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Fisheries Research 75 (2005) 120–137

FISHERIES RESEARCH

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Demersal assemblages off Portugal: Mapping, seasonal, and temporal patterns

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Received 3 September 2003; received in revised form 21 February 2005; accepted 23 March 2005

Abstract

Analysis of trawl surveys (1989–1999, 22 surveys) conducted off Portugal (36–710 m depth) indicated the existence of five spatially distinct fish assemblages: shallow and intermediate (northern and southern), and deep assemblages. Depth and latitude correlated with major directions of biological turnover on the shelf, and accordingly, determined the geographical location of the assemblage boundaries. These did not change significantly between the summer and fall surveys, but there were seasonal changes in relative species composition within assemblages, which are discussed in light of known patterns of planktonic production associated with the seasonal upwelling. On the shelf plateau (<150 m), horse mackerel (*Trachurus trachurus*) was more important in autumn assemblages, whereas the pelagic crab (*Polybius henslowii*), and boarfish (*Capros aper*) dominated summer assemblages to the north and south, respectively. On the upper slope, the fish community was dominated by blue whiting (*Micromesistius poutassou*). Most species were confined to certain depth and latitudinal ranges, and in ubiquitous species (European hake, *Merluccius merluccius*, horse mackerel), mean body size increased from the shallower to the deeper assemblages.

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Keywords: Fish assemblages; Continental shelf; Portugal; Blue whiting; Boarfish; European hake; Horse mackerel; Pelagic crab

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1. Introduction

An understanding of the ecological context within which fisheries take place, is essential to minimize the adverse impacts of those activities, preserve biodiversity, and assess the long-term ability of the ecosystem to sustain the catches. In that sense, a call for the incorporation of more ecological concepts into fisheries management has recurrently appeared in the literature (Mercer, 1982; May, 1984; Caddy and Sharp, 1986; Sherman, 1991; Gomes, 1993), and more recently, the European Union adopted a common fisheries policy that, where appropriate, is to be based onto a whole-system approach to fisheries management (COM,

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doi:10.1016/j.fishres.2005.03.012

2002). The differences between the geographical distribution of fish populations and the management areas of interest to fisheries have been recently recognized as of primordial concern (Gislason et al., 2000). In this sense, a reasonable initial approach to ecosystem understanding is a good description of the biological community involved and of its major environmental correlates.

The goal of this paper is to present a description of the demersal marine community inhabiting the continental margin off Portugal, how it organizes into fish assemblages, their spatial distribution, and the environmental factors that they are associated with. This description is based on the larger biological data set currently available for the area, collected over the past 11 years by research trawl surveys of the Portuguese Institute for Fisheries and Sea Research (IPIMAR).

Fager and Longhurst (1968) and Day and Pearcy (1968) were pioneers in describing and mapping large marine communities on continental shelves. Later, the accumulation of data collected by fisheries and survey activities, allied to the increasing availability of computational means, led to an increasing number of similar studies, initially centered on fishing grounds in the Northwest Atlantic (Tyler et al., 1982; Colvocoresses and Musick, 1984; Mahon et al., 1984, 1998; Gabriel, 1989; Gomes et al., 1992, 1995) and later on continental margins all over the world (e.g. Bianchi, 1991; Jin, 1995; Barber et al., 1997; Adjeroud et al., 1998). Demersal fish assemblages off Portugal have also been previously identified and characterized based on 4 years of survey data (1985–1988) (Gomes et al., 2001). The authors emphasized the relationship between the structure of fish assemblages and major oceanographic features in the area, discussing the dominant routes of trophic flow in the assemblages. Here, we use an 11-year time series, the community patterns described are thus less vulnerable to anomalous years or to eventual artifacts caused by the methods of analysis.

2. Methods

2.1. Data sources and selection

IPIMAR has conducted demersal research trawl surveys on the Portuguese continental margin since 1979. The surveys followed a fixed grid of 97 sampling stations, spread throughout the shelf between 36 and 710 m (Fig. 1). In this study, we analyze an 11-year time series (1989–1999) of data collected by 22 surveys, conducted in the fall (11 surveys), summer (9 surveys), and winter (2 surveys) (Table 1). The target duration of each tow was 60 min and further details on the methodology, research vessels, and gear characteristics of the surveys can be found in Cardador et al. (1997).

Each survey yields a two-way data matrix (stations × species) whose entry (i, j) is the catch of species j at station i. The number of stations by survey ranged from 57 to 96 in the autumn of 1992 in the summer of 1990 (Table 1). The initial data basis included 343 taxa (species or groups of species), including fish, crustaceans, and cephalopods. The selection of taxa for the analysis followed similar studies regarding dem-

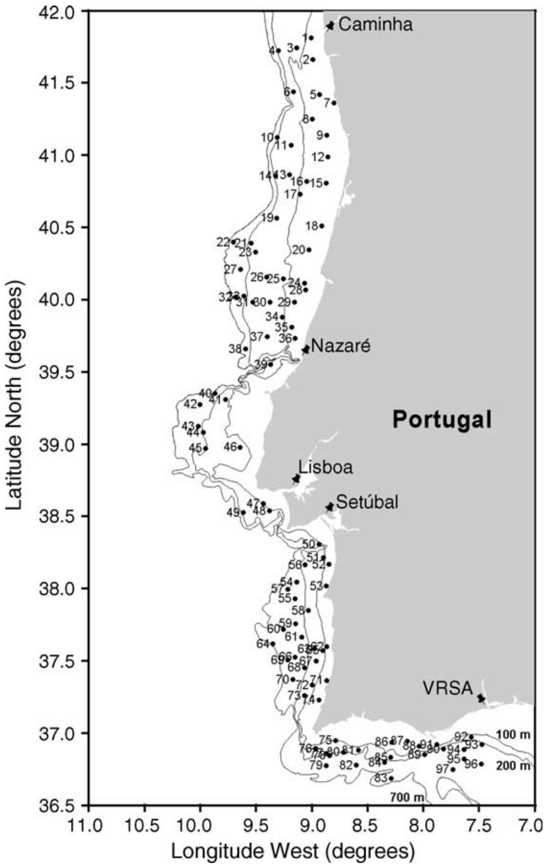

Fig. 1. Portuguese continental margin, showing the 97 fixed sampling stations and the 100, 200, and 700 m bathymetrics.

Table 1
Year, season and number of valid tows

Year	Season	Sampling effort
1989	Summer	83
	Autumn	67
1990	Summer	96
	Autumn	93
1991	Summer	92
	Autumn	90
1992	Winter	87
	Summer	76
	Autumn	57
1993	Winter	75
	Summer	66
	Autumn	65
1994	Autumn	82
1995	Summer	75
	Autumn	86
1996	Autumn	70
1997	Summer	86
	Autumn	58
1998	Summer	85
	Autumn	74
1999	Summer	64
	Autumn	79

ersal communities (e.g. Fariña et al., 1997; Mahon et al., 1998; Ungaro et al., 1999). Although species with strictly pelagic habitats were discarded, certain pelagics were retained in our analysis because they exhibit significant demersal behavior and comprise a high proportion of the catches along the Portuguese shelf. These species included blue whiting (*Micromesistius poutassou*), horse mackerel (*Trachurus trachurus*), blue jack mackerel (*Trachurus picturatus*), Atlantic mackerel (*Scomber scombrus*), chub mackerel (*Scomber japonicus*),[2] and John dory (*Zeus faber*) (Silva, 1999). In order to avoid an excess of zero entries in the data matrices to be analyzed, rare species were excluded by adopting cutting thresholds. A taxon was eliminated from the analysis if caught in less than 80% of the surveys or if the overall (1989–1999) percentage of tows containing the taxon was less than 2.5%. Other criteria for excluding a taxon was its contribution being less than 0.05% to total numbers or total weight. A final selection of 54 taxa (Table 2) preserved 98.9 and 99.3% of the overall demersal catches in weight and number, respectively.

2.2. Data analysis

2.2.1. Data transformation

Data were log-transformed [$\ln(x + 1)$, x = catch in numbers] before the analysis, in order to reduce the influence of the most abundant taxa in the results (Overholtz and Tyler, 1985; Mahon et al., 1998; Gomes et al., 1992, 1995, 2001). For correspondence analysis (COA), the log-transformed data were further converted to the nearest integer.

2.2.2. Multivariate analysis

Two techniques of multivariate analysis, correspondence analysis, and cluster analysis (CA), were undertaken. COA is an ordination method (Gauch, 1982; Greenacre, 1984; Hair et al., 1995), originally developed for contingency tables, which arranges species and stations in a low-dimensional space, where similar stations (in regard to species composition) are close together, and dissimilar ones are far apart. Separate analyses were performed for each survey data matrix.

Hierarchical CA is a classification technique that joins groups of stations sequentially, based on their species composition. CA was performed for each survey, using Ward's clustering algorithm (Ward, 1963) run over matrices of Euclidean distances between the sampling stations. The optimal number of groups was decided based on the following sequence of steps: (1) visual inspection of the dendrograms to identify the most probable range in the number of groups; (2) graphical analysis of the fusion coefficients, i.e. the distances at which two groups are joined along the clustering process. When coefficients are plot against the classification step, the appearance of an elbow-like structure indicates there is no justification for any further clustering and the process stops (Aldenderfer and Blashfield, 1984; Sharma, 1996), retaining the number of groups (g) formed at that point, that is $g = n -$ step, where n = total number of observations; (3) analysis of group homogeneity. The concept of loss of homogene-

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[2] Final report of the SESITS Project (Study Contract 96-029) carried out with the financial assistance of the European Commission, DG XIV (available through cardador@ipimar.pt).

Table 2
List of demersal taxa caught in the surveys, included in this study

Group	Family	Scientific name	English name	Portuguese name	FAO code
Cephalopods	Loliginidae	*Alloteuthis* spp.	Squids	Lulas bicudas	ALL
		Loligo vulgaris	European squid	Lula-vulgar	SQR
	Octopodidae	*Octopus vulgaris*	Common octopus	Polvo-vulgar	OCC
	Ommastrephidae	*Illex coindetii*	Broadtail shortfin squid	Pota-voadora	SQM
Crustaceans	Aristeinae	*Aristeus antennatus*	Blue and red shrimp	Camarão-vermelho	ARA
	Homaridae	*Nephrops norvegicus*	Norway lobster	Lagostim	NEP
	Pandalidae	*Plesionika heterocarpus*	Arrow shrimp	Camarão-marreco-flecha	PLH
		Plesionika martia	Golden shrimp	Camarão-marreco-do-alto	PLM
	Pasiphaeidae	*Pasiphaea sivado*	White glass shrimp	Camarão-cristal-branco	PAS
	Penaeidae	*Parapenaeus longirostris*	Deepwater rose shrimp	Gamba-branca	DPS
	Portunidae	*Polybius henslowi*	Pelagic crab	Pilado	POH
Fishes	Argentinidae	*Argentina* spp.	Argentine	Argentina-branca	ARG
	Callionymidae	*Callionymus lyra*	Common dragonet	Peixe-pau-lira	CAL
	Caproidae	*Capros aper*	Boarfish	Pimpim (mini-saia)	BOC
	Carangidae	*Trachurus picturatus*	Blue jack mackerel	Carapau-negrão	JAA
		Trachurus trachurus	Atlantic horse mackerel	Carapau	HOM
	Chimaeridae	*Chimaera monstrosa*	Rabbit fish	Ratazana	CMO
	Congridae	*Conger conger*	European conger	Congro	COE
	Gadidae	*Gadiculus argenteus argenteus*	Silvery pout	Badejinho	GAA
		Micromesistius poutassou	Blue whiting	Verdinho	WHB
		Phycis blennoides	Greater forkbeard	Abrótea-do-alto	GFB
		Trisopterus luscus	Pouting	Faneca	BIB
	Lophiidae	*Lophius budegassa*	Blackbellied angler	Tamboril-preto	ANK
		Lophius piscatorius	Monk	Tamboril	MON
	Merlucciidae	*Merluccius merluccius*	European hake, hake	Pescada	HKE
	Mullidae	*Mullus barbatus barbatus*	Red mullet	Salmonete-da-vasa	MUT
		Mullus surmuletus	Red mullet	Salmonete-legítimo	MUR
	Myctophidae	Myctophidae	Lanternfishes	Mictofídeos	LXX
	Rajidae	*Raja brachyura*	Blonde ray	Raia-pontuada	RJH
		Raja clavata	Thornback ray	Raia-lenga	RJC
	Scombridae	*Scomber japonicus*	Chub mackerel	Cavala	MAS
		Scomber scombrus	Atlantic mackerel	Sarda	MAC
	Scophthalmidae	*Lepidorhombus boscii*	Four-spot megrim	Areeiro-de-quatro-manchas	LDB
	Scorpaenidae	*Helicolenus dactylopterus*	Blackbelly rosefish	Cantarilho-legítimo	BRF
	Scyliorhinidae	*Galeus melastomus*	Blackmouth catshark	Leitão	SHO
		Scyliorhinus canicula	Small-spotted catshark	Pata-roxa	SYC
	Serranidae	*Serranus hepatus*	Brown comber	Serrano-ferreiro	SEH
	Soleidae	*Microchirus variegatus*	Thickback sole	Azevia-raiada	MIV
	Sparidae	*Boops boops*	Bogue	Boga-do-mar	BOG
		Diplodus vulgaris	Common two-banded seabream	Sargo-safia	CTB
		Pagellus acarne	Axillary seabream	Besugo	SBA
		Pagellus bogaraveo	Blackspot seabream	Goraz	SBR
		Pagellus erythrinus	Common pandora	Bica	PAC
		Sparus pagrus	Red porgy	Pargo-legítimo	RPG
		Spondyliosoma cantharus	Black seabream	Choupa	BRB

Table 2 (*Continued*)

Group	Family	Scientific name	English name	Portuguese name	FAO code
	Squalidae	*Deania calceus*	Birdbeak dogfish	Sapata	DCA
		Etmopterus pusillus	Smooth lanternshark	Xarinha-preta	ETP
		Etmopterus spinax	Velvet belly	Lixinha-da-fundura	ETX
	Trachinidae	*Trachinus draco*	Greater weever	Peixe-aranha-maior	WEG
	Trichiuridae	*Benthodesmus elongatus symoni*	Frost-fish	Espada-de-má-água	BES
		Lepidopus caudatus	Silver scabbardfish	Peixe-espada	SFS
	Triglidae	*Aspitrigla cuculus*	Red gurnard	Cabra-vermelha	GUR
		Lepidotrigla cavillone	Large scaled gurnard	Ruivo	LEC
	Zeidae	*Zeus faber*	John dory	Peixe-galo-negro	JOD

Group, family and scientific, English and Portuguese names, as well as the FAO code, are presented.

ity (Sharma, 1996; Everitt, 1993) states that the fusion of g groups into $g-1$ groups is only reliable if the internal homogeneity (evaluated by covariance matrices) of the $g-1$ groups is not substantially reduced when compared to the internal homogeneity of the g groups.

2.2.3. *Depth distribution*

Species ubiquity over depth was assessed by dividing the continental margin into 50 m wide depth regions and building an empirical cumulative distribution function (CDF) over depth, with data of the 22 surveys. This CDF was weighted by the number of individuals caught at each depth region (Paz and Casas, 1996). If a given species was randomly distributed over depth, its CDF should be similar to the overall distribution function of sampling stations. Otherwise, preferences by shallow or deep waters are to appear as marked deviations from the overall distribution.

3. Results

3.1. *Ordination and classification of sampling stations*

The first axis of COA always ordinated stations along the depth gradient, ranging between shallow (usually <150 m) and deep (usually >300 m) stations and their associated species (Fig. 2). The secondary gradient in the data separated northern and southern stations. This latitudinal gradient was usually recognized along the third axis, as in most surveys the second axis exhibited the so-called arch or Guttman effect (Gauch, 1982; Greenacre, 1984). In four surveys (summers of 1990 and 1995, autumn 1993, winter 1995), however, the two main gradients were depicted in the first ordination plane (Fig. 2). The range of the percentage of inertia explained by the first ordination axis in the 22 surveys was 14.5–20.2%; for the first five axes, the cumulative percentage of inertia ranged from 44.9 to 53.7%.

The CDFs confirmed the preference of some species for restricted depth ranges (Fig. 3). Squids (*Alloteuthis* spp.), the sparid bogue (*Boops boops*), and to a lesser extent, horse mackerel, were associated with shallow grounds. The crustaceans Norway lobster (*Nephrops norvegicus*), white glass shrimp (*Pasiphaea sivado*) and golden shrimp (*Plesionika martia*) exhibit a strong preference for deeper habitats, as their empirical curves are always under the curve of overall cumulative depths. European hake (*Merluccius merluccius*), hereafter referred to as hake, crosses this curve and appears rather ubiquitous in so far as depth is concerned. Boarfish (*Capros aper*) and blue whiting, two other abundant species, exhibit a preference for shallower and deeper grounds, respectively (Fig. 3).

Throughout the 11-year time series, the groups of stations formed by CA were always associated with depth (shallow, intermediate and deep) and often with latitude (north and south), confirming the results of COA ordination (Fig. 4). The number of groups ranged between 3 and 5, depending on survey. In surveys with three groups (autumn 1994) and four groups (several surveys), the depth gradient was present (shallow, intermediate, and deep groups were identified) but the latitude gradient was not recognized, appearing an overall (north–south) group.

Table 3 summarizes the groups of stations identified by survey and their association with the depth and lati-

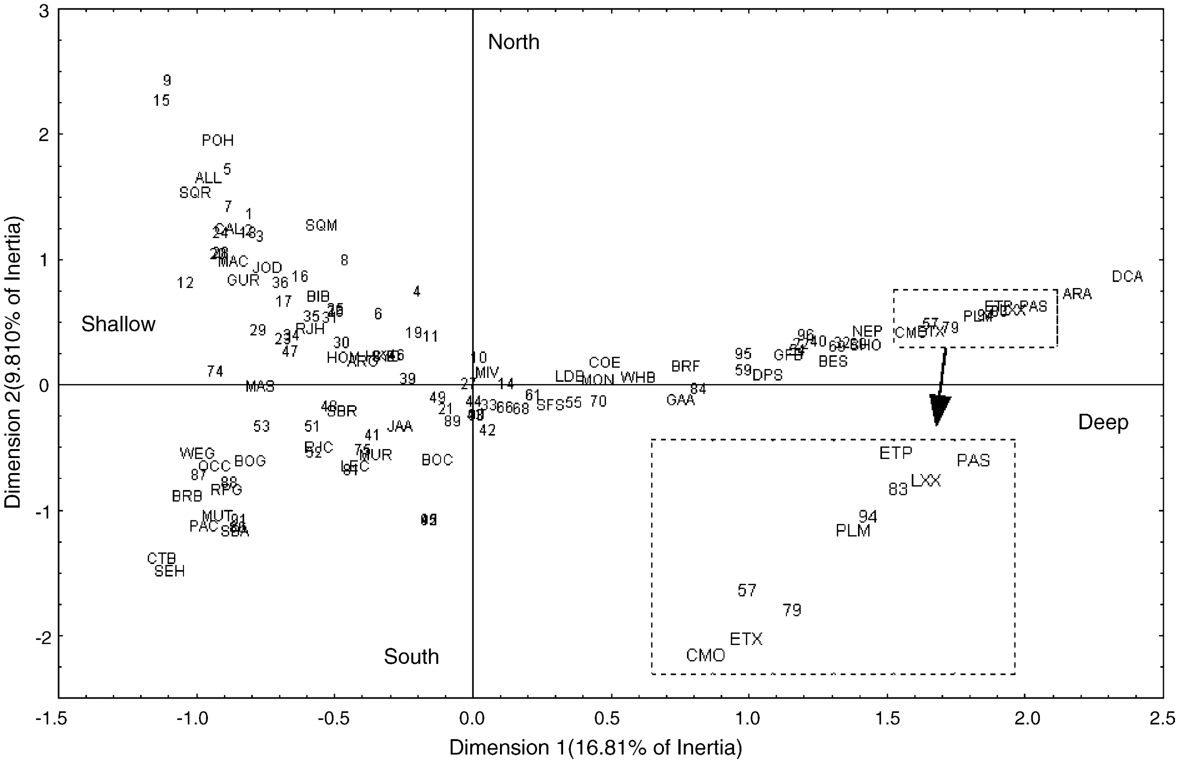


Fig. 2. First two axes of the COA ordination for the summer 1995 survey. The first axis differentiates between shallow and deep stations. The former associates with species like the black seabream (BRB), the common pandora (PAC) and the two-banded seabream (CTB), whereas deep stations associate, for example, to the birdbeak dogfish (DCA), and the blue and red shrimp (ARA). The second axis correlates with a north–south gradient. Northern stations, like 9 (41°7′N) and 15 (40°47′N) associate with species that occur preferentially to the north, like the pelagic crab (POH), and squids (ALL), whereas southern stations, like 88 and 91 (both 36°55′N), associate with species that occur mostly to the south, such as CTB.

Table 3
Demersal assemblages by survey

Depth	Latitude	Summer, 1989	Autumn, 1989	Summer, 1990	Autumn, 1990	Summer, 1991	Autumn, 1991	Winter, 1992	Summer, 1992	Autumn, 1992	Winter, 1993	Summer, 1993	Autumn, 1993	Autumn, 1994	Summer, 1995	Autumn, 1995	Autumn, 1996	Summer, 1997	Autumn, 1997	Summer, 1998	Autumn, 1998	Summer, 1999	Autumn, 1999	Persistence (%)
Shallow	N	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	100
	S	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	100
Intermediate	overall	□	□	□	■	□	□	■	□	□	□	■	□	□	■	□	□	□	□	□	□	□	□	18
	N	■	□	■	□	■	□	□	■	■	□	□	□	□	□	■	■	■	■	□	■	■	■	55
	S	□	■	■	□	■	■	□	■	■	■	□	■	□	□	■	■	■	■	■	■	■	■	73
Deep	overall	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	■	100
Number of groups		4	4	5	4	5	4	4	5	5	4	4	4	3	4	5	5	5	5	4	5	5	5	

Persistence (P) scaling: □ P <= 50% ▨ 50 < P < 100% ■ 100%

The persistence of the assemblages is defined as the relative presence (%) of the assemblage in the 22 surveys. Latitude ‘overall’ means that the assemblage did not show a clear latitudinal confinement.

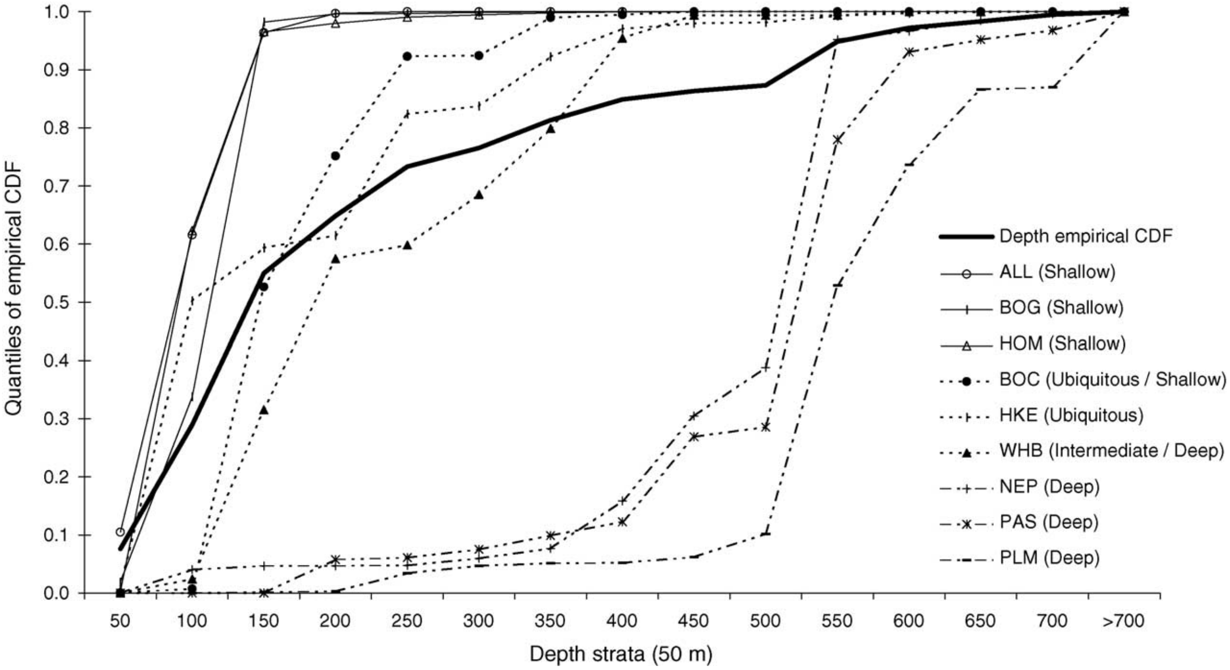


Fig. 3. Empirical cumulative distribution function (CDF) curves built with the catch data of 22 surveys (1989–1999) over 50 m depth strata. The curve of each individual species is to be compared with the overall curve (continuous bold) built from the depths of all tows pooled over the 22 surveys. Species preference are shallow (ALL, squids; BOG, bogue; HOM, horse mackerel), ubiquitous/intermediate (BOC, boarfish), ubiquitous (HKE, hake), ubiquitous/deep (WHB, blue whiting) or deep (NEP, Norway lobster; PAS, white glass shrimp; PLM, golden shrimp), depending both on whether their curve lie above, across, or below the overall curve and on the crossing patterns of the curves.

tude gradients. A percentual indicator of the persistence of each group (number of group occurrences/number of surveys) along the 11-year period is also shown. Fig. 5 presents a geographic mapping of the demersal assemblages in the summer of 1990 (Fig. 5a) and summer of 1995 (Fig. 5b) as examples of typical profiles of five and four groups. Deep (overall) and shallow (northern and southern) groups were present in all 22 surveys (100% persistent); the former never showed marked evidence of major biological heterogeneity along latitude, whereas the latter always did. Intermediate groups were less persistent than the deep and shallow ones (18% the intermediate overall, 55% the intermediate northern, and 73% the intermediate southern). Overall, five groups were more than 50% persistent throughout the 22 survey series: deep, shallow (northern and southern) and intermediate (northern and southern). Global COA and CA analysis, combining all years or seasons, did not add any new information as the same groups appear, though with a less pronounced latitudinal gradient than in analysis of isolated surveys.

No clear seasonal patterns in number and distribution of groups were recognized. However, two major periods could be distinguished between 1989 and 1999. Prior to the autumn of 1995, intermediate groups occurred inconsistently, but from then on, the latitude profile of the intermediate groups changed little, originating a recurrent pattern of five groups, namely, shallow northern and southern, intermediate northern and southern and deep (a brief description of each group follows; for geographical references, see Fig. 1).

3.1.1. *Shallow northern group*

This group of stations extends from Caminha at the northern limits of the Portuguese shelf, down to the region of Nazaré, covering depths from 38 m (S.D. = 4) to 130 m (S.D. = 37). On average, the group comprised 21.7 ± 6.6% of the total number of sampling stations.

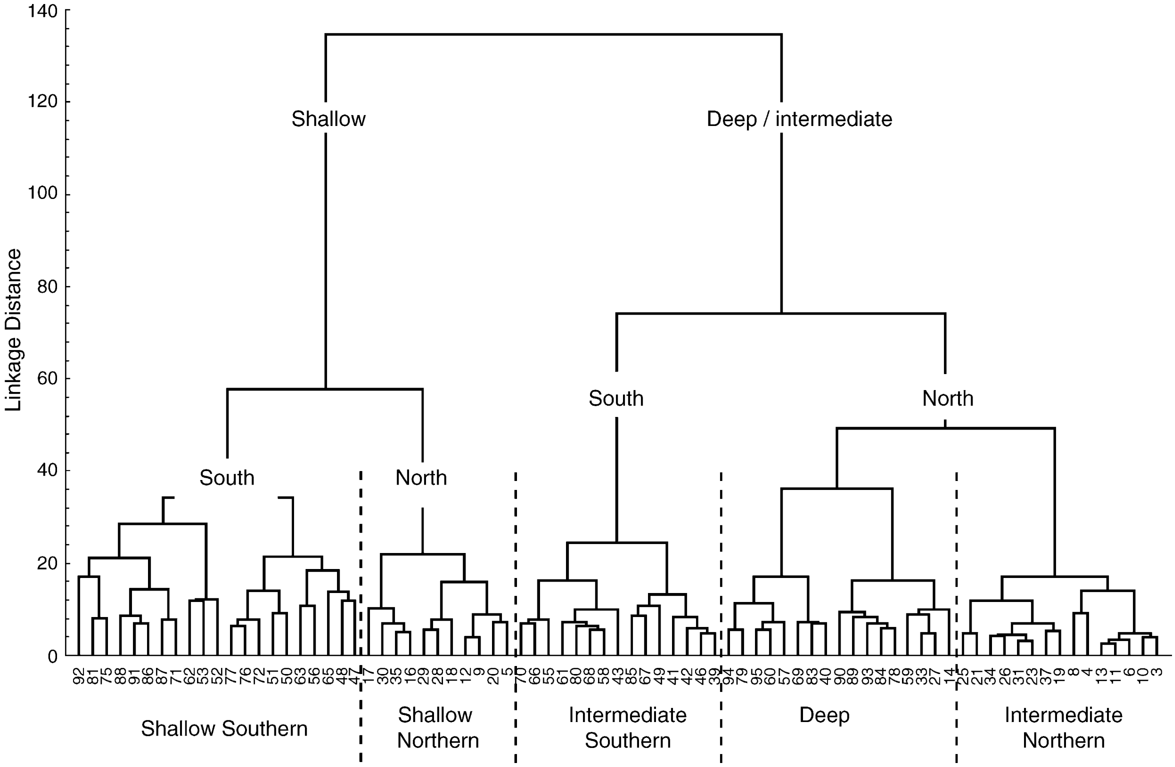


Fig. 4. Typical results of CA with the Ward's clustering algorithm (in this case, the autumn 1999 survey). The major groups of stations are identified and the ordinates are Euclidian distances.

3.1.2. Shallow southern group

Extends from Setúbal down to V.R. Santo António at the extreme southeast (SE) of Portugal. Stations in this group ranged from 44 m (S.D. = 18) to 179 m (S.D. = 29) deep. The average percentage of stations affected to the group was 21.6 ± 6.8%. The geographic gap between the northern and southern shallow assemblages was due to the inexistence of sampling sites below the bathymetric of 100 m between Nazaré and Setúbal, on account of non-trawlable grounds in the area.

3.1.3. Deep group

Under constraints of a fixed grid of stations, the recognition of a deep group depended on sampling at stations located on the deeper parts of the slope. To the north, for example, stations 1–21 (Fig. 1) are shallower than 210 m and thus not likely to cluster with the deep group. Only station 22 (532 m deep) was likely to yield a catch composition characteristic of the deep group and failure to tow there may cause this group to pass unnoticed in the north. That is probably why the deep group was identified above station 22 in only 7 surveys. In five out of these seven, there was no intermediate northern group, so the deep group extended to shallower areas of the shelf. The deep group ranged from 226 m (S.D. = 124) to 659 m (S.D. = 127), reaching 711 m in almost half the surveys. This group is also the one that accounted for the greatest proportion of stations (25.3 ± 12.3%).

3.1.4. Intermediate groups

The intermediate northern group extended from the northern tip of the shelf down to Nazaré, a latitudinal range similar to that of the shallow northern group. Stations in the group were between 103 m (S.D. = 2) and 232 m (S.D. = 71), reaching the shelf-break, and comprised 9.9 ± 9.6% of the total number of stations. The latitudinal boundary with the intermediate southern group was always located off Nazaré, from where

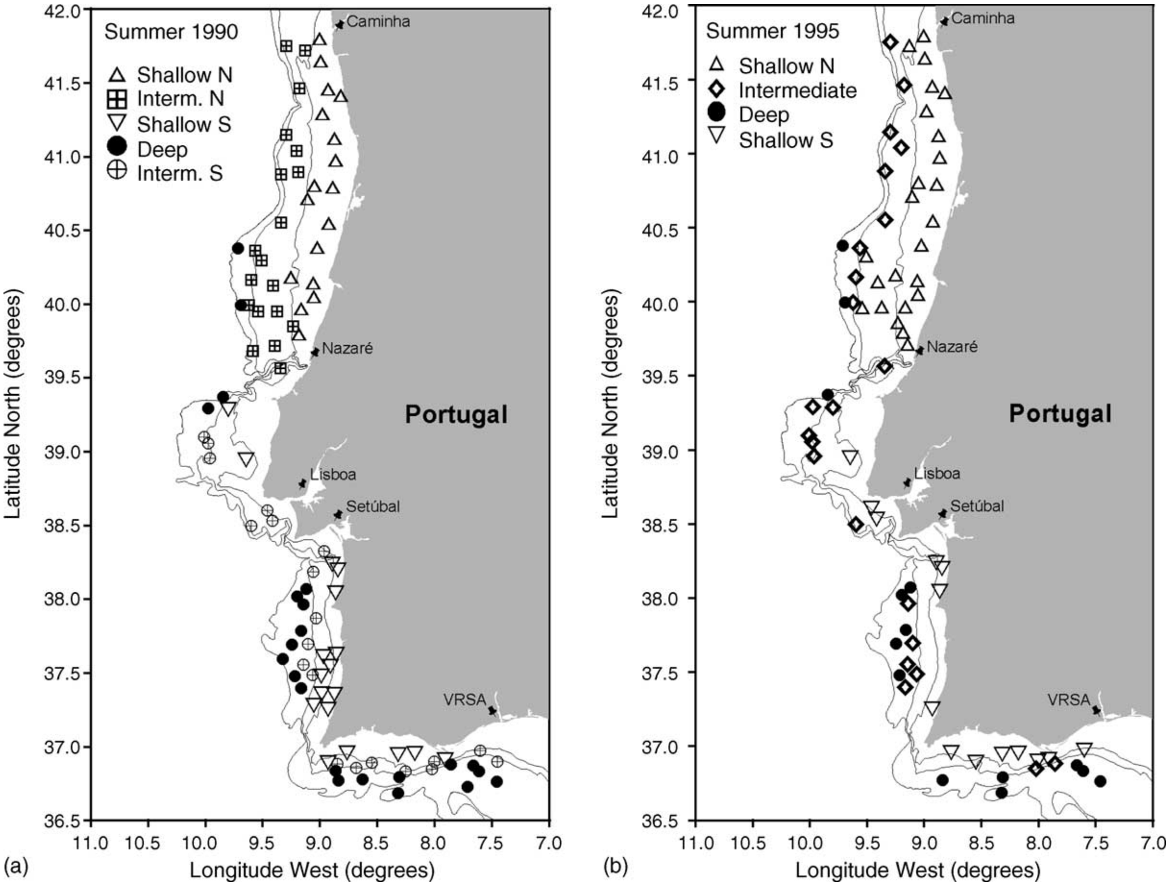


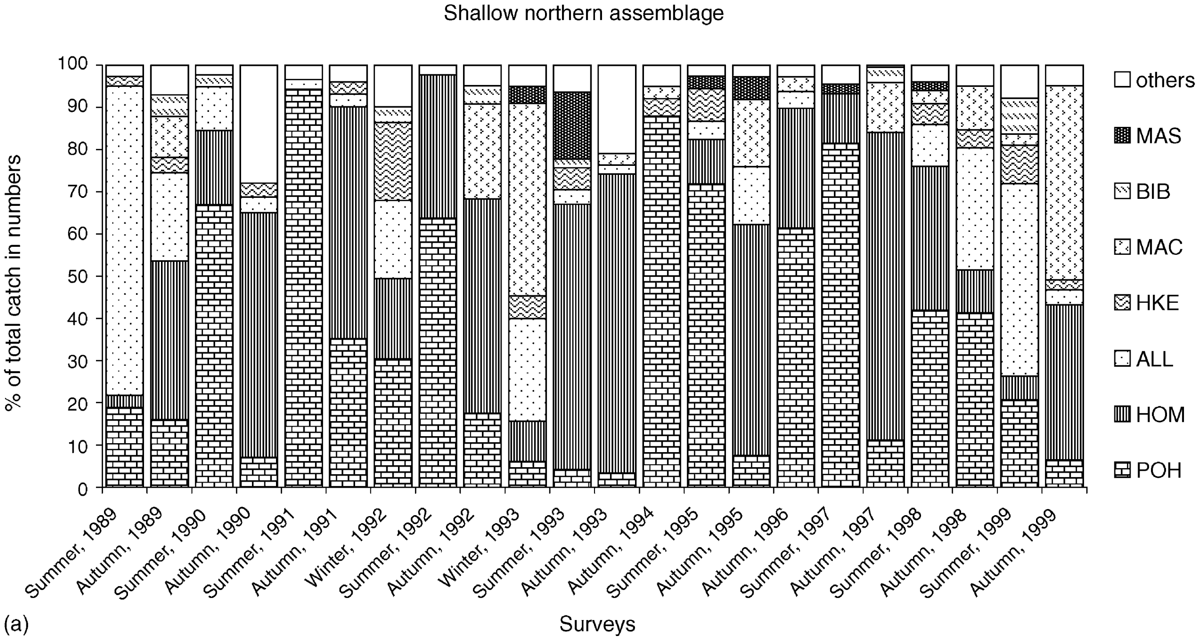
Fig. 5. Map of the demersal assemblages in the summer of: (a) 1990 and (b) 1995. Two intermediate assemblages are observed in the summer of 1990, whereas one single overall intermediate group is present in the summer of 1995.

the latter extends down to the extreme SE of the shelf at V.R. Santo António. The intermediate southern group extends deeper on the slope than the intermediate northern group, ranging from 108 m (S.D. = 25) to 369 m (S.D. = 71). On average, the intermediate southern comprised 15 ± 11.5% of the total number of stations and also covered the shelf-break. The segregation between the two intermediate groups did not take place in 4 out of the 22 surveys (Table 3), when an overall intermediate group extended from the northern tip down to the extreme SE of the shelf. The depth range of this group, from 92 ± 31 to 439 ± 68 m, was wider than that of the northern and southern intermediate groups. When the overall intermediate occurred, the shallow groups were usually restricted to shallower than usual depth ranges, and the deep group started deeper (>316 m) than average (226 m). The overall intermediate group, when present, accounted for 35.8 ± 10.1% of stations and could not be clearly linked to any particular season of the year.

3.2. *Biological interpretation of groups*

3.2.1. *Shallow northern assemblage*

The pelagic crab *Polybius henslowii* (36.2 ± 30.3% of catches) and the horse mackerel (34.1 ± 22.9%) were the most abundant species in the shallow northern group with 100 and 91% persistence, respectively (Fig. 6a). There was an alternation of dominance between these species throughout the time series, as relative high catches of one species were usually accompanied by low catches of the other. Their occurrence in



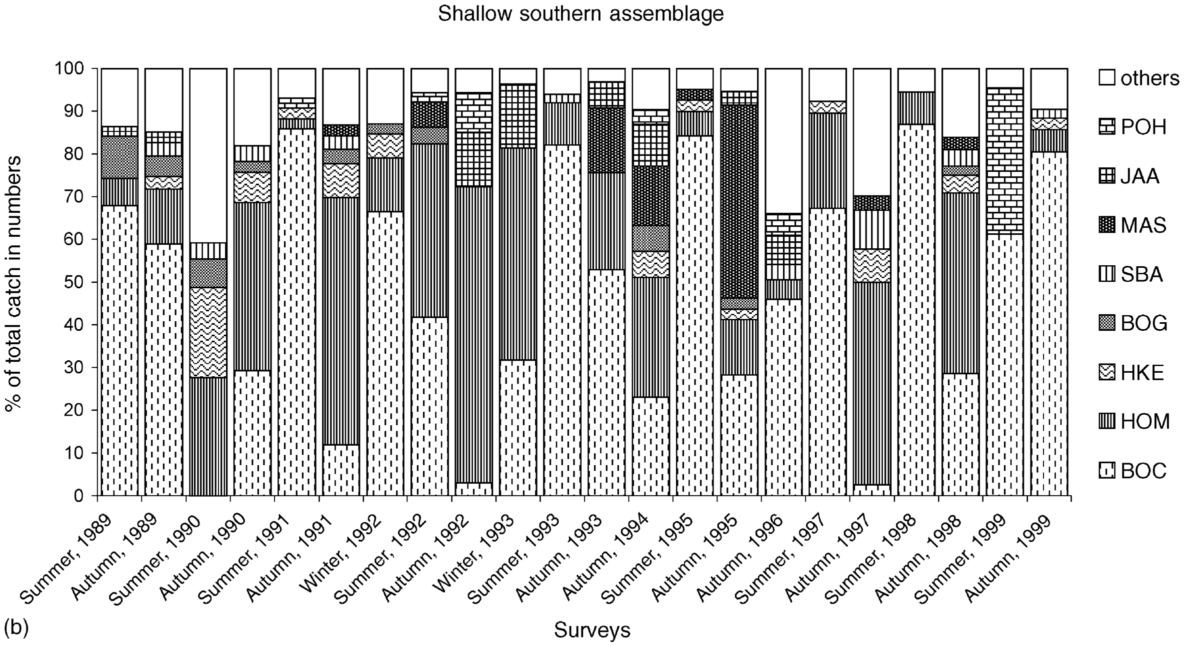


Fig. 6. Species relative compositions (%) of the total catch in numbers of the: (a) shallow northern; (b) shallow southern; (c) deep; (d) intermediate northern; (e) intermediate southern assemblages. FAO codes are: ALL, squid; ARA, blue and red shrimp; BIB, pouting; BOC, boarfish; BOG, bogue; DPS, deepwater rose shrimp; HKE, hake; HOM, horse mackerel; JAA, blue jack mackerel; MAC, Atlantic mackerel; MAS, chub mackerel; PAS, white glass shrimp; PLM, golden shrimp; POH, pelagic crab; SBA, axillary seabream; WHB, blue whiting.

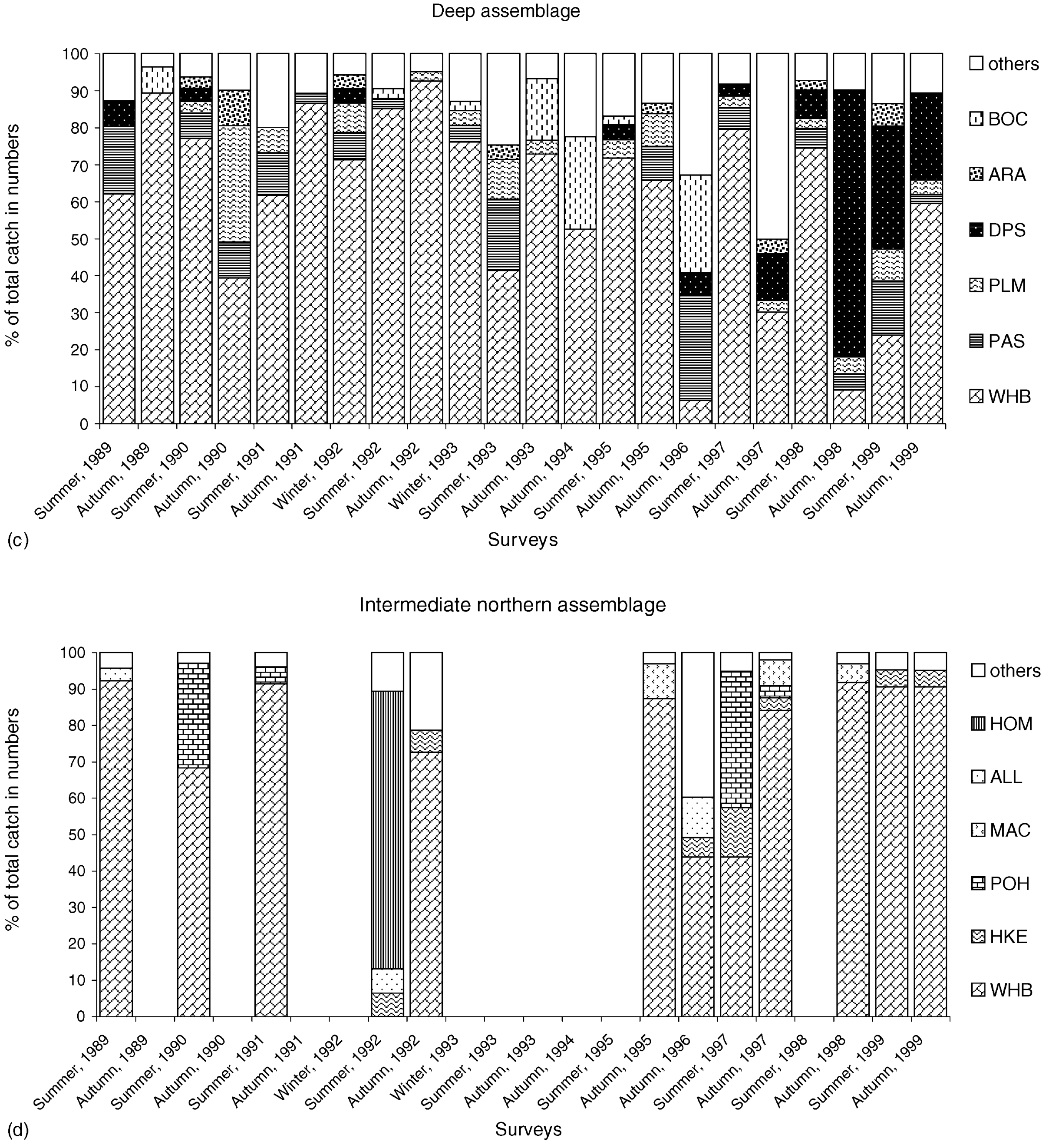


Fig. 6. (*Continued*)

similar proportions took place in a few surveys, especially in the winter. The pelagic crab tended to dominate in the summer, whereas the horse mackerel was most abundant in autumn. The two other very persistent taxa, squids and hake did not exhibit clear seasonal patterns (Fig. 6a). Atlantic mackerel exhibited high variability (14.7 ± 15.8% of catches), and was more abundant in autumn and winter (Fig. 6a).

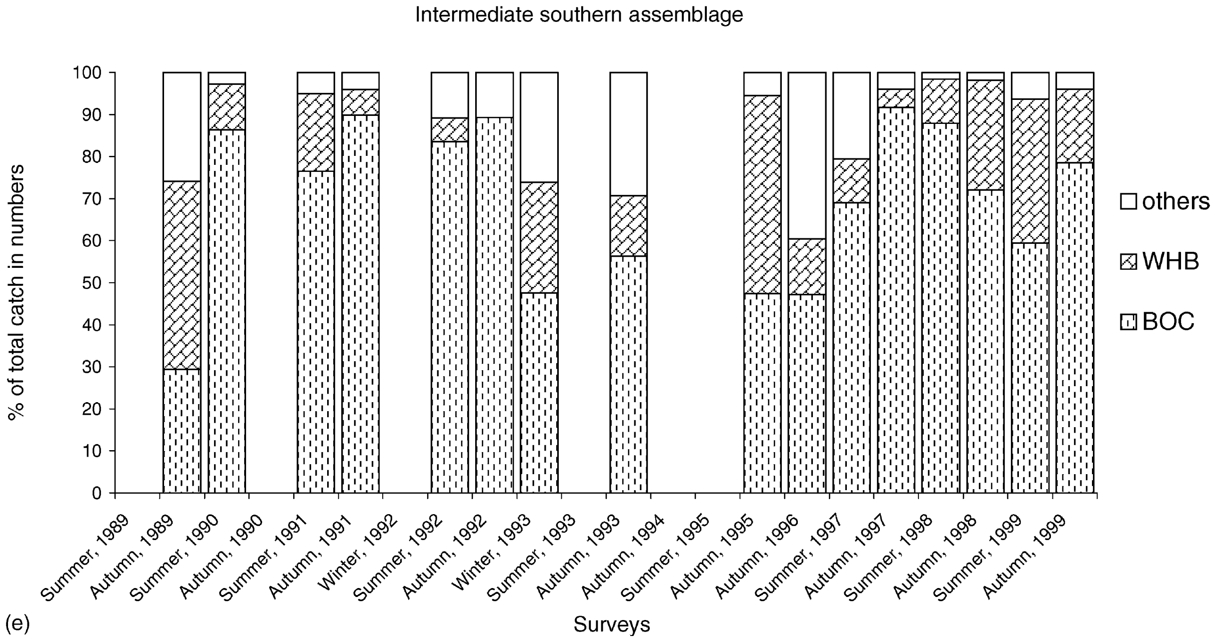


Fig. 6. (*Continued*).

3.2.2. *Shallow southern assemblage*

The most abundant species in the group was boarfish (averaging 49.6 ± 27.7% of the catches), and the second most abundant was horse mackerel (24.0 ± 13.4%) (Fig. 6b). The shallow southern group had the highest number of persistent species. There were six additional species, which recurred in at least 25% of the surveys: hake, bogue, axillary seabream (*Pagellus acarne*), Atlantic mackerel, blue jack mackerel, and pelagic crab. Species richness was the highest among the assemblages. The sparids (including bogue and axillary seabream) were a distinct feature of this assemblage, as they were rare in catches elsewhere. Other distinct species in the assemblage were blue jack mackerel and Atlantic mackerel. As for seasonal patterns, horse mackerel dominated a substantial proportion of the surveys, mostly in autumn. Boarfish dominated in the summer, reaching percentages of total catches above 80% in the summers of 1991, 1993, 1995, and 1998.

3.2.3. *Deep assemblage*

Blue whiting dominated the deep assemblage (60.4 ± 25.2% of catches, 100% persistence), and with the exception of crustaceans, relative catches of other species were low (Fig. 6c). Such was the case of boarfish (11.8 ± 10.7% of catches, 30% persistence). Deepwater shrimps were the most important species next to the blue whiting, and these included white glass shrimp, golden shrimp, deepwater rose shrimp (*Parapenaeus longirostris*) and blue and red shrimp (*Aristeus antennatus*). The rose shrimp persisted in the last seven surveys (autumn 1996–1999), was a dominant species in the autumn of 1998 (72.1% of catches), and was also very important in the summer of 1999 (Fig. 6c).

3.2.4. *Intermediate assemblages*

Blue whiting in the north and boarfish in the south dominated the intermediate assemblages. The largest abundances of boarfish occurred in the summer. Accordingly, the intermediate overall assemblage in the summer (1993 and 1995) was dominated by boarfish, whereas the two other occurrences of this assemblage (autumn 1990 and winter 1992) were dominated by blue whiting. Intermediate assemblages were relatively stable in species composition and catches were distributed by a small number of species. In the intermediate northern, five species persisted in at least 25% of the surveys: blue whiting, hake, pelagic crab, Atlantic mackerel, and squids (Fig. 6d). In the intermediate southern, only two species persisted in at least 25% surveys: boarfish and blue whiting (Fig. 6e).

Abundance trends within the assemblages were assessed from catch per unit effort (cpue) indices for the most important species. The catches of both commercially targeted (e.g. hake, sparids, and horse mackerel) and non-commercial (pelagic crab and boarfish) species exhibited oscillations with no clear pattern or

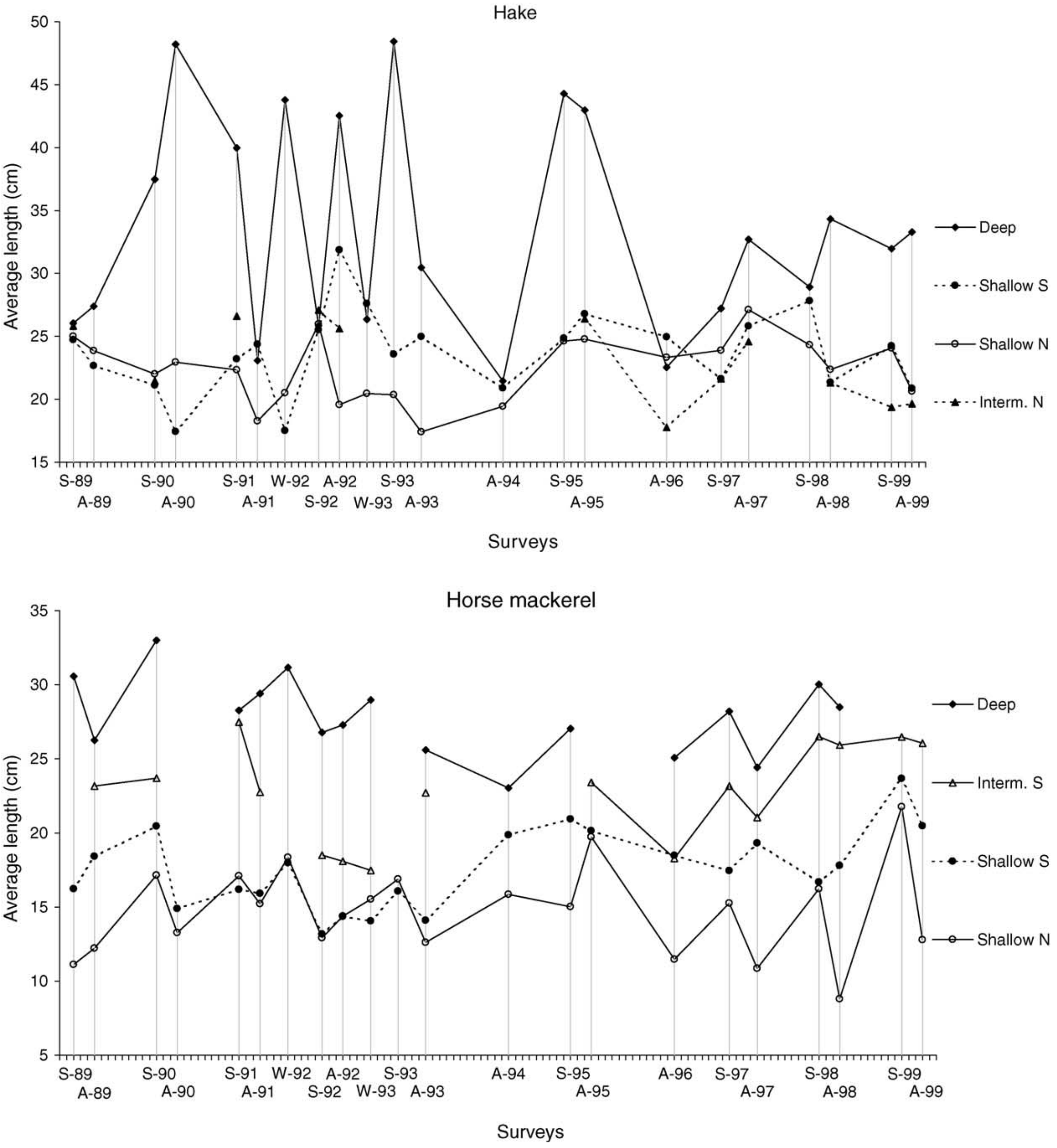


Fig. 7. Average lengths of the most ubiquitous species on the Portuguese shelf by assemblage: (a) hake and (b) horse mackerel.

persistent trends over the 11 years of surveys. Oscillations had the largest amplitudes in the pelagic crab, horse mackerel, boarfish, and deepwater rose shrimp. The latter exhibited the most persistent cpue increase of all species, beginning in the summer of 1995 and staying relatively high since then.

3.3. *Size distribution of main commercial species*

The mean length of two widespread commercial species on the shelf, European hake and horse mackerel, were computed for each assemblage and survey (Fig. 7a and b). There was a positive correlation between mean size and depth in both species, especially consistent in the horse mackerel. Mean lengths of horse mackerel ranged between 23 and 33 cm at the deep assemblage, decreased to 19–27 cm in the intermediate southern, 14–24 cm in the shallow southern, and 8–22 cm in the shallow northern assemblage. Variability in the size of hake in the deep assemblage (Fig. 7a) is probably explained by two facts. First, only about 6.2% of the catches are from the deep assemblage, second, the upper limits of the deep assemblage varied considerably in the surveys. The highest peaks in hake size (autumn 1990 and summer 1993) coincide with an upper depth limit of 487 m, whereas in autumn 1994, when the mean length was only 22 cm, the upper limit was at about 100 m.

4. Discussion

4.1. *Ecological gradients on the Portuguese continental margin*

Five spatially distinct and temporally persistent fish assemblages were identified on the Portuguese continental margin (shallow northern, shallow southern, intermediate northern, intermediate southern, and deep). The results of multivariate techniques indicated that these assemblages were associated primarily with a depth gradient, a pattern already reported for other parts of the Atlantic (Mahon et al., 1984; Overholtz and Tyler, 1985; Bianchi, 1992; Gomes et al., 1992; Fariña et al., 1997). In the relatively narrow Portuguese shelf, the strong influence of depth is suggested by the arch effect recurrently observed in the second axis of COA. This effect results from non-linear responses of species abundance (e.g. Gaussian response) to the environmental gradient (Gauch, 1982; Greenacre, 1984) and is known to occur when sampling takes place over gradients that induce high rates of species turnover along them (also known as beta diversity) (Pielou, 1975; Gauch, 1982). Southern groups extended deeper than northern groups. In particular, the depth range of the southern intermediate group was almost twice that of the northern intermediate group, both having an upper limit around 100 m. These differences are probably related to bottom topography, as the shelf is much steeper and less regular to the south than in the north (Fig. 1), where it is relatively flat and shallow.

The second gradient observed in the Portuguese marine community was associated with latitude. In most surveys, both the shallow and intermediate groups subdivided into groups of stations aligned with latitude. The latitudinal boundary appears to be located around the Nazaré Canyon (39°30′N), a sharp physical discontinuity on the shelf (Fig. 1). This canyon, the biggest in Europe, crosses the entire platform with an extension of about 170 km and rises from 5000 m deep up to about 50 m, very close to the coastline, with a longitudinal slope of 30 m/km (Freire de Andrade, 1937; Vanney and Mougenot, 1981). However, the north–south biological discontinuity is not exclusively due to this canyon, but rather to differences in shelf and coastal morphology, bathymetry, river runoff, and ocean currents along the north and southern parts of the shelf. In the northern margin, the coastline is more regular, has no important capes, northern winds stress is more constant, and the amount of river runoff is greater. Less saline waters induce the development of a saline shelf-break front during winter as the amount of heat that reaches the sea surface is lower and the thermocline is weaker, leading to a more persistent coastal upwelling (Cunha, 2001). On the southern margin, the irregular coastline, the narrower shelf area, and the presence of several capes, induce different oceanographic conditions that lead to lower primary and secondary production compared to the north (Cunha, 2001).

4.2. *Seasonal variations in community patterns*

The most striking seasonal patterns in demersal assemblages took place within the assemblages themselves, rather than in the positioning of their geographical limits. The boundaries of the groups, particularly the shallow ones, did not vary substantially round the year, a fact previously reported for the Portuguese margin (Gomes et al., 2001) and for other areas in the Atlantic (Gabriel, 1992; Gomes et al., 1995). Seasonality was more pronounced within the shallow southern assemblage, but differences between seasons were also observed in the shallow northern and in the intermediate southern assemblage. Pelagic crab dominated in the summer catches, whereas horse mackerel and Atlantic mackerel were relatively more important in autumn (shallow northern); boarfish was relatively more abundant in the summer (southern shallow and intermediate) whereas horse mackerel increased its relative proportion in autumn (shallow southern and northern).

The Portuguese continental shelf is under the influence of a summer upwelling, particularly active between June and September (Fiúza, 1982). The upwelling is likely the most important driving force of seasonally patterned oceanographic and biological processes on the shelf. In the spring, there is an increase in zooplankton biomass, in response to the supply of phytoplankton driven by upwelled nutrients, reaching biomass maximums in late spring and early summer (Cunha, 2001). However, on the northern shelf, biomass decreases in the late summer, whereas on the southern shelf, the high levels of zooplankton biomass are maintained throughout the upwelling season (June–October), possibly by advection from the northern shelf by the prevailing surface circulation (Cunha, 2001).

At the time of the summer surveys (July), zooplankton biomass is close to its peak throughout the shelf. It is tempting to associate the high summer concentrations of the pelagic crab, in northern shallow waters, and the concentrations of boarfish, in shallow intermediate southern waters, with the spring–summer bloom. Planktonic Polybiinae larvae prevail among the first annual peak of decapod larvae, from January to March (Santos, 1999, personal communication). The fast-growing characteristic of the pelagic crab (González-Gurriarán, 1987) and the occurrence of higher zooplankton biomasses on the northern coast (Cunha, 2001) could therefore be related to the summer peaks of pelagic crab on the shallow northern assemblage. Boarfish is a zooplankton feeder with euphausiids preferred by larger (10–15 cm long) boarfish and copepods and Euphausiid larvae dominating the diet of smaller (3–9 cm) individuals (Macpherson, 1979). Boarfishes observed off Portugal usually ranged between 7 and 12 cm, and the higher zooplankton diversity reported for the southern shelf (Cunha, 2001) suggests that, in the summer, food is available there for both small (≤9 cm) and large (>9 cm) boarfish. The marked seasonal patterns in the abundance of boarfish underlie observed differences in diversity and evenness (Sousa, 2005, personal communication), between the summer and autumn shallow southern assemblages, with higher values in autumn, when boarfish tends to be much less abundant.

4.3. Temporal patterns of fish assemblages

Long-term studies of groundfish assemblages have shown that, although spatial assemblage patterns are broadly consistent over time, some surveys yield atypical results (Mahon et al., 1984; Gomes et al., 1995). This may be because the proportions of individual species within assemblages are unusual and/or their geographic boundaries are displaced from usual locations. When data are available for a small number of years, it is difficult to decide whether such anomalies are real or a mere consequence of the random noise associated with ecological samples. It is thus reassuring to have long time series and different methodological approaches to analyze data with the high level of variability that characterizes groundfish surveys.

In our 11-year study, three groundfish assemblages (shallow northern, shallow southern, and deep assemblage) persisted on the Portuguese margin, without major changes in their geographic boundaries. The persistence of these assemblages was examined at the light of trends in the catch per unit effort indices of the main species to conclude that both commercially targeted (e.g. hake, sparids, and horse mackerel) and non-commercial (pelagic crab and boarfish) species, exhibited oscillations with no clear pattern or persistent trends over the 11 years of surveys. As for hake, this is in agreement with reports from the Portuguese trawl fishing fleet (1989–1999). Trawl effort shows a downward trend from 1992 to 1999, but the trawl cpue of hake shows a stable behaviour since 1989, with a maximum in 1995 (ICES, 2003).

The intermediate (northern and southern) assemblages were dominated by two species, blue whiting and boarfish, respectively, and have remained relatively stable since the summer of 1995. These differences may be explained by trends in the abundance of blue whiting and of deepwater crustaceans in the deep assemblage. Until the summer of 1995, blue whiting accounted for 70 ± 17% of catches in the deep assemblage, and to the north, this group frequently extended to shallower (intermediate) grounds. The net result was the inability of multivariate methods to distinguish an intermediate northern assemblage therein. After the summer of 1995, the cpue of deepwater rose shrimp in the deep assemblage increased and this was matched by an increase of both commercial cpue of the crustacean trawl fishery (Afonso-Dias, 2002, personal communication) and abundance indices from trawl surveys (Silva, 2001), suggesting recovery from a state of overexploitation reported in the early nineties (Cadima, 1995, personal communication). As a consequence, dominance of the deep stations was shared between the blue whiting and the rising deepwater crustaceans, faunistic differences with intermediate stations increased, and the intermediate northern assemblage emerged as a separate group. The same applies in the southern shelf, but because the blue whiting is relatively less important in the intermediate southern assemblage, the latter was more persistent (16 out of 22 surveys) than the intermediate northern one (12 out of 22 surveys).

The number of assemblages identified and their main characteristics did not differ much from a previous study by Gomes et al. (2001) that used data from only four demersal autumn surveys (1985–1988) and described five autumn assemblages along similar gradients of depth and latitude. In the shallow assemblages, the major differences between our results and those of Gomes et al. (2001) have to do with the greater role played by boarfish and chub mackerel in the shallow southern assemblage since 1989. In both studies, all stations on the shelf-break and beyond (deep groups) were clearly dominated by the blue whiting.

4.4. Spatial confinement and size distribution

Previous descriptions of fish assemblages show that marine species differ in their tendency to be confined to a given area and absent from elsewhere (Mahon et al., 1984; Gabriel, 1989; Gomes et al., 1992, 1995). Our analysis shows that some species are strongly associated with a single assemblage, whereas others are quite ubiquitous on the shelf. Area confinement may have to do with depth (Fig. 3), latitude, bottom substract, or other factors. For example, Norway lobster has a clear preference for depths below 400 m, where it is associated with sandy-muddy bottoms, and blue whiting occurs generally deeper than 150 m. The sparids and the blue jack mackerel are present at the shallow intermediate part of the southern shelf and practically absent elsewhere. The pelagic crab, pouting, squids, and Atlantic mackerel, have a preference for the northern part of the shelf.

In the other extreme, the European hake and the horse mackerel are very ubiquitous species that comprised a significant proportion of total catches. The ontogenic stages of these species, however, appear to have different ecological requirements as their length range was clearly different among the assemblages. At the same latitude, larger hake, and horse mackerel tend to be at deeper assemblages, and within the shallow and intermediate assemblages, hake, and horse mackerel tend to be larger in the southern than in the northern assemblages (Fig. 7a and b). Growth in hake and horse mackerel is known to be associated with a change in feeding habits. Both species gradually shift from exclusive zooplankton feeding, at early life stages, to preying upon fish of increasing size at adult stages (Sánchez, 1993). Blue whiting, for example, is an important forage species for adult hakes larger than 25 cm (Silva et al., 1997) and for adult horse mackerels larger than 36 cm (Cabral and Murta, 2002; Silva et al., 1997). The average size of the blue whiting increased with depth and it only reaches high densities below 200 m (Bailey, 1982). The inclusion of blue whiting in the diet of hake and horse mackerel provides evidence that these species move deeper as they grow.

Assuming a tendency for larger fish to feed upon larger prey items (Kerr and Dickie, 2001), the observed differences in fish size by latitude, appears to be in agreement with the claim that species diversity of zooplankton is lower to the north, with shorter food chains and smaller organisms, leading directly to smaller planktivorous fish. The advection of plankton biomass by the surface flow, under the influence of predominantly northern winds, is responsible for the accumulation of particulate matter on the southern shelf, a diverse benthic community, and demersal fish that feed upon it (Cunha, 2001). This is a possible explanation for the presence of larger fish on the southern shelf, within the same species at the same depth.

Acknowledgements

Financial support for Pedro Sousa has been provided by the Fundação para a Ciência e Tecnologia (Programa PRAXIS XXI), Lisbon, Portugal, in a Ph.D. scholarship programme. This work was conducted within the scope of Project NeoMAv–INIAP–IPIMAR (QCA-3/MARE, FEDER). We are indebted to the Portuguese Institute for Fisheries and Sea Research staff, as their overall planning and sustained fieldwork made this work possible. In particular, we express our gratitude to Dra. Fátima Cardador (IPIMAR) for assistance with data handling. Pedro Sousa also thanks Dr. Manuel Afonso-Dias (University of Algarve, Portugal) for his support at the early stages of this work.

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