Aquat. Living Resour. 19, 93–103 (2006)
© EDP Sciences, IFREMER, IRD 2006
DOI: 10.1051/alr:2006009
www.edpsciences.org/alr

Aquatic
Living
Resources

Species-richness patterns in space, depth, and time (1989-1999) of the Portuguese fauna sampled by bottom trawl

Pedro Sousa[1,a], Manuela Azevedo[1] and Manuel C. Gomes[2]

[1] DRM, IPIMAR, Portuguese Institute for Fisheries and Sea Research, Av. de Brasília, 1449-006 Lisbon, Portugal
[2] DBV, Faculty of Sciences, Univ. Lisbon, Campo Grande, 1749-016 Lisbon, Portugal

Received 14 August 2005; Accepted 3 March 2006

Abstract – We have analyzed a series of 22 groundfish surveys conducted between 1989 and 1999 on the Portuguese shelf and upper slope (97 sampling station grid, 36−710 m) in the summer, autumn, and winter, to address the hypotheses of latitudinal and depth trends in species richness (number of species) and whether these patterns changed over time and among seasons. Richness was modelled by means of a Generalized Additive Model (GAM) with significant covariates being latitude and longitude, in a joint-spatial smooth, and depth, chronological time, and season. A decrease in richness was detected along the continental margin, when moving higher in latitude, with lowest richness being found in the shallow northern area. Thus, although our study spanned only about 5 degrees in latitude, we found no exception to the equator-pole latitudinal decrease in richness commonly acknowledged by ecologists. There is no common agreement on the way marine fish species richness varies with depth, yet our findings were consistent for the entire eleven-year period: richness decreases slightly with depth, from the coastline to the shelf break (200−300 m), steadily increasing afterwards down the slope. The patterns of change in latitude and depth persisted in time and among seasons but their magnitude changed. Richness was higher in the winter compared to the other seasons.

Key words: Biodiversity / Depth gradients / GAM / Groundfish surveys / Latitudinal gradients / Species richness / NE Atlantic Ocean

Résumé – Nous analysons une série de 22 campagnes de chalutage de fond conduites entre 1989 et 1999 sur le plateau et le niveau supérieur de la pente continentale du Portugal (97 stations, entre 36 et 710 m de profondeur) en été, automne et hiver, pour vérifier les hypothèses liées à la variation du nombre d'espèces en fonction de la latitude et de la profondeur, et si ces tendances varient avec le temps ou selon les saisons. Le nombre d'espèces est modélisé au moyen du modèle additif généralisé (GAM) avec comme co-variables significatives la latitude-longitude, la profondeur, la chronologie et la saison. Une diminution du nombre d'espèces a été détectée le long de la marge continentale, augmentant avec la latitude, avec le plus faible nombre dans des zones septentrionales les moins profondes. Ainsi, bien que notre étude couvre seulement 5 degrés en latitude, nous n'avons pas trouvé d'exception à la diminution latitudinale du nombre d'espèces de l'équateur au pôle communément observée par les écologistes. Les opinions sont partagées en ce qui concerne la variation du nombre d'espèces de poisson en fonction de la profondeur ; nos résultats se sont révélés constants sur l'ensemble des 11 années de la période d'étude : le nombre d'espèces diminue légèrement avec la profondeur, de la côte vers les accores (200−300 m), puis augmente régulièrement le long de la pente continentale. Le schéma du changement en latitude et profondeur a persisté dans le temps, et selon les saisons, mais sa magnitude a changé. Le nombre d'espèce est plus élevé en hiver, comparé aux autres saisons.

1 Introduction

The Convention on Biological Diversity of the United Nations signed by an extensive number of governments in 1992 included the conservation of biological diversity and the sustainable use of its components among its main objectives. Since then, the scientific community has been increasingly concerned with the assessment and preservation of biodiversity and its direct implications on biological communities as well as its side effects on mankind (Edwards et al. 1994; Perrings et al. 1995; Kunin and Lawton 1996). This has led to an exponential increase of biodiversity studies in the literature (Hawksworth 1995; Willig et al. 2003). Regarding the marine environment, the Commission for the Protection of the Marine Environment of the North-East Atlantic (OSPAR Commission) has set up a strategy for biological diversity and ecosystem conservation. Biodiversity indices can be viewed as part of a broader range of ecological indicators proposed

---

[a] Corresponding author: `psousa@ipimar.pt`

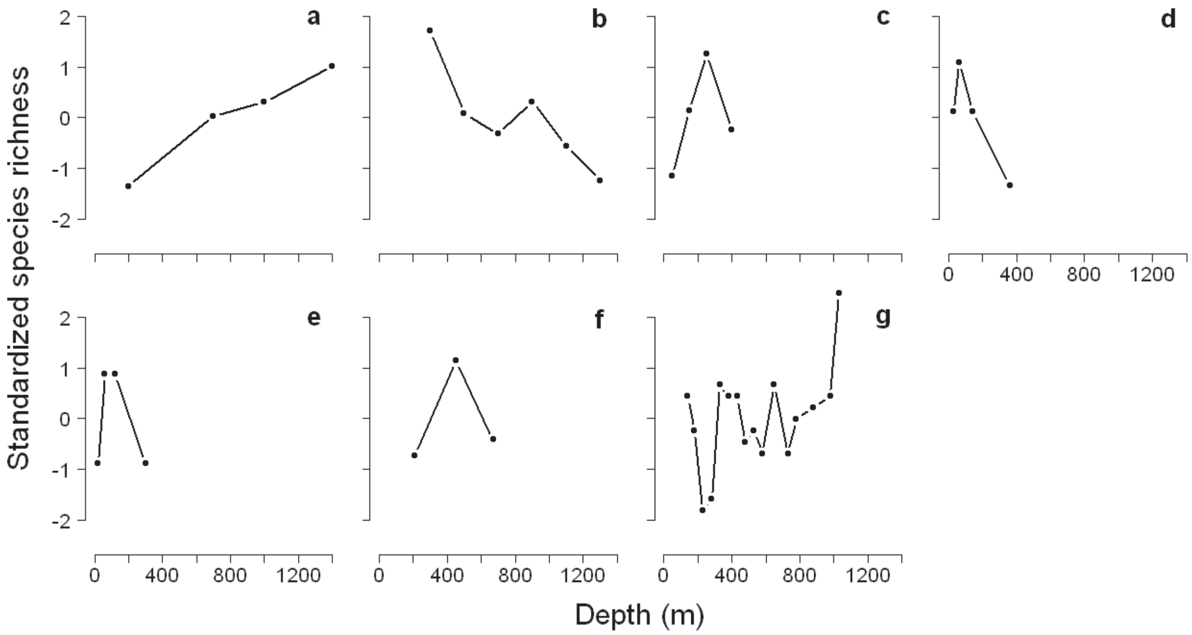


Fig. 1. Standardized (centered and reduced) species richness trends with depth from different data sources. a) Flach and Bruin (1999), NE Atlantic macrobenthos; b) Koslow et al. (1997), W Australian slope demersal fish; c) Mueter and Norcross (2002), Alaskan shelf and upper slope demersal fish; d) Labropoulou and Papaconstantinou (2004), Aegean Sea shelf and upper slope demersal fish; e) Labropoulou and Papaconstantinou (2004), Tracian Sea shelf and upper slope demersal fish; f) Paz and Casas (1996), Flemish Cap demersal fish; g) Jinao and Yanhong (1989), East China Sea demersal fish.

for use in assessing impacts of fishing in marine communities (Fulton et al. 2005). Diversity measures, which summarize the multispecific characteristics of marine communities, have been used in several recent studies (e.g., Blanchard 2001; Fock et al. 2002; Magnussen 2002; Price 2002; Lobry et al. 2003).

As pointed out by Flach and Bruin (1999) the term *diversity* is not defined in the literature, leading to some confusion. Diversity or biodiversity can be measured by species richness (the total number of species) or by weighted measures, such as evenness (how the abundance data are distributed among the species) and the Shannon index (Magurran 1988; Willig et al. 2003). Among these, species richness has been by far the most used measure in the literature with a substantial contribution from studies in the marine environment. Trends of species richness in latitude (Gray 2001; Willig et al. 2003) and depth (Macpherson and Duarte 1994; Gray 2001; Macpherson 2002) have been described for different regions of the world's oceans. In a contemporary revision, Gray (2001) showed that the scale, accuracy and technical characteristics of sampling have played in the past a much greater role in estimating species richness of marine areas than initially thought and that in light of recent sampling technologies current data provides a substantially improved source of information. He also supported the theory that marine species richness decreases when moving high in latitude, similarly to the pattern observed for terrestrial environments, at least for the northern hemisphere (see also Poore and Wilson 1993). This trend in latitude has also been described by Macpherson and Duarte (1994) for east-Atlantic fish populations. Failures to validate the latitudinal pattern in previous studies could be due to the interaction between depth and latitude, given the amount of variability in species richness explained by depth (Macpherson and Duarte 1994).

As for depth, there is no clear pattern of change in species richness (Gray 2001). In the past, authors have presented profiles of richness with depth for several marine areas (e.g., Macpherson and Duarte 1994; Koslow et al. 1997; Mueter and Norcross 2002; Labropoulou and Papaconstantinou 2004) but there is no agreement among the resulting trends. These are shown in Fig. 1, after data standardization for comparison.

We used a large data series of groundfish surveys conducted on the Portuguese continental shelf and upper slope to investigate the hypotheses of latitudinal and depth trends in species richness in this area of the Atlantic. As previous studies of richness patterns have largely ignored temporal effects, we have also examined whether latitudinal and depth patterns in richness change over time. Since the structure of the marine community on the Portuguese margin is under the influence of a seasonal upwelling (Sousa et al. 2005), we have further investigated whether species richness changes among seasons.

2 Methods

Since 1989, the Portuguese Institute for Fisheries and Sea Research (IPIMAR) has been conducting bottom trawl surveys following a fixed grid of 97 sampling stations, spread throughout the shelf between 36 and 710 m (Fig. 2). The target duration of each tow was 60 min and further details about methodology, research vessels, and gear characteristics of the surveys can be found in Cardador et al. (1997). We used the data from

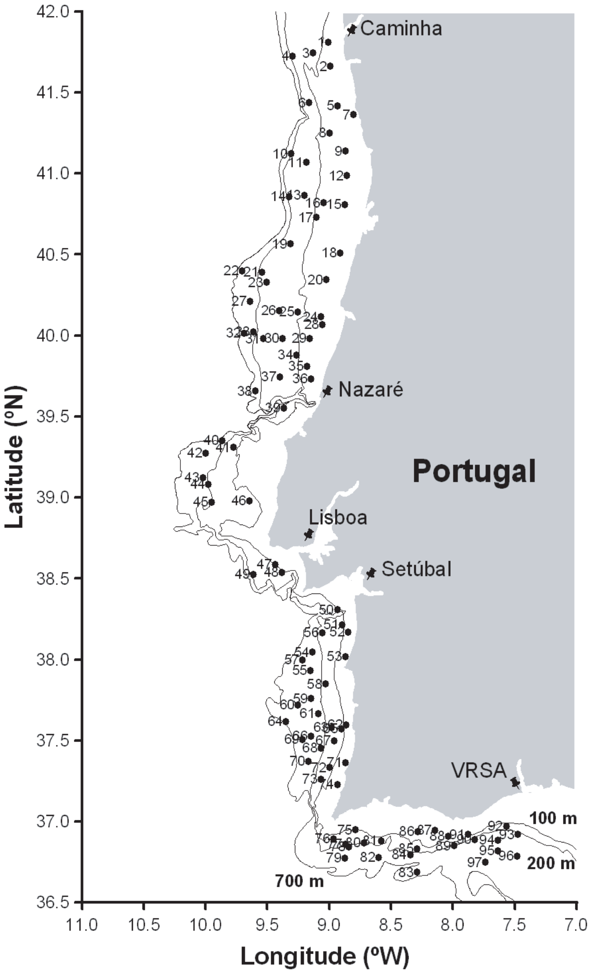


Fig. 2. Geography of the Portuguese continental margin showing the sampling stations (1-97) grid and the 100, 200 and 700 bathymetrics.

22 of these surveys, conducted between 1989 and 1999 and covering summer (9 surveys), autumn (11) and winter (2) comprising a total of $n = 1704$ observations.

Species richness was estimated at each sampling station (Fig. 2) and modeled by Generalized Additive Models (GAM – Hastie and Tibshirani 1990), based on a selected set of covariates. GAM are themselves a generalization of GLM – Generalized Linear Models (McCulagh and Nelder 1989) as they may include flexible, non-parametric terms. These models have recently proved to be very useful in ecology as they are able to accommodate the natural non-linearities of the biological responses to environmental gradients (Augustin et al. 1998; Frescino et al. 2001; Austin 2002; Guisan et al. 2002; Lehmann et al. 2002a,b; Stratoudakis et al. 2003; Venables and Dichmont 2004). In addition, GAM share helpful properties of GLM, namely, the ability to analyze the partial effects of each explanatory variable in the response. A GAM may include both parametric and non-parametric (smoothed) terms and, in this case, the expected value of the response variable Y $[E(Y_i) \equiv \mu_i]$ is given by

$$E\left(Y_i\right) \equiv \mu_i = g^{-1}\left[X_i\beta + \sum_{j=1}^{p} f_j\left(x_{ji}\right)\right] \qquad (1)$$

where μ_i is related to the additive predictor on the right hand side of Eq. (1) through a monotonic link function $g(.)$ whose form is related to the statistical distribution (picked from the exponential family) assumed for Y (Hastie and Tibshirani 1990). The parametric component is represented by $X_i\beta$, where X_i is the i-th row of a $1 + p$ matrix of coefficients, p being the number of explanatory variables, and β is the corresponding vector of parameters, including the intercept. x_{ji} is the i-th observation of explanatory variable j and $f_j(.)$ are smooth functions of the explanatory variables.

A multiplicity of smoothers exists, the majority of them based on weighting the observed values by a number of neighboring points. Such is not the case of cubic smoothing splines (CS) which consist on minimizing a penalized residual sum of squares between the observed values of the response and the univariate smoothing functions over each predictor x. In CS, the amount of smoothing is controlled by the degrees of freedom associated with the function, the fewer the degrees of freedom, the greater the smoothing.

Model building involves the adoption of a distribution for the response variable, the choice of a link function and the set of covariates to include based on a backward stepwise selection procedure. To address the hypotheses raised in this study the covariates depth (meters), longitude (°W), latitude (°N), chronological time (1989-1999), and season (summer, autumn, winter) were included in the model. Time was handled as a categorical variable and thus the models included both non-parametric (smoothed) terms (depth, latitude and longitude) and parametric terms (factors *time* and *season*) (Eq. (1)). Since it is more appropriate to consider the dependence of species richness on spatial location as a response surface, latitude and longitude were smoothed as interaction terms, using tensor products (Wood 2004).

Analyses were conducted using the *mgcv* package, in R (R development core team 2005). The amount of smoothing in the continuous covariates was evaluated by computing generalized cross validation (GCV) scores (Wood 2001). To decide on whether or not to exclude terms from the model, we have used GCV and the analysis of the partial significances (p-values) of the covariates. Model validation was carried out by checking the statistical assumptions of normality of residuals and constant variance.

3 Results

From 1989 until 1999 the groundfish survey data included more than 340 different taxa, including species and groups of species. However, the large majority of the catches was dominated by a small number of taxa: snipefish – *Macroramphosus* spp., boarfish – *Capros aper*, blue whiting – *Micromesistius poutassou* and horse mackerel – *Trachurus trachurus* comprised about 95% of the total catches in numbers (1989-1999). Species that accounted for about 99.9% of the total catch in numbers are listed by decreasing order of importance, including scientific, English and Portuguese name as well as the corresponding taxonomic group and family (Table 1).

Species richness (S) was highly variable, ranging from 2 to 41 species. Although S is a positive discrete variable, its empirical distribution is bell shaped (Fig. 3) thus supporting

Table 1. List of demersal species included in this study in decreasing order of importance of proportional catch in numbers. Scientific, English and Portuguese names are included, as well as their taxonomic group and family.

Scientific name	English name	Portuguese name	Group, Family	Percentage of catch in numbers (1989-1999)
Macroramphosus spp.	Snipefishes	Trombeteiros	Fish, MACRORAMPHOSIDAE	80.573
Capros aper	Boarfish	Pimpim (mini-saia)	Fish, CAPROIDAE	8.692
Micromesistius poutassou	Blue whiting	Verdinho	Fish, GADIDAE	4.738
Trachurus trachurus	Atlantic horse mackerel	Carapau	Fish, CARANGIDAE	1.804
Polybius henslowi	Pelagic crab	Pilado	Crustacean, PORTUNIDAE	1.358
Sardina pilchardus	European sardine	Sardinha	Fish, CLUPEIDAE	0.377
Trachurus picturatus	Blue jack mackerel	Carapau-negrão	Fish, CARANGIDAE	0.333
Merluccius merluccius	European hake	Pescada	Fish, MERLUCCIIDAE	0.248
Alloteuthis spp.	Squids	Lulas bicudas	Cephalopod, LOLIGINIDAE	0.230
Scomber japonicus	Chub mackerel	Cavala	Fish, SCOMBRIDAE	0.223
Parapenaeus longirostris	Deepwater rose shrimp	Gamba-branca	Crustacean, PENAEIDAE	0.193
Scomber scombrus	Atlantic mackerel	Sarda	Fish, SCOMBRIDAE	0.158
Pasiphaea sivado	White glass shrimp	Camarão-cristal-branco	Crustacean, PASIPHAEIDAE	0.142
Boops boops	Bogue	Boga-do-mar	Fish, SPARIDAE	0.096
Engraulis encrasicholus	European anchovy	Biqueirão	Fish, ENGRAULIDAE	0.084
Plesionika heterocarpus	Arrow shrimp	Camarão-marreco-flecha	Crustacean, PANDALIDAE	0.067
Lepidopus caudatus	Silver scabbardfish	Peixe-espada	Fish, TRICHIURIDAE	0.065
Plesionika martia	Golden shrimp	Camarão-marreco-do-alto	Crustacean, PANDALIDAE	0.060
Trisopterus luscus	Pouting	Faneca	Fish, GADIDAE	0.049
Pagellus acarne	Axillary seabream	Besugo	Fish, SPARIDAE	0.044
Serranus hepatus	Brown comber	Serrano-ferreiro	Fish, SERRANIDAE	0.036
Lepidotrigla cavillone	Large scaled gurnard	Ruivo	Fish, TRIGLIDAE	0.026
Helicolenus dactylopterus	Blackbelly rosefish	Cantarilho-legítimo	Fish, SCORPAENIDAE	0.022
Nephrops norvegicus	Norway lobster	Lagostim	Crustacean, NEPHROPIDAE	0.022
Gadiculus argenteus argenteus	Silvery pout	Badejinho	Fish, GADIDAE	0.021
Aristeus antennatus	Blue and red shrimp	Camarão-vermelho	Crustacean, ARISTEIDAE	0.021
Loligo vulgaris	European squid	Lula-vulgar	Cephalopod, LOLIGINIDAE	0.019
Illex coindetii	Broadtail shortfin squid	Pota-voadora	Cephalopod, OMMASTREPHIDAE	0.017
Hoplostethus mediterraneus	Mediterranean slimehead	Olho-de-vidro	Fish, TRACHICHTHYDAE	0.017
Scyliorhinus canicula	Small-spotted catshark	Pata-roxa	Fish, SCYLIORHINIDAE	0.015
Galeus melastomus	Blackmouth catshark	Leitão	Fish, SCYLIORHINIDAE	0.015
Argentina spp.	Argentine	Argentina-branca	Fish, ARGENTINIDAE	0.013
Etmopterus spinax	Velvet belly	Lixinha-da-fundura	Fish, SQUALIDAE	0.012
Microchirus variegatus	Thickback sole	Azevia-raiada	Fish, SOLEIDAE	0.010
Myctophidae	Lanternfishes	Mictofídeos	Fish, MYCTOPHIDAE	0.010
Pagellus bogaraveo	Blackspot seabream	Goraz	Fish, SPARIDAE	0.008
Arnoglossus laterna	Mediterranean scaldfish	Carta do Mediterrâneo	Fish, BOTHIDAE	0.008
Etmopterus pusillus	Smooth lanternshark	Xarinha-preta	Fish, SQUALIDAE	0.007
Spondyliosoma cantharus	Black seabream	Choupa	Fish, SPARIDAE	0.007
Nezumia sclerorhynchus	Roughtip grenadier	Lagartixa-áspera	Fish, MACROURIDAE	0.007
Callionymus lyra	Common dragonet	Peixe-pau-lira	Fish, CALLIONYMIDAE	0.007
Zeus faber	John dory	Galo-negro	Fish, ZEIDAE	0.006
Diplodus vulgaris	Common two-banded seabream	Sargo-safia	Fish, SPARIDAE	0.006
Trachyrhynchus scabrus	Roughsnout grenadier	Furão	Fish, MACROURIDAE	0.005
Conger conger	European conger	Congro	Fish, CONGRIDAE	0.005
Lepidorhombus boscii	Four-spot megrim	Areeiro-de-quatro-manchas	Fish, SCOPHTHALMIDAE	0.005
Solenocera membranacea	Atlantic mud shrimp	Camarão-da-vasa	Crustacean, SOLENOCERIDAE	0.005
Aristaeomorpha foliacea	Red royal prawn	Camarão-púrpura	Crustacean, ARISTEIDAE	0.005
Anthias anthias	Swallowtail seaperch	Canário-do-mar	Fish, SERRANIDAE	0.004
Trisopterus minutus minutus	Poor cod	Fanecão	Fish, GADIDAE	0.004

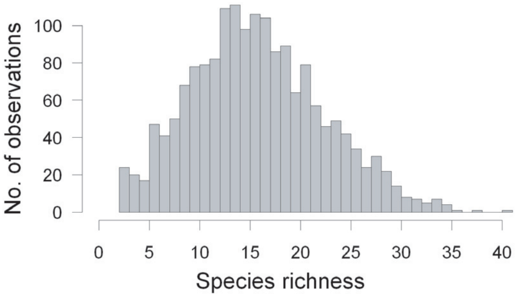


Fig. 3. Histogram of species richness at all sampling stations for the 22 surveys conducted between 1989 and 1999 (n = 1704).

the adoption of a Gaussian model for the GAM fitting. The stepwise selection kept all predictors as being significant ($p <$ 0.01), resulting in the following model:

$$S \sim \text{te(Long, Lat)} + \text{s(depth)} + \text{season} + \text{time}, \qquad (2)$$

where "s" are univariate cubic spline functions and "te" are tensor product smoothing functions. Residual diagnostics showed no departures from the assumptions (Fig. 4a,b) indicating an adequate fit, although the adjusted r-square of the model was small (~0.24).

3.1 Effects of covariates on species richness

Table 2 presents approximate significances (p-values) of non-parametric terms, parameter estimates, their standard errors and significances for levels of the parametric terms. Smoothed terms (longitude × latitude, depth) were found to be highly significant ($p \sim 0$, Table 2). The interpretation of smoothed terms in a GAM requires the analysis of their partial effects on the response. These are the additive contribution of each of the terms in the model, keeping all covariates fixed but the one under analysis (Hastie and Tibshirani 1990). Smooth functions are constrained to have zero mean in order for the models to be identifiable, thus the ordinates of the partial plots are scaled to zero. Whenever a joint smooth of two variables is under analysis the way to interpret its effect is to look at a 3-d plot, where regions of positive and negative effects are displayed as contour lines. This is the case for the partial effect of the joint smooth of longitude and latitude on species richness (Fig. 5a). Negative contour lines irradiating west from shallow northern areas (~40°–41°N) indicate relatively low species richness. Increasing positive contours to the shallow southeast (~37°N, 7.5°W) and in deep areas at intermediate latitudes (~39°N, 10°W) indicate relatively high species richness. The partial effect of depth shows a pattern of slight reduction in species richness from shallow grounds to about 250 meters, with richness increasing with depth thereafter (Fig. 5b). It should be noted, however, that between 40.5°N and 42°N the fixed sampling grid lacks stations below ~200 m depth (Fig. 2) therefore, uncertainty remains at this range regarding the pattern depicted for greater depths.

The majority of year levels were significantly higher than the first one (1989), taken for reference (Table 2). Years of particularly high species richness were 1996 (coef. = 9.78), 1990 (coef. = 4.79), 1994 (coef. = 3.98) and 1999 (coef. = 3.78). No significant differences were detected between autumn and summer (the reference level) surveys but the winter coefficient (2.17) was significantly higher ($p < 0.001$) than the other seasons, indicating higher richness in the winter.

Table 2. Species richness model – approximate significances (p-values) of non-parametric (smoothed) terms and parameter estimates, standard errors and significances for the parametric terms (year and season). The following significance indicators are used: ** significant at the 0.001 level; * significant at 0.05.

Model term	Coefficient	Std. error	p
Intercept	14.60	0.52	$< 2 \times 10^{-16}$**
te (long,lat)	-	-	$< 2 \times 10^{-16}$**
s (depth)	-	-	$< 2 \times 10^{-16}$**
Season (autumn)	0.15	0.31	0.630
Season (winter)	2.17	0.59	2.7×10^{-4}**
Year (1990)	4.79	0.63	4.7×10^{-14}**
Year (1991)	2.86	0.64	7.3×10^{-6}**
Year (1992)	2.91	0.65	8.6×10^{-6}**
Year (1993)	2.95	0.65	6.6×10^{-6}**
Year (1994)	3.98	0.81	9.7×10^{-7}**
Year (1995)	0.49	0.65	0.457
Year (1996)	9.78	0.85	$< 2 \times 10^{-16}$**
Year (1997)	2.68	0.67	7.2×10^{-5}**
Year (1998)	1.66	0.66	0.011*
Year (1999)	3.78	0.68	2.5×10^{-8}**

3.2 Predictions

The adopted model was used to make predictions of species richness in order to examine patterns in time (1989-1999), depth and space (longitude × latitude), with an increasing number of fixed covariates. Temporal patterns of predicted species richness are shown in Fig. 6 using boxplots by year. In this case only time levels are represented, pooling the effects of the remaining covariates by year. Richness has not remained stable over time. A sharp discrepancy is observed between lower richness in 1989 and 1995, and the highest in 1996. Between 1990 and 1994 richness remained relatively constant and after 1996 it decreased to slightly lower levels (Fig. 6).

Predicted profiles in depth were drawn between summer and winter (Fig. 7a,b). The autumn was not found to be significantly different than the summer (Table 2) thus the corresponding plot is not shown. The trends are smooth functions of the predictions whereas data points are observed richness (Fig. 7). Trends in species richness by depth are similar between summer and winter but differ by a scaling factor, with higher species richness in the winter.

Temporal differences in trends of species richness with depth were investigated by making predictions for separate surveys. Furthermore, since predictions are the outcome of the additive effects of the spatial, yearly and seasonal terms, these plots enable a relative comparison of the goodness of fit by survey. Trends of the predicted values were superimposed on observed data for this purpose (Fig. 8).

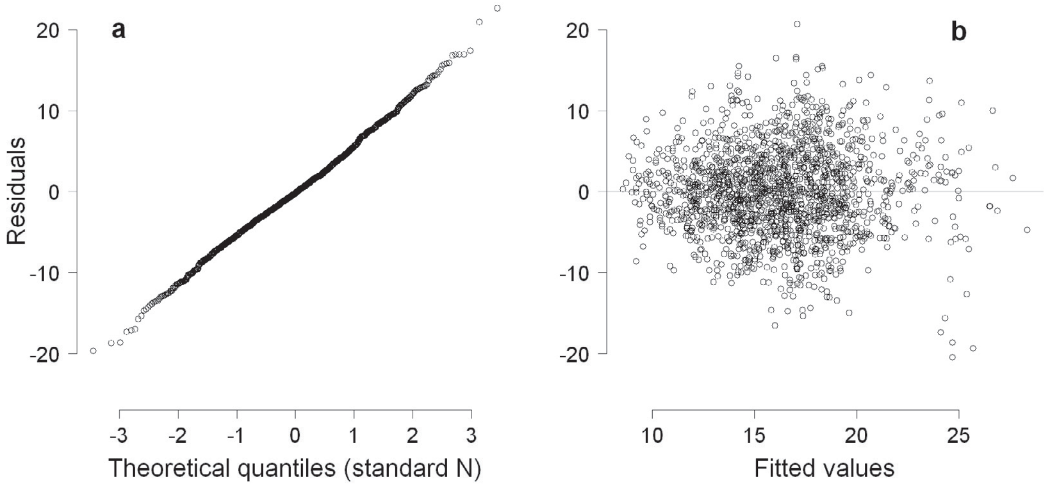


Fig. 4. Diagnostics for the species richness model: a) quantile-quantile plots showing sorted residuals against corresponding quantiles of the standard Normal distribution; b) residuals against fitted values.

The increase in species richness with depth from about 250 m, as revealed by the partial effect of depth (Fig. 5b), is clearly seen in all surveys (Fig. 8). Still, the slight reduction pattern from shallower grounds to about 250 m deep (Fig. 5b) is absent from some surveys, with no distinct pattern in time, a probable consequence of the high variability in richness of shallow grounds. Overall, it can be perceived from Fig. 8 that the trends of predictions accommodate relatively well the scatterplots of observed data. Yet, a few exceptions exist both translating into overestimation, i.e., trends clearly above the scatterplots (autumn of 1989), and underestimation (autumn of 1993).

Spatial predictions were made keeping values for depth set to its mean and controlling the levels of season and year. The degree of spatial interpolation was controlled in order to avoid predicting too far from the observed locations (i.e., sampling stations, Fig. 2). The spatial predictions were mapped for eight surveys selected for highlighting sharp differences in species richness. For example, winter 1992 was included since species richness in this season was found to be significantly higher than in the summer and autumn, 1989 was selected for being the year with lowest richness, and 1996 was included for having the highest richness. Maps are shown as contours of predicted species richness over space, richness increasing from darker to lighter colour/shading (Fig. 9).

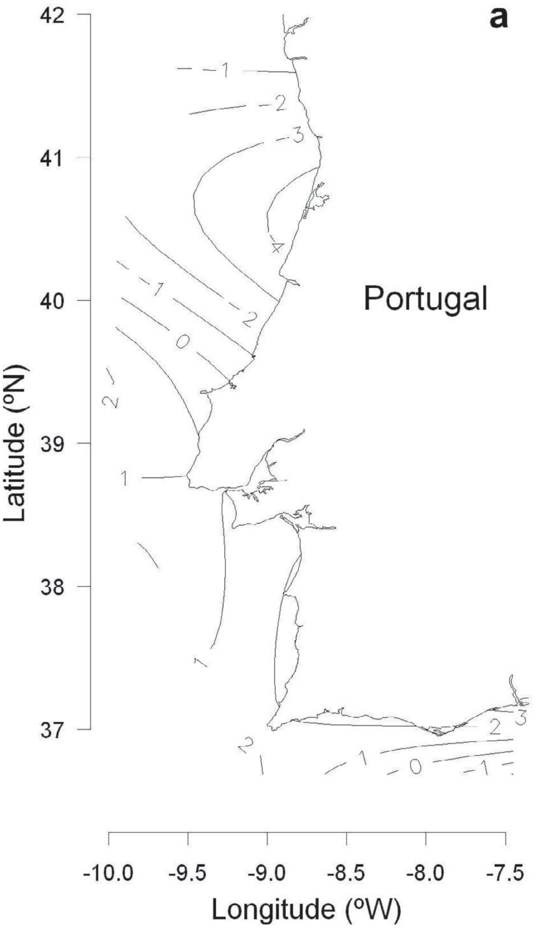
The overall pattern depicted in Fig. 9 does not change between surveys. There is lower species richness to the north and higher to the south, as expected from the partial effect of the joint smooth of longitude and latitude (Fig. 5a). The south-north reduction in the number of species varied between 20 and 40%. Substantial scale differences occurred between surveys, for example, the increase in species richness between the summer of 1989 and the autumn of 1990. Nevertheless, the most striking difference apparent in Fig. 9 is the highest species richness predicted for the autumn of 1996, followed by a subsequent decrease to average levels in the remaining surveys. The species caught in 1996 were distributed among several taxonomic groups including fish, crustaceans, cephalopods and others. The technical characteristics of sampling, area covered, and the species identification procedure in this survey were no different than usual. It thus does not seem that richness in 1996 could arise due to an artefact of methodology or as a result of unusual increases in a single taxonomic group.

4 Discussion

We have provided the most comprehensive description of marine species richness and its covariates on the Portuguese continental margin to date. Latitude, longitude, depth, seasonality and chronological time were all found to be statistically significant predictors of variation in species richness. Nevertheless, the model only explained about 24% of the total variability in the data, which is in agreement with the r-square of 0.25 obtained by Mueter and Norcross (2002) for the GAM fit to species richness of demersal fish in Alaska. The fact that a relatively long time series has been used – 22 surveys conducted over a period of 11 years and covering summer autumn and winter – prevents years or seasons with anomalous patterns from being adopted as typical for the area.

We have been able to detect seasonal differences in richness, with greater richness observed in the winter season. Because there were only two winter surveys (1992-1993), uncertainty remains as to whether this is a general pattern or only due to a specific phenomenon that happened to occur in the winters of 1992 and 1993. These years have coincided with a regime shift in seasonal upwelling conditions on the Iberian margin, changing from a period of relatively weak upwelling to a period of a stronger one, which included the winter, a traditionally non-upwelling season on the margin (Santos et al. 2005). Furthermore, these authors have shown that the winter NAO index in these years was the highest in the past 40 years.

Species richness reduces from the southern to the northern part of the Portuguese margin. This pattern persisted throughout the 22 surveys and is in agreement with one of the longest recognized ecological trends: decreasing richness from the



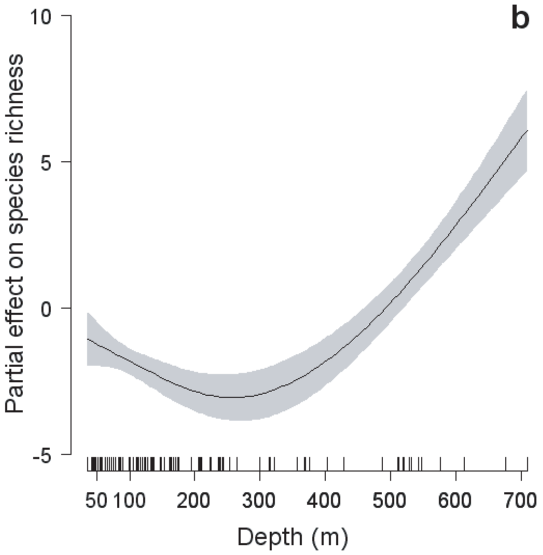


Fig. 5. Partial effects of smooth terms of the species richness model. a) spatial (latitude × longitude) smooth. Partial effects are presented as contour lines, following the geographical joint smooth of latitude and longitude: negative contour lines indicate areas of relatively low species richness whereas the opposite is revealed by positive contours. Contour lines are restricted to a neighbourhood of sampling locations; b) depth smooth. The shaded area represents approximate 95% confidence limits of the regression line with a rugged x-axis to show sampling intensity.

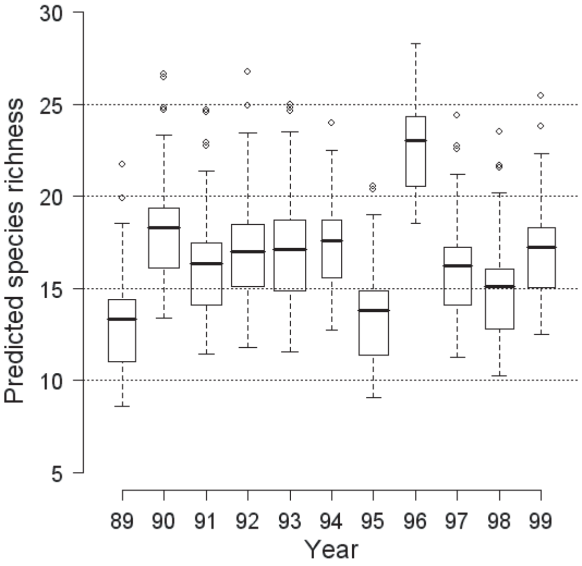


Fig. 6. Boxplots of predicted species richness by year. Within each year, the remaining covariates of the final model (longitude, latitude, depth and season) are aggregated. Boxes width is proportional to the number of observations. Box sections represent quartiles and whiskers are minimum and maximum values after excluding outliers and extremes.

equatorial to the polar regions (with a few notable exceptions, Willig et al. 2003). In the marine domain, this pattern has been recognized for the northern hemisphere, although it did not turn up so clearly for the southern hemisphere (Poore and Wilson 1993; Gray 2001). Most exceptions to the classical pattern were associated with scale, as they were based on studies extending over short latitudinal ranges (<20° latitude). Our sampled area covers only about 5 latitudinal degrees, but agrees with the general pattern.

Species richness also changes with depth on the Portuguese continental margin. There is a slight reduction in the number of species from the coast (50 m) down to the shelf break (200−300 m), increasing steadily afterwards along the slope, down to the deepest sampling stations at approximately 700 m. This is in agreement with Macpherson and Duarte (1994) who used a large database for fish taxa in the east-Atlantic, to show an increase in richness with depth to about 1000 m, followed by a decrease.

To our knowledge, a pattern of increase in species richness with depth has not been recognized as being common to fish communities on continental margins (see also Fig. 1 and Gray 2001). A number of explanations for this are possible. First, the number of studies similar to ours, where fish comprise a very significant proportion of the fauna, is rather small (Willig et al. 2003). Second, most authors have aggregated data within depth ranges, presenting indices by range (Jinao and Yanhong 1989; Paz and Casas 1996; Koslow et al. 1997; Labropoulou and Papaconstantinou 2004). By not considering the continuous nature of depth, aggregation may mask underlying patterns in species richness. Third, studies based on a very limited period of time (e.g. 1 or 2 surveys) and/or a small sampling

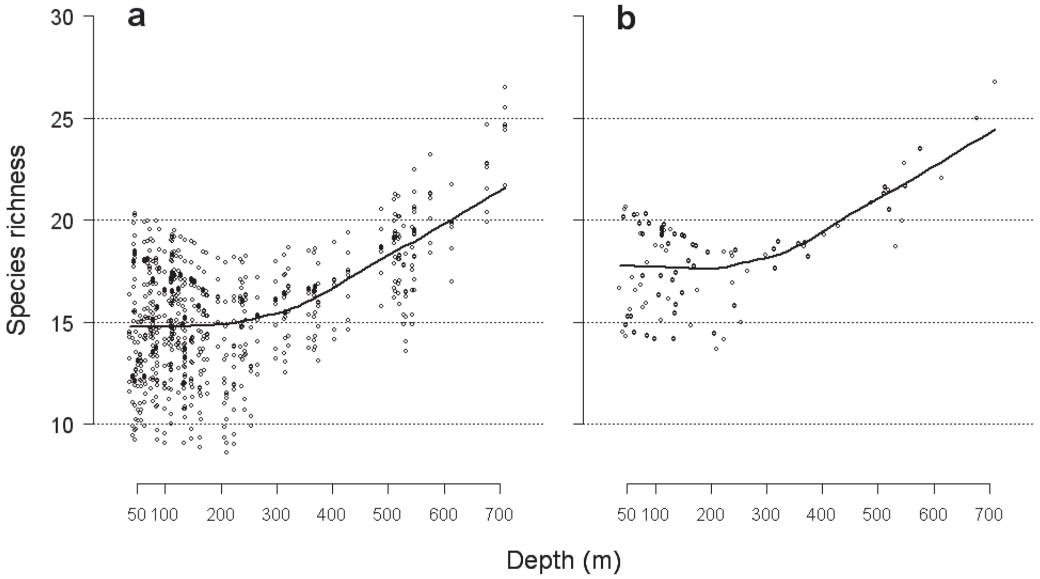


Fig. 7. Trend lines of predicted species richness with depth superimposed on observed richness (circles); a) summer; b) winter.

coverage over depth, may not show more general patterns very clearly (Koslow et al. 1997; Colloca et al. 2003).

There is a broad range of hypotheses to explain the latitudinal pattern of species richness, as recently synthesized by Willig et al. (2003). Indeed, latitude is a surrogate for a number of primary environmental gradients, such as shelf morphology, substrate characteristics, hydrological and oceanographic features, primary production, and food availability. These same gradients are correlates of depth, although other factors interfere in species adaptation to depth, like pressure, dissolved oxygen, and temperature range.

The northern part of the Portuguese continental shelf is much wider, with a steeper shelf break, than the southern area (Fig. 2). As for bottom sediments, there are also major differences. Extensive areas on the southern shelf consist primarily of mud bottom types, whereas mud is practically nonexistent on the northern shelf. A large number of benthic species which are prey to demersal fishes are known to require different types of muddy sediments which, themselves, are highly heterogeneous in regard to composition and granulometry (Schwinghammer 1981; Parsons et al. 1984).

There are also major differences in oceanographic hydrological features between the northern and southern parts of the Portuguese margin. A permanent feature over the slope of the northern part is the presence of the Iberian Poleward Current (IPC), with greater intensity in the winter (Peliz et al. 2005), whereas the southern part is under the influence of the main pathway of circulation of the Mediterranean Water (MW) into the Atlantic (Fiúza 1982), which tends to follow northward the contours of the Portuguese southwestern slope. According to Ambar et al. (1986), this warmer and saltier water mass is part of an undercurrent that may extend from the bottom of the surface mixed layer down to 1500 m. Mesoscale eddies are common features of the western Iberian region, owing to both the presence of the IPC and the poleward flow of the MW interacting with the topography (Peliz et al. 2002).

As Willig et al. (2003) stated, the hypothesis that greater biological production at the bottom of the food web results in greater species richness, everything else being equal, requires validation. On the Portuguese margin, conditions for primary and secondary marine production are better off the northern than off the southern coast, as a result of more persistent upwelling. Moreover, the diversity of zooplankton species is lower to the north, with shorter food chains (Cunha 2001). We therefore find that the area of higher production corresponds to the area of lower species richness. This is empirical evidence for a negative correlation between measures of ocean production and species richness, as previously reported by Macpherson (2002) using data of eastern and western Atlantic fishes and invertebrates.

We are not aware of any established straightforward mechanisms relating physical and biological features to the increase of species richness with depth. It is unlikely that any one variable will entirely account for richness gradients. However, one potentially important factor might be changes in richness of benthic fauna with depth. Recent studies on the Portuguese shelf indicate a decrease in richness of macrobenthos as one moves from the coast down to the shelf break (Gaudêncio, pers. comm. 2005). To our knowledge, there is no information available about benthic faunal richness on the Portuguese slope. However, other studies in the Northern Atlantic have reported either an increase with depth of all benthic taxa beyond the shelf break (Haedrich et al. 1980) or depth zonation on the slope (Rowe and Menzies 1969; Haedrich et al. 1975; Rowe 1981). Parsons et al. (1984) state that similar turnovers in benthic fauna might be related to the boundary between shallow and deep water masses which account for differences in sediment texture and stability. On the Portuguese margin the transition zone around 200−300 m, where species richness starts to increase, coincides with the upper limit of the range of influence of the all-year-round IPC along the north-western coast and the MW in the south.

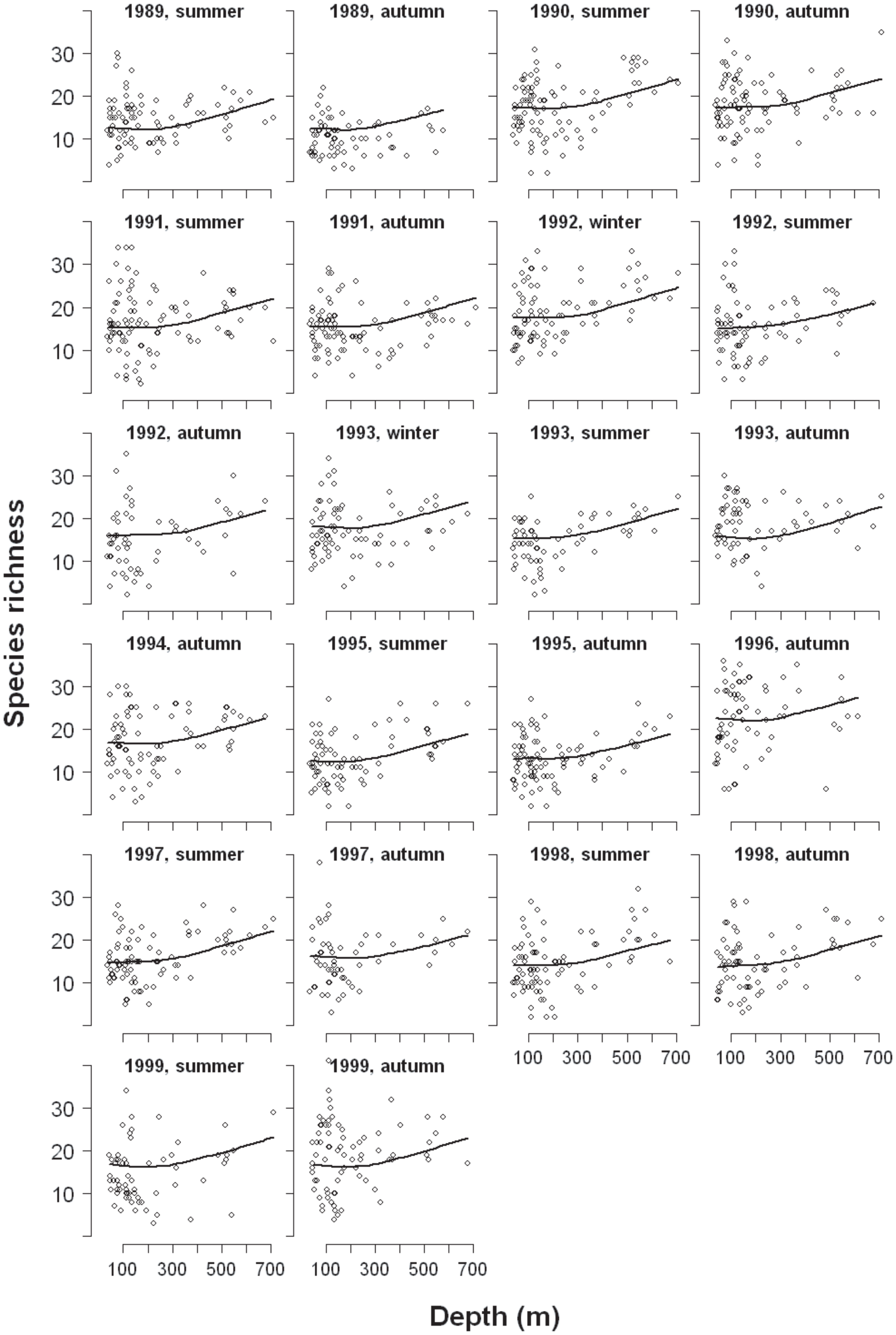


Fig. 8. Trend lines of predicted species richness with depth by year and season superimposed on observed richness (circles).

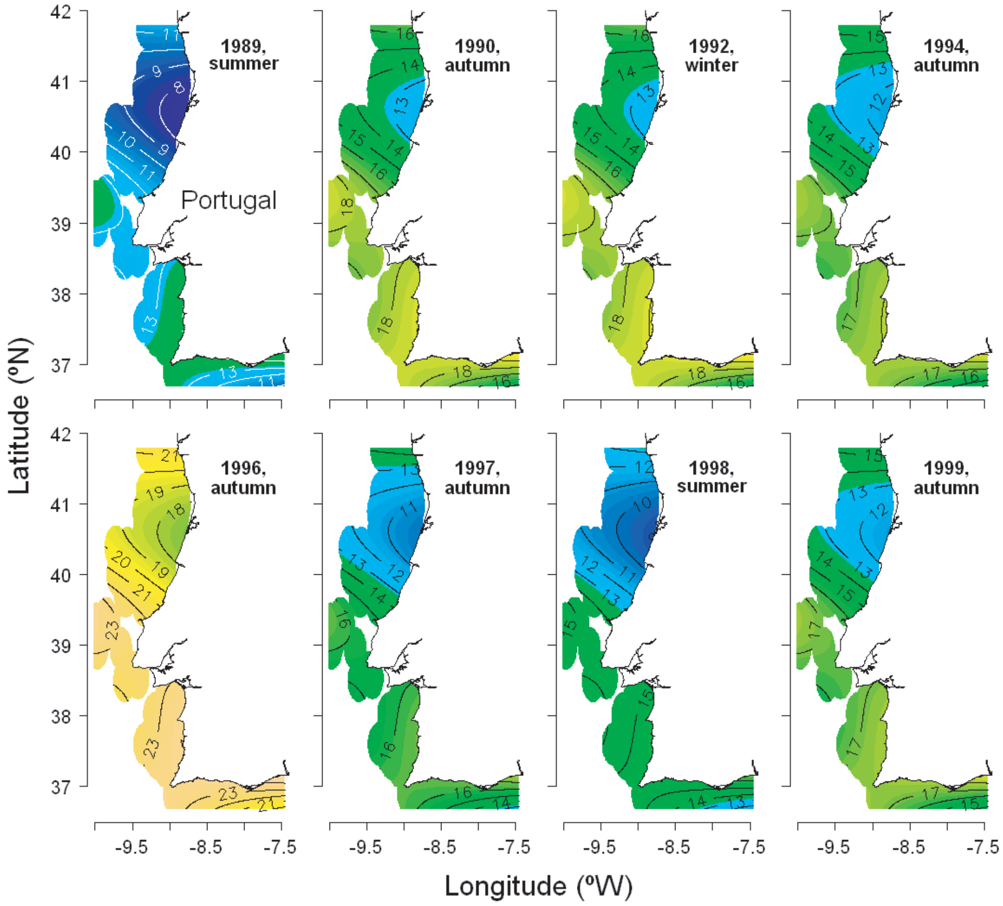


Fig. 9. Contour plots with predicted species richness over space for a selection of years and seasons (lighter colour/shading – higher richness; darker colour/shading – lower richness).

Our study contributes to an improved understanding of spatial patterns of biodiversity in the marine environment, in line with recent recommendations by Willig et al. (2003). We also provide background information for the adoption of conservation strategies at a local scale, following current guidelines of the European Commission for biodiversity.

Acknowledgements. Financial support for Pedro Sousa has been provided by the Fundação para a Ciência e a Tecnologia (Programa PRAXIS XXI), Lisbon, Portugal, in a PhD scholarship programme. This work was conducted within the scope of Project NeoMAv (INIAP-IPIMAR, UE co-financed), some of the surveys being funded by PNAB/Data Collection. We express our gratitude to Dra. Fátima Cardador (IPIMAR) for assistance with data handling and to Dr. Simon Wood (University of Bath) for his contribution to GAM modelling. We thank an anonymous referee for useful comments that helped to improve the manuscript.

References

Ambar I., Fiúza A.F.G., Boyd T.J., Frouin R., 1986, Observations of a warm oceanic current flowing northward along the coasts of Portugal and Spain during November-December 1983. EOS Trans. Am. Geophys. Union 67, 1054.

Augustin N.H., Borchers D.L., Clarke E.D., Buckland S.T., Walsh M., 1998, Spatiotemporal modelling for the annual egg production method of stock assessment using generalized additive models. Can. J. Fish. Aquat. Sci. 55, 2608-2621.

Austin M.P., 2002, Spatial prediction of species distribution: an interface between ecological theory and statistical modelling. Ecol. Model. 157, 101-118.

Blanchard F., 2001, Une approche de la dynamique des peuplements de poissons démersaux exploités: analyse comparée de la diversité spécifique dans le golfe de Gascogne (océan Atlantique) et dans le golfe du Lion (mer Méditerranée). Aquat. Living Resour. 14, 29-40.

Cardador F., Sanchéz F., Pereiro F.J., Borges M.F., Caramelo A.M., Azevedo M., Silva A., Pérez N., Martins M.M., Olaso I., Pestana G., Trujillo V., Fernandez A., 1997, Groundfish surveys in the Atlantic Iberian waters (ICES divisions VIIIc and IXa): history and perspectives. ICES CM 1997/Y:8, p. 29.

Colloca F., Cardinale M., Belluscio A., Ardizzone G., 2003, Pattern of distribution and diversity of demersal assemblages in the central Mediterranean sea. Estuar. Coast. Shelf Sci. 56, 469-480.

Cunha M.E., 2001, Physical control of biological processes in a coastal upwelling system: comparison of the effects of coastal topography, river run-off and physical oceanography in the Northern and Southern parts of the western Portuguese coastal waters. PhD thesis, FCL, Lisboa.

Edwards P.J., May R.M., Webb N.R. (Eds.), 1994, Large-scale ecology and conservation biology. Blackwell Science.

Flach E., Bruin W.D., 1999, Diversity patterns of macrobenthos across a continental slope in the NE Atlantic. J. Sea Res. 42, 303-323.

Fiúza A.F., 1982, The Portuguese upwelling system. Actual problems of oceanography in Portugal, pp. 45-71. Seminar, Lisbon, 20-21 Nov. 1980, Junta Nacional de Investigação Científica e Tecnológica – NATO Marine Sciences Panel.

Fock H., Uiblein F., Köster F., von Westernhagen H., 2002, Biodiversity and species-environment relationships of the demersal fish assemblage at the Great Meteor Seamount (subtropical NE Atlantic), sampled by different trawls. Mar. Biol. 141, 185-199.

Frescino T.S., Edwards Jr. T.C., Moisen G.G., 2001, Modelling spatially explicit forest structural attributes using generalized additive models. J. Veg. Sci. 12, 15-26.

Fulton E.A., Smith A.D.M., Punt A.E., 2005, Which ecological indicators can robustly detect effects of fishing? ICES J. Mar. Sci. 62, 540-551.

Gray J., 2001, Marine diversity: the paradigms in patterns of species richness examined. Sci. Mar. 65 (Suppl. 2), 41-56.

Guisan A., Edwards Jr. T.C., Hastie T., 2002, Generalized linear and generalized additive models in studies of species distributions: setting the scene. Ecol. Model. 157, 89-100.

Haedrich R., Rowe G.T., Polloni P.T., 1975, Zonation and faunal composition of epibenthic populations on the continental slope south of New England. J. Mar. Sci. 33, 191-212.

Haedrich R.L., Rowe G.T., Polloni P.T., 1980, The megabenthic fauna in the deep sea south of New England, USA. Mar. Biol. 57, 165-179.

Hastie T.J., Tibshirani R.J., 1990, Generalized Additive Models. Chapman & Hall.

Hawksworth D.L. (ed.), 1995, Biodiversity. Measurement and Estimation. Chapman & Hall.

Jinao S., Yanhong C., 1989, On the demersal fish communities of the East China Sea. Chin. J. Oceanol. Limnol. 7, 159-168.

Koslow J.A., Williams A., Paxton J.R., 1997, How many demersal fish species in the deep sea? A test of a method to extrapolate from local to global diversity. Biodiversity Conserv. 6, 1523-1532.

Kunin W.E., Lawton J.H., 1996, Does biodiversity matter? Evaluating the case for conserving species. In: Gaston K. J. (Ed.). Biodiversity. A Biology of Numbers and Difference, Blackwell Science, pp. 283-307.

Labropoulou M., Papaconstantinou C., 2004, Community structure and diversity of demersal fish assemblages: the role of fishery. Sci. Mar. 68 (Suppl. 1), 215-226.

Lehmann A., Leathwick J.R., Overton J.McC., 2002a, Assessing New Zealand fern diversity from spatial predictions of species assemblages. Biodiversity Conserv. 11, 2217-2238.

Lehmann A., Overton J.McC., Leathwick J.R., 2002b, GRASP: generalized regression analysis and spatial prediction. Ecol. Model. 157, 189-207.

Lobry J., Gascuel D., Domain F., 2003, La biodiversité spécifique des ressources démersales du plateau continental guinéen : utilisation d'indices classiques pour un diagnostic sur l'évolution de l'écosystème. Aquat. Living Resour. 16, 59-68.

Macpherson E., 2002, Large-scale species-richness gradients in the Atlantic Ocean. Proc. R. Soc. Lond. B 269, 1715-1720.

Macpherson E., Duarte C.M., 1994, Patterns in species richness, size and latitudinal range of East Atlantic Fishes. Ecography 17, 242-248.

Magnussen E., 2002, Demersal fish assemblages of Faroe Bank: species composition, distribution, biomass spectrum and diversity. Mar. Ecol. Prog. Ser. 238, 211-225.

Magurran A.E., 1988, Ecological Diversity and Its Measurement. Princeton University Press. Princeton, New Jersey.

McCullagh P., Nelder J.A., 1989, Generalized Linear Models. Chapman & Hall. Mueter F.J., Norcross B.L., 2002, Spatial and temporal patterns in the demersal fish community on the shelf and upper slope regions of the Gulf of Alaska. Fish. Bull. 100, 559-581.

Paz J., Casas J.M., 1996, Zonation and associations of dominant fish fauna on Flemish Cap. NAFO Sci. Counc. Stud. 25, 67-75.

Perrings C., Mäller K.-G., Folke C., Holling C.S., Jansson B.-O. (Eds.), 1995, Biodiversity loss. Economic and ecological issues. Cambridge University Press.

Parsons T.R., Takahashi M., Hargrave B., 1984, Biological oceanographic processes. Pergamon Press.

Peliz A., Dubert J., Santos A.M.P., Oliveira P.B., Le Cann B., 2005, Winter upper ocean circulation in the Western Iberian Basic – Fronts, Eddies and Poleward Flows: an overview. Deep-Sea Res. I 52, 621-646.

Peliz A., Rosa T., Santos A.M.P., Pissarra J., 2002, Fronts, jets and counter-flows in the Western Iberia Upwelling System. J. Mar. Syst. 35, 61-77.

Poore G.C.B., Wilson G.D.F., 1993, Marine species richness. Nature 361, 597-598.

Price A.R.G., 2002, Simultaneous "hotspots" and "coldspots" of marine biodiversity and implications for global conservation. Mar. Ecol. Prog. Ser. 241, 23-27.

R Development Core Team, 2005, R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL `http://www.R-project.org`.

Rowe G.T., 1981, The deep sea ecosystem. In: Longhurst A.R. (Ed.). Analysis of Marine Ecosystems, Academic Press, pp. 235-267.

Rowe G.T., Menzies R.J., 1969, Zonation of large benthic invertebrates in the deep sea off the Carolinas. Deep-Sea Res. 16, 531-581.

Santos M.A., Kazmin A.S., Peliz A., 2005, Decadal changes in the Canary upwelling system as revealed by satellite observations: Their impact on productivity. J. Mar. Res. 63, 359-379.

Schwinghamer P., 1981, Characteristic size distributions of integral benthic communities. Can. J. Fish. Aquat. Sci. 38, 1255-1263.

Sousa P., Azevedo M., Gomes M.C., 2005, Demersal assemblages off Portugal: mapping, seasonal, and temporal patterns. Fish. Res. 75, 120-137.

Stratoudakis Y., Bernal M., Borchers D.L., Borges M.F., 2003, Changes in the distribution of sardine eggs and larvae off Portugal, 1985-2000. Fish. Oceanogr. 12, 1-12.

Venables W.N., Dichmont C.M., 2004, GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fish. Res. 70, 319-337.

Willig M.R., Kaufman D.M., Stevens R.D., 2003, Latitudinal gradients of biodiversity: patterns, process, scale, and synthesis. Ann. Rev. Ecol. Evol. Syst. 34, 273-309.

Wood S.N., 2001, mgcv: GAMs and Generalized Ridge Regression for R. R News 1(2), 20-25.

Wood S.N., 2004, Low rank scale invariant tensor product smooths for generalized additive mixed models. Tech. Rep. 04-13. Depart. Statistics, University of Glasgow.