commonly considered appropriate in

the fisheries context due to its sensitivity to the most abundant and usually commercially important species (Gabriel, 1983; Sinclair, 1985; Gomes, 1993). The stations were clustered using the hierarchical agglomerative strategy of Group Average (Clifford and Stephenson, 1975) run under the CLUSTAN package (Wishart, 1978). The clusters identified by this method were mapped and geographical continuity of stations belonging to the same cluster was considered an indication of cluster validity. The recurrent appearance of clusters with the same faunistic composition and geographical location over the years was also taken as a confirmation that these clusters were neither sporadic nor an artifact of the method.

#### Interpretation method

Different techniques have been suggested for the interpretation of cluster analysis results. Examples are the inverse clustering of variables followed by nodal analysis (Lambert and Williams, 1962) or the computation of cluster statistics. However, inverse clustering of species held little attraction because of the discrete nature of exclusive classifications that lead to the inclusion of each species into a single cluster, no matter how ubiquitous that species may be. Moreover, ecologists have often defended the advantages of using polythetic divisive methods as opposed to agglomerative ones (Lambert *et al.*, 1973; Boesch, 1977; Gauch, 1982). Agglomerative methods begin by joining the pair of units which are more similar in respect to a set of variables. In each subsequent step, similarities between objects (units and pre-formed clusters) are re-evaluated and the two most similar objects are combined. In ecology, this step-by-step aggregation leads to classifications that are sensitive to the random noise commonly found in the basic ecological samples upon which it builds. Instead, we have used a divisive method proposed by Hill *et al.* (1975) and later refined and computerized by Hill (1979) under the name of TWINSpan. The method makes an initial ordination of species and samples using correspondence analysis. A rough division of samples is done based on scores on the first factorial axis and “differential” species are identified by their preference to one or the other side of the dichotomy. A second, “refined”, ordination is then achieved by using “differential” species and the new ordination is divided to derive a final dichotomy. The process proceeds in the same way over the two sides of this dichotomy. The final results of TWINSpan are displayed in a two-way table that fulfills requirements of non-exclusivity. An ubiquitous species can therefore be associated with more than one cluster of stations by simple visual inspection. Inspection of such two-way tables allowed the recognition of biological features of each of the main station clusters previously identified by cluster analysis.

Table 1. List of taxa caught in groundfish surveys that were included in this study. Common vernacular names of species, in portuguese and english, are included.

Cephalopods	Portuguese	English
<b>Loliginidae</b>		
<i>Alloteuthis</i> spp.	lula pequena	
<i>Loligo vulgaris</i> (Lamarck 1798)	lula	European squid
<b>Ommastrephidae</b>		
<i>Illex coindetii</i> (Verany 1837)	pota	shortfin squid
<b>Decapod crustaceans</b>		
<b>Nephropidae</b>		
<i>Nephrops norvegicus</i> (Linnaeus 1758)	lagostim	Norway lobster
<b>Penaeidae</b>		
<i>Parapenaeus longirostris</i> (Lucas 1846)	gamba	deepwater rose shrimp
<b>Portunidae</b>		
<i>Polybius henslowi</i> (Leach 1820)	pilado	pelagic crab
<b>Batoid fishes and sharks</b>		
<b>Rajidae</b>		
<i>Raja (Raja) clavata</i> (Linnaeus 1758)	raia	thornback ray
<b>Scyliorhinidae</b>		
<i>Scyliorhinus canicula</i> (Linnaeus 1758)	pata-roxa	small spotted dogfish
<b>Bony fishes</b>		
<b>Gadidae</b>		
<i>Micromesistius poutassou</i> (Risso 1826)	verdinho	blue whiting
<i>Trisopterus luscus</i> (Linnaeus 1758)	faneca	pout
<i>Trisopterus minutus</i> (Linnaeus 1758)	fanecão	poor cod
<b>Merlucciidae</b>		
<i>Merluccius merluccius</i> (Linnaeus 1758)	pescada	European hake
<b>Congridae</b>		
<i>Conger conger</i> (Linnaeus 1758)	safio	conger eel
<b>Scophthalmidae</b>		
<i>Lepidorhombus boscii</i> (Risso 1810)	areeiro de 4 manchas	four-spot-megrim
<b>Soleidae</b>		
<i>Microchirus variegatus</i> (Donovan 1808)	solha	plaice
<b>Argentinidae</b>		
<i>Argentina sphyraena</i> (Linnaeus 1758)	argentina	argentine
<b>Clupeidae</b>		
<i>Sardina pilchardus</i> (Walbaum 1792)	sardinha	sardine
<b>Callionymidae</b>		
<i>Callionymus lyra</i> (Linnaeus 1758)	peixe-pau	common dragonet
<b>Carangidae</b>		
<i>Trachurus trachurus</i> (Linnaeus 1758)	carapau	horse-mackerel
<b>Scombridae</b>		
<i>Scomber (scomber) scombrus</i> (Linnaeus 1758)	sarda	mackerel
<b>Sparidae</b>		
<i>Boops boops</i> (Linnaeus 1758)	boga	bogue
<i>Diplodus vulgaris</i> (Saint-Hilaire 1817)	sargo, safia	two-banded seabream
<i>Pagellus acarne</i> (Risso 1826)	besugo	axillary seabream
<i>Spondyllosoma cantharus</i> (Linnaeus 1758)	choupa	black seabream
<b>Trichiuridae</b>		
<i>Lepidopus caudatus</i> (Euphrasen 1788)	peixe-espada	scabbard fish
<b>Triglidae</b>		
<i>Aspitrigla cuculus</i> (Linnaeus 1758)	ruivo	gurnards
<i>Lepidotrigla cavillone</i> (Lacepede 1801)	ruivo	red gurnard
<i>Trigla lucerna</i> (Linnaeus 1758)	ruivo	tub gurnard, saphirine gurnard
<b>Macrorhamphosidae</b>		
<i>Macrorhamphosus gracilis</i> (Lowe 1839)	apara-lápis	
<i>Macrorhamphosus scolopax</i> (Linnaeus 1758)	apara-lápis	snipefish
<b>Caproidae</b>		
<i>Capros aper</i> (Linnaeus 1758)	mini-saia	boarfish
<b>Zeidae</b>		
<i>Zeus faber</i> (Linnaeus 1758)	peixe-galo	John dory

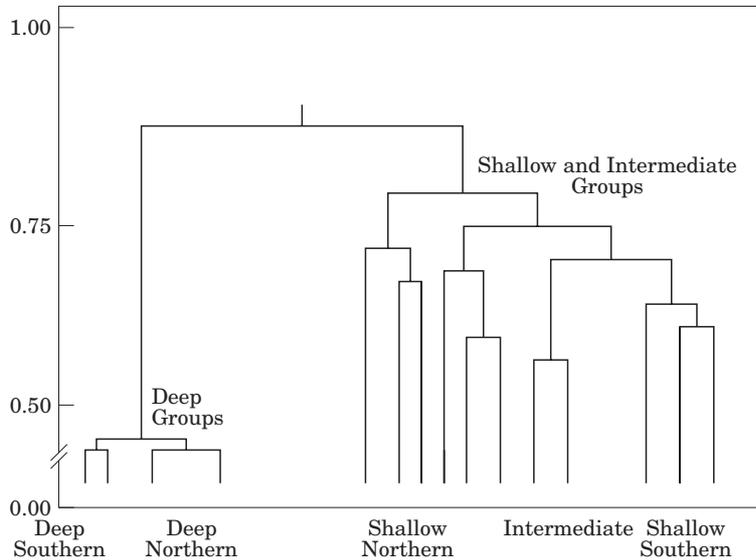


Figure 2. Typical result of cluster analysis with the Group Average algorithm (in this case fall 1988). The dendrogram is cut at a high hierarchical level and the major groups of stations are identified as well as the number of stations at each group. The ordinate scale is the Bray-Curtis measure of dissimilarity.

## Results

### Groundfish assemblages: the depth and latitude dichotomies

The major dichotomy in the multivariate analysis was always between sampling stations shallower than approximately 100 m and deeper stations commonly beyond the 150 m isobath. The sharpest zoogeographic contrast on the Portuguese Shelf is thus associated with depth, defining what may be called a “Shallow Group” and a “Deep Group” of stations (Figures 2 and 3). The most abundant species in shallow stations are the horse-mackerel (*Trachurus trachurus*) and sardine (*Sardina pilchardus*) (all along the coast), mackerel (*Scomber scombrus*) (to the north of Lisbon), and sparids, especially the axillary seabream (*Pagellus acarne*) (to the south of Lisbon). The most important biological transition of the Portuguese margin takes place as one moves from the shallow nearshore (20–120 m) towards stations deeper than the 150 m isobath. In these stations of the Deep Group, i.e. from 150 m down to at least 400 m, the biomass is dominated by the blue whiting (*Micromesistius poutassou*). This species forms large concentrations along the shelf break, accounting for the relatively high values of total biomass found in deep stations. The other species caught in large amounts beyond 150 m are the European hake (*Merluccius merluccius*), an ubiquitous and abundant species throughout the shelf and, occasionally, boarfish (*Capros aper*) to the south.

Within the shallow and deep clusters of stations, the major separation was associated with latitude (Figures 2 and 4). Both the Shallow and the Deep Groups sub-

divided into a group whose vast majority of stations was located to the north of Lisbon and one other group whose stations were located to the south and off Algarve. The exact latitude where this north–south separation took place varied from year to year between Peniche and Setubal. We thus have a “Shallow-Northern Group”, a “Shallow-Southern Group”, a “Deep-Northern Group”, and a “Deep-Southern Group” of stations (Figure 4). In three of the surveys (fall 1985, fall 1986, fall 1988) stations belonging to the Shallow-Southern Group could be further subdivided into two groups associated with depth. There was a cluster of stations between 20 and 100 m (Figure 3), with a biological composition typical of the Shallow-Southern Group, and a cluster between 80 m and 180 m with a composition that appears to be in transition to the Deep-Southern Group. This 80–180 m cluster was named the “Intermediate Group”; it was a characteristic feature in only three out of five surveys, along the southwest coast.

Clusters of stations at lower hierarchical levels did not recur, in other words, it was not possible to recognize their biological or geographical features in at least two of the surveys. This led us to conclude that any further subdivision of the above mentioned groups risked being merely a result of fortuitous circumstances at the time of the survey rather than a true mesoscale biogeographic feature of the Portuguese Shelf.

### Shallow Groups

Stations in the Shallow Groups were usually between 20 and 100 m, although they might reach the 120 m isobath

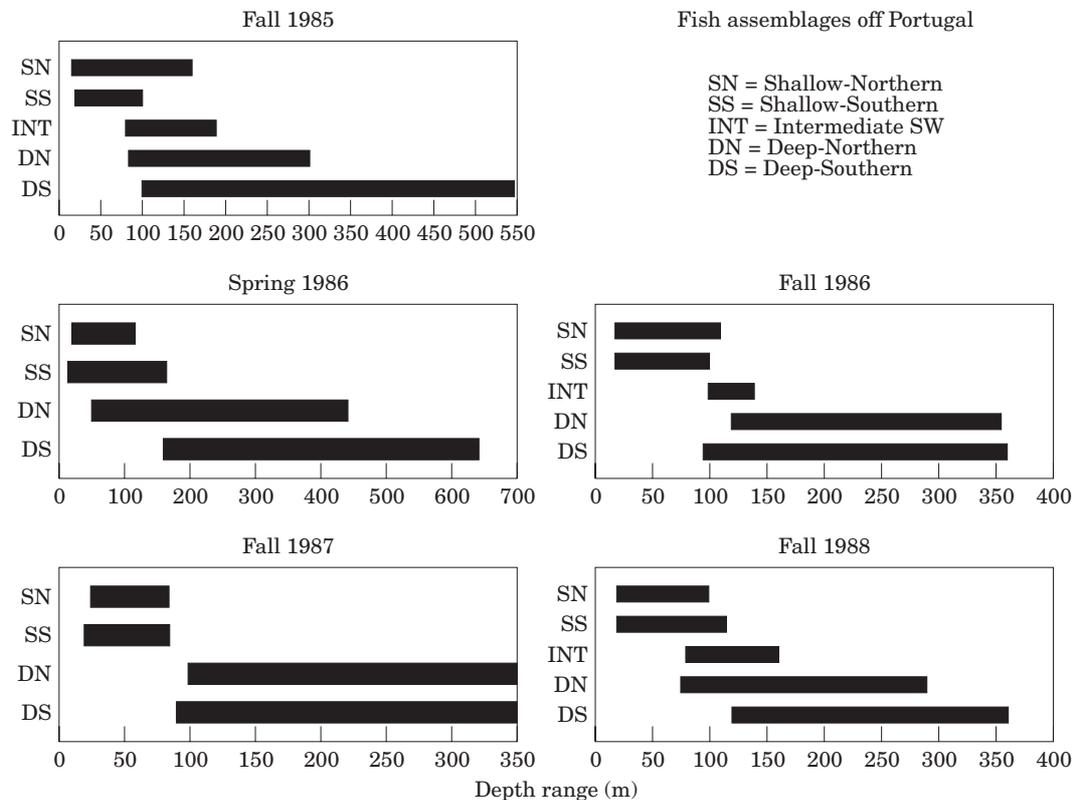


Figure 3. Depth range of clusters of stations that define every fish assemblage off Portugal, by survey.

(Figure 3). No single species dominated the biomass at these stations in any of the surveys. In the Shallow-Northern Group, each of the following species accounted for more than 20% of the biomass of catches in at least one of the surveys (Figure 5): sardine (spring 1986, fall 1986, fall 1988), mackerel (fall 1985, fall 1988), horse-mackerel (fall 1986, fall 1987), and European squid (*Loligo vulgaris*) (fall 1987). Altogether, these four species always accounted for more than 80% of total biomass in the catches. However, alone, each species exhibited a very high variability in abundance (Figure 5). Other species routinely caught in the Shallow-Northern Group were European hake, pout (*Trisopterus luscus*), pelagic crab (*Polybius henslowi*), and poor cod (*Trisopterus minutus*). The presence of pout, poor cod, and mackerel, in particular, is very typical in the group. The total catch per unit effort (CPUE) also exhibited high variability, ranging from about 15 Kg tow<sup>-1</sup> in 1987 to 117 Kg tow<sup>-1</sup> in 1986 (Figure 5).

The geographic boundary between the Shallow-Northern and Shallow-Southern Groups is in the region of Setubal and its location did not vary much in the course of the four years studied. As one moves southward across this region, the relative proportion of mack-

erel in the catches decreases significantly, whereas the importance of sparids increases (Figure 5). In most surveys there was also evidence for the southward decrease of species of the genus *Trisopterus* (pout and poor cod). In the Shallow-Southern Group, horse-mackerel and the axillary seabream usually composed more than 50% of total biomass in the catches (Figure 5). Other species routinely accounting for 1–10% of the biomass were the European hake, sardine, European squid, John dory (*Zeus faber*), and the seabreams *Diplodus vulgaris*, *Spondilyosoma cantharus* and *Boops boops*. The presence of various species of seabreams is probably the most characteristic feature of the southwestern nearshore, as it distinguishes this area biogeographically from the region to the north of Lisbon. The total CPUE exhibited a clear increasing trend during the study period, from about 14 Kg tow<sup>-1</sup> in 1985 to 123 Kg tow<sup>-1</sup> in 1988, mainly due to increases in axillary seabream (in 1986–1987) and horse-mackerel (in 1988).

It is arguable whether the Intermediate Group (80–180 m) should be kept apart from the Shallow-Southern Group or be merely considered a deeper section of the latter. The group was only recognized in three surveys, and to the exception of *Allotheuthis spp.* and John dory,

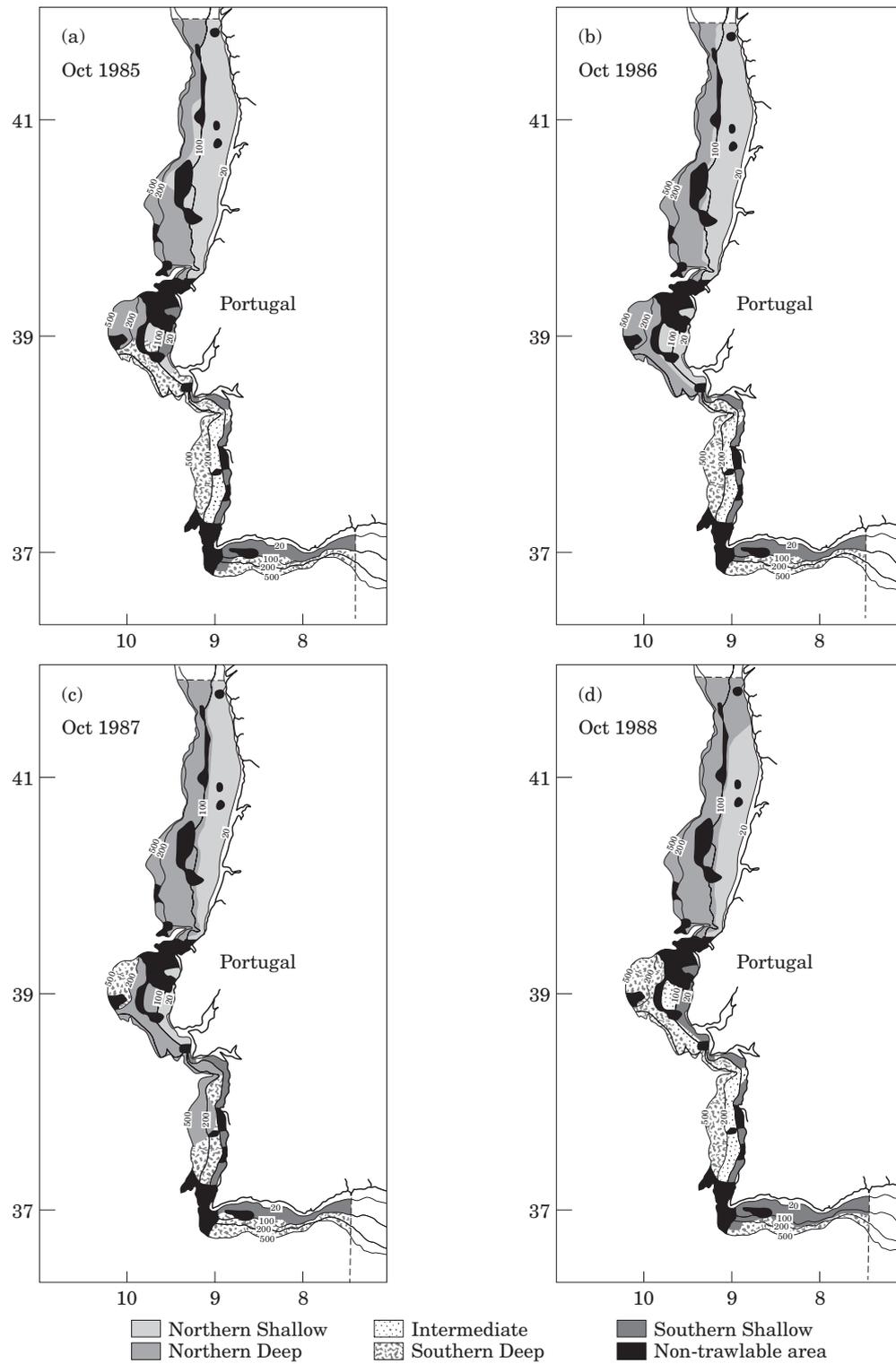


Figure 4. Areas covered by the major fish assemblages off Portugal in the fall (1985–1988).

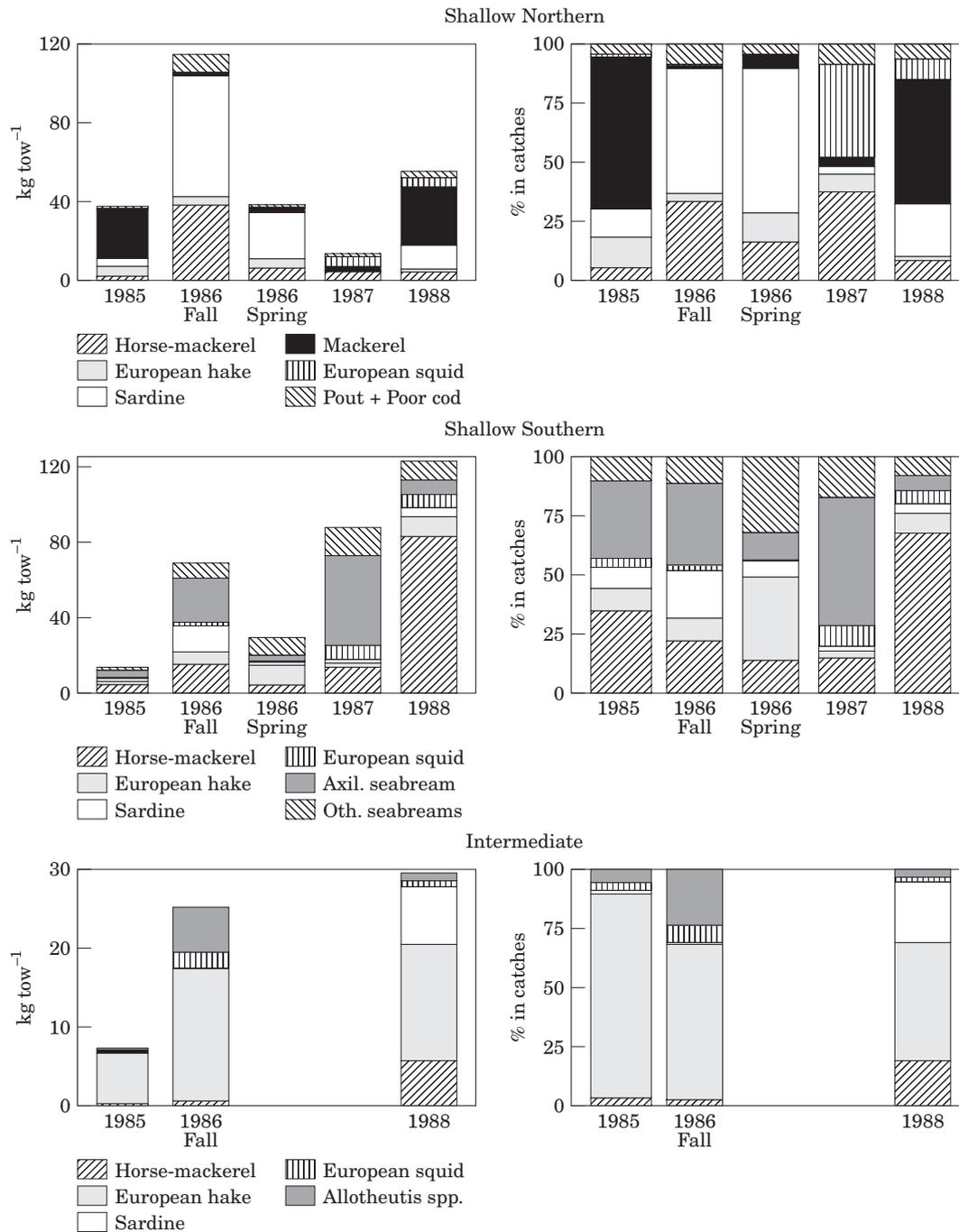


Figure 5. Biomass composition of catches (in kg per tow on the left and in weight percentage on the right) at the five main clusters of stations identified on the Portuguese Shelf in four fall surveys and one spring survey, from 1985–1988.

all species of the Intermediate Group (European hake, sardine, squid, horse-mackerel) were found at stations of the Shallow-Southern Group (Figure 5). The most distinguishing feature of the Intermediate Group was the

dominance of the European hake in the catches (47–80% of the biomass). The total CPUE was relatively low, attaining its highest value in 1988, with 30 Kg tow<sup>-1</sup>. It is possible that this group reflects the presence of the

major nursery of hake in the area (Cardador, 1995), as discussed below. In such case, the irregular appearance of the group might then reflect biomass movements of hake recruits between depths of 100 m and 300 m.

### Deep Groups

About 50 species were routinely caught by the groundfish surveys beyond the 150 m isobath, along the shelf and upper slope of the Portuguese continental margin (Deep-Northern and Deep-Southern Groups). The vast majority of these species, however, represented always less than 0.1% of the biomass in the catches. Usually three to nine species accounted for almost all of the biomass in the Deep Groups. Among these, the blue whiting was the most abundant species, usually composing 70–90% of the biomass in the catches. Stations in the Deep Groups were also distinguished by their relatively high catch rates. In a total of eight fall observations conducted in the Deep Groups (four in the north plus four in the south), the CPUEs were only once lower than 100 Kg tow<sup>-1</sup> (Deep-Southern Group in 1985) (Figure 5).

In the Deep-Northern Group blue-whiting made up most of the catches with the remaining biomass almost totally composed of the European hake. Two other ubiquitous species, pout and John dory, represented little biomass but made frequent appearances in the shallower stations of the group. Total catch rates were relatively stable, staying around 250–300 Kg tow<sup>-1</sup> between 1985 and 1987, and dropping to 115 Kg tow<sup>-1</sup> in 1988. Unlike the north–south boundary between the two Shallow Groups, the exact location of the north–south boundary between the Deep Groups was highly variable among surveys (Figure 5). In the Deep-Southern Group, to the south of Lisbon and off Algarve, the biomass was still dominated by blue whiting, but a few other species were usually caught in significant amounts. These were boarfish (3–49% of the biomass), European hake (4–9%), and the decapod crustaceans Norway lobster (*Nephrops norvegicus*) and deepwater rose shrimp (*Parapenaeus longirostris*) (altogether 1–2% of the biomass). Total CPUE was highly variable, ranging from 92 Kg tow<sup>-1</sup> in 1985 to 545 Kg tow<sup>-1</sup> in 1988 (Figure 5).

### Discussion

#### Recurrent fish assemblages on North Atlantic shelves: persistence, change, and uncertainty

Analysis of four years of groundfish data from the Portuguese Shelf indicated a high degree of spatial consistency in the clustering pattern of stations and in its species composition throughout most of the shelf. We could thus map and describe four broad recurrent areas,

characterized by relatively homogeneous fish assemblages (Figure 4) in the five surveys analysed, plus a fifth area that was identified in three of the surveys. In general, the geographic contours of these areas did not change very much from year-to-year, although the relative proportion of species within each assemblage varied considerably especially in the inshore assemblages (Figure 5). These results are in agreement with the general description of continental shelves and upper slopes depicted by similar studies (Colvocoresses and Musick, 1984; Mahon *et al.*, 1984; Overholtz and Tyler, 1985; Gabriel, 1992; Gomes *et al.*, 1992, 1995), which have revealed the existence of relatively homogeneous fish assemblages covering broad areas of continental shelves and slopes in the Northwest Atlantic. Apparently these assemblages are persistent, retaining their species compositions over periods of time at least as long as the average life span of their component species. There is also strong evidence for the mesoscale persistence of the geographic boundaries of the assemblages. Their geographic limits are usually relatively predictable and may be associated with the bottom topography or other physical features in the area.

In spite of this general picture of persistence and geographic predictability, long-term studies have also shown that, every once in a while, there is a year (or season) when assemblage patterns seem to be rather atypical (Colvocoresses and Musick, 1984; Mahon *et al.*, 1984; Gomes, 1993; Gomes *et al.*, 1995). In such years the biomass proportions of individual species within the assemblages are unusual and/or some boundaries seem to be displaced from their usual geographic locations. It is usually possible to identify a few assemblage boundaries that are more prone to displacement. For example, boundaries of the Avalon assemblage on the Grand Banks of Newfoundland, shifted conspicuously in a sequence of maps for 16 years of groundfish data (Gomes, 1993). When data are available only for a single year such anomalies pass undetected. With data for a small number of years, one or two being anomalous, it is difficult to decide whether we are witnessing artifacts caused by an inappropriate sampling plan or actual boundary displacements. More drastic changes in assemblage composition and location are also possible although more rarely reported. Gomes *et al.* (1995) described the drastic disruption of a long standing assemblage structure on the Labrador Shelf, Canada, probably due to the combined effect of changing environmental conditions and overexploitation by the fishery, illustrating how these factors can sweep away apparently stable fish assemblages over a relatively short number of years.

In this study we present a biogeographic portrait of the Portuguese shelf that appears to be robust at the regional scale of a few hundred kilometers. The five year time-series analysed, however, is relatively short to draw

safe conclusions about assemblage patterns at the scale of tens of kilometers. For example, it is uncertain whether the Intermediate Group, identified from 80–180 m off the southwest coast, corresponds to a persistent assemblage or to a faunistically intermediate region that is formed only in some years. Alternatively, it may merely be an artifact due to inadequate sampling in the area. The presence of year-round high concentrations of hake in the 100–200 m band along the SW coast had been previously reported by Cardador (1995), but the existence of a faunistically distinct area also depends on the relative abundance of the species that are companion to the hake therein.

Other small-scale features could only be illuminated by increasing the number of sampling stations in strata that appear to be critical for the spatial discrimination of the assemblages. In every survey there was a great deal of uncertainty concerning the geographic location of the latitudinal boundary between northern and southern assemblages. The location of the boundary between the Deep-Northern and Deep-Southern assemblages, for example, appeared to be highly variable between Peniche and Setúbal. These two assemblages were dominated by the blue whiting, which often composed more than 90% of biomass in the catches. It would take a greater sampling intensity to detect the transition from one assemblage to the other based on the co-occurring species that contribute much less to total biomass. It should be acknowledged, however, that the main purpose of groundfish surveys, yielding the sort of information that has proved useful in defining assemblages along continental shelves, is rarely patterns of spatial distribution by themselves. The principal purpose of these surveys was to estimate standing stocks and monitoring a small number of commercial species. Only by coincidence will a sampling plan designed to minimize the variance of biomass estimators also be the most suitable to identify spatial patterns of biological variation.

### A depth-aligned distribution

On continental shelves of the Northwest Atlantic, depth was consistently associated with biological variation. It has been relatively easy to recognize assemblages of groundfish species that dominate the shallow portion of the shelves (usually <100 m). Examples are the yellow-tail flounder, longhorn sculpin, little skate, and window-pane flounder in the Middle Atlantic Bight and on the Georges Bank (Overholtz and Tyler, 1985; Gabriel, 1992). Easily recognizable also are assemblages of deeper dwellers (usually beyond 150 m) dominating part of the upper continental slope. Redfish, white hake, common grenadier, longfin hake and witch flounder are examples drawn from the Scotian Shelf (Mahon *et al.*, 1984). Deep assemblages tend to have a much broader

depth range than do the shallow ones (Snelgrove and Haedrich, 1985), even if occupying narrower areas in two-dimensional mapping. Depth contours are much closer there and ambient conditions tend to stay homogeneous along broader depth ranges than in the larger shallow areas. On the Grand Banks of Newfoundland (Gomes *et al.*, 1992), for example, the shallow assemblage is usually found between 40–100 m, whereas the deep assemblage occurs beyond the 200 m isobath and down to at least 400 m. Assemblages falling intermediate between the shallow and deep extremes have been identified, but are usually more difficult to characterize. They tend to be a mix of species from the shallow and deep assemblages with no abundant distinctive species of their own.

Major changes in the composition of the demersal community off the Portuguese Shelf are also associated with depth. This led us to use a Shallow-Deep terminology to name the main groups of stations. Biological change is particularly sharp between the 100 and 200 m isobaths, where separation between the two main groups takes place. Species like the seabreams, the European squid, and the horse-mackerel were strongly associated with the narrow 20–100 m depth band, whereas the blue whiting characterizes a much wider and deeper depth range, from approximately 150 m to the maximum depth attained in the surveys (usually 450–500 m). As in previous studies of fish assemblages in the Atlantic, in some years we have identified a transition strip between the Shallow and the Deep groups. Again, this intermediate zone had no distinctive species of its own, rather being an unusual combination of species that are found in the assemblages nearby. Our time-series was not long enough to either validate it as a permanent feature in the area or to recognize it as dependent on changes in the depth range of hake recruits in the area as suggested below.

Some of the most abundant species on the Portuguese margin, namely horse-mackerel and European hake, occur both in deep and shallow assemblages. Several studies suggest that these species are at different ontogenic stages in these different assemblages. The juveniles of horse-mackerel form nearshore concentrations between 20–100 m, along all continental shelf, with higher abundance in the southwest coast (Borges, 1983, 1984), whereas adults are distributed from 20–200 m, with higher abundance between 100 and 200 m (Borges, 1988). Apparently they move to deeper waters after the winter-spring spawning and can be caught in the wide 200–500 m depth range in the summer (Borges and Gordo, 1991; Murta and Borges, 1994). The biomass of horse-mackerel caught in our Shallow Assemblages was therefore probably dominated by juveniles, whereas the few horse-mackerel caught in the Deep Assemblages were post- and pre-spawning adults. There is also evidence for a differential size distribution

of the European hake. Although its biomass spreads down to 400 m, hake recruits (age 0, <17 cm) along the northwest coast of the Iberian Peninsula have higher catch rates between 100–200 m at all seasons (Pereiro and Pineiro, 1985; Cardador, 1984, 1995). The main nursery area of hake in Portuguese waters is along the southwest coast to the south of Lisbon (Cardador, 1995). The depth preferred by the recruits therein seems to shift between the 100–200 m and the 200–300 m depth ranges (Cardador, 1995). If survey stations in the area are done at a time when the bulk of recruit biomass is between 100 and 200 m, it is possible that methods of multivariate data analysis recognize stations in this depth range as faunistically distinct. That probably explains the identification of the Intermediate Assemblage in our fall surveys of 1985, 1986, and 1988.

#### Oceanography, trophic links and fish assemblages off Portugal

Most long-term studies of fish assemblages on the Northwest Atlantic (e.g. Colvocoresses and Musick, 1984; Mahon *et al.*, 1984; Gomes *et al.*, 1992) have attempted to draw associations between major assemblages and either water masses or thermal structures on continental shelves. Four of the surveys analyzed in our study took place in October–November, after the end of the upwelling season on the Portuguese shelf. The surveys were conducted during a transition period between this season and the vertical homogenization that characterizes the winter cooling, when oceanographic circulation and thermal structure nearshore are less understood off Portugal. The single spring survey analyzed took place in June, about one month before the average upwelling season. There were no prominent differences in assemblage structure in this survey, when compared to the fall surveys, although it should be kept in mind that our study would only recognize mesoscale differences between the spring and the fall. The mesh size of the station grid is too coarse to detect changes in the distribution of fishes within the assemblages.

The biological significance of physical oceanographic processes is well described for planktonic organisms with very limited locomotory capacity (Landry, 1977; Longhurst, 1981; Parsons *et al.*, 1983). The effect of physical processes on the movements, distribution, and food web organization of actively swimming nekton, however, has received much less investigation, perhaps because the relevant time scales are set as much by the swimming velocities of the larger animals as by the velocity of the physical processes themselves. Marine communities in coastal upwelling ecosystems, however, exhibit global patterns of trophic and spatial organization that are worth a brief allusion because of their striking similarities with those on the Portuguese shelf.

Much of the primary production in coastal upwelling ecosystems is transported away by water circulation from the immediate centre of upwelling, thus lower trophic levels in upwelling areas are often displaced with respect to one another, progressively away from the centre of upwelling (Vinogradov and Shushkina, 1978; Barber and Smith, 1981; Vinogradov, 1981). In areas of seasonal upwelling, fishes are required to have a certain degree of mobility that displaces them as much away from the centre of production as they rank higher in the trophic structure. On the Portuguese shelf, such mesoscale pattern of fish distribution led us to expect that species closer to primary production, like sardine, should distribute closer to shore, whereas species closer to secondary and tertiary production, like adult hakes and adult horse-mackerel, should extend their distribution further offshore. Our depth-aligned description of fish assemblages appears to fit such expectations.

In common, stereotyped, descriptions of upwelling systems, successive levels up the food web are dominated by euphausiids, small fish like sardine and anchovy that may exploit the primary production directly, and larger predators like hakes and jack mackerels (Ryther, 1969; Landry, 1977; Boje and Tomczak, 1978; Cushing, 1982; Caddy and Sharp, 1986). Although this is obviously a gross oversimplification, the addition of a few important components, namely the blue whiting, cephalopods, and sparids, makes this description quite compatible with the composition of the marine community on the Portuguese shelf described in this study. Euphausiids are probably major competitors of sardine for primary production and they are likely to be the major link through which primary production is transferred to fish on the Portuguese shelf, either directly or indirectly through the blue whiting. In our Deep Assemblages (shelf break and upper slope), biomass is dominated by the blue whiting, whose diet is mostly dependent on zooplanktonic crustacea, mostly copepods and euphausiids (Cabral, 1992). On the Portuguese shelf, the blue whiting are heavily preyed upon by hake greater than 20 cm (Trindade, 1983; Cabral, 1992), which was the second most important fish identified in the Deep Assemblages, as well as by large mackerel (Murta, 1992) (Figure 6). Euphausiids have also been reported to comprise a very important proportion of the diet of hakes smaller than 20 cm (Trindade, 1983; Cabral, 1992), of mackerel smaller than 25 cm (Murta, 1992), and of horse-mackerel at all sizes (Murta, 1992). A simplified picture of major trophic links within our Shallow Assemblages (Figure 6) thus positions sardine and euphausiids competing for primary production and being preyed upon by horse-mackerel, the younger stages of hake and, to the north of Lisbon, by mackerel (Figure 6). The sparids are very important in the Shallow Southern Assemblage but we are not aware of comprehensive studies of their diet off Portugal.

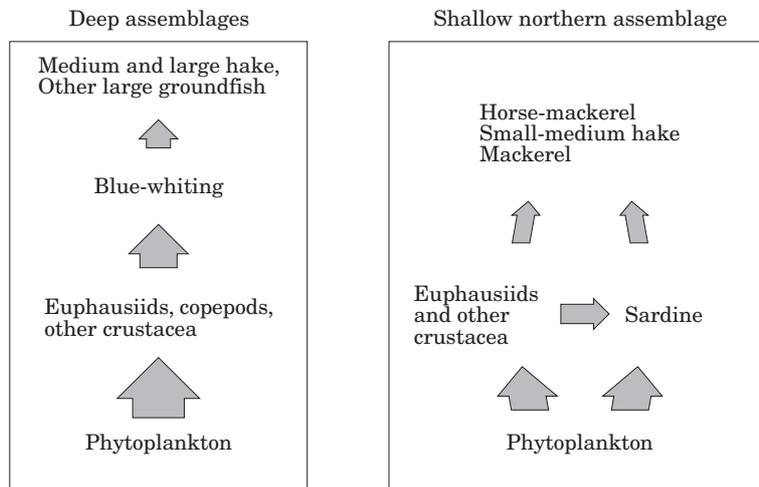


Figure 6. Major directions of energy flow in the Deep assemblages and in the Deep Northern assemblage areas.

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