

Analysis of horse mackerel, blue whiting, and hake catch data from Portuguese surveys (1989–1999) using an integrated GLM approach

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Abstract – Catch rates (kg hour^{-1}) of horse mackerel (*Trachurus trachurus*), blue whiting (*Micromesistius poutassou*) and hake (*Merluccius merluccius*) from a series of 22 groundfish surveys conducted off Portugal between 1989 and 1999 were analysed using integrated logistic and gamma Generalized Linear Models (GLM). This methodology deals with the large amount of zeros in survey data matrices by modelling the probability of catch and the amount of positive catch separately, and then integrating the two sub-models into a single catch rate model of abundance. Among the explanatory variables included in the models, the geographic areas occupied by fish assemblages, i.e., groups of persistent co-occurring species, explained most of the variability observed for horse mackerel and blue whiting, while depth was the most important factor for hake. Because of hake's ubiquity on the Portuguese margin, models for this species were less parsimonious and explained a lower proportion of total variability compared with the other species. The abundance of horse mackerel is much higher in the winter and reduces with depth. Blue whiting and horse mackerel exhibited opposite trends in abundance from 1991 to 1994, with the latter species presenting a higher abundance throughout this period. No clear temporal trends of abundance were detected for hake. The effect of trawling hour in models suggested that horse mackerel and blue whiting exhibit vertical migrations, staying close to the bottom by day, when abundance is higher. The current approach proved to cope well with sparse catch data matrices and brought out novel information on the ecology of fish species in the Portuguese continental margin by successfully integrating environmental information into the analysis of fish abundance.

Key words: Abundance / Fisheries / Blue whiting / Hake / Horse mackerel / GLM

Résumé – Analyse des captures de chinchard, merlan bleu et merlu à partir des données de campagnes de pêche portugaises (1989–1999) au moyen d'une approche GLM intégrée. Les taux de capture (kg h^{-1}) de chinchard (*Trachurus trachurus*), merlan bleu (*Micromesistius poutassou*) et merlu (*Merluccius merluccius*) d'une série de 22 campagnes de chalutage de fond conduites au large du Portugal entre 1989 et 1999 sont analysés au moyen de modèles logistiques linéaires généralisés gamma (GLM). Cette méthode fonctionne avec un grand nombre de zéros dans les matrices de données de campagnes en modélisant la probabilité de capture et la somme de captures séparément, puis en intégrant les 2 sous-modèles en un seul modèle de taux de capture et d'abondance. Parmi les variables explicatives incluses dans le modèle, les aires géographiques occupées par les assemblages de poissons, c'est-à-dire les espèces rencontrées ensemble, expliquent plus de la moitié de la variabilité observée pour le chinchard et le merlan bleu, tandis que la profondeur est le facteur le plus important pour le merlu. A cause de l'ubiquité du merlu sur le plateau continental portugais, les modèles pour cette espèce sont moins parcimonieux et expliquent une plus faible proportion de la variabilité totale comparée aux autres espèces. L'abondance du chinchard est beaucoup plus élevée en hiver et diminue avec la profondeur. Le merlan bleu et le chinchard présentent des tendances opposées en abondance, de 1991 à 1994, le chinchard étant plus abondant durant cette période. Aucune tendance claire n'a été détectée pour le merlu. L'effet de l'heure de chalutage, dans les modèles, suggère que le chinchard et le merlan bleu présentent des migrations verticales, restant près du fond durant le jour, lorsque l'abondance est élevée. L'approche courante fonctionne bien avec des matrices de données de capture éparées et apportent une information nouvelle sur l'écologie de ces espèces du plateau continental portugais, en intégrant avec succès des informations environnementales, dans l'analyse des abondances de poissons.

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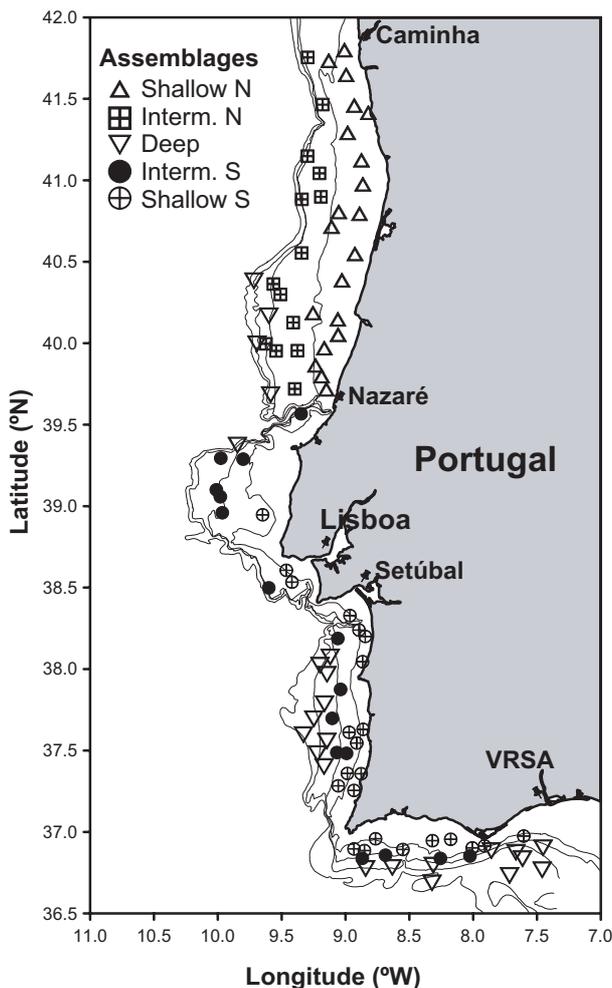


Fig. 1. Geography of Portuguese demersal assemblages. Contour lines are bathymetrics of 100, 200, 500 and 700 m. All symbols are positioned at sampling stations and each symbol associates a station to one of five assemblages, as in the legend. VRSA: Vila Real de Santo António.

1 Introduction

Groundfish research surveys have been conducted off the Portuguese continental margin since the late seventies by the Portuguese Institute for Fisheries and Sea Research (IPIMAR). The main objective of the surveys is to estimate the abundance and distribution of the most important commercial species of the Portuguese trawl fishery: European hake (*Merluccius merluccius*), horse mackerel (*Trachurus trachurus*) and blue whiting (*Micromesistius poutassou*), among others.

Marine survey data are often characterised by comprising a substantial proportion of zeros (zero catch of species x at site y). Furthermore, the distribution of the non-zero values is often highly positively skewed. Model-based methods have been proposed to overcome these particular features of the data, namely the delta distribution (Pennington 1983, 1996; Lo et al. 1992) and geostatistical methods (Conan 1985; Petitgas 1993). These methods however, are not exempt from problems (Myers and Pepin 1986; Stefánsson 1996). The log-normal distribution, assumed by the delta method, has been shown to

produce no better results than the Weibull or gamma distributions in so far as non-zero observations are concerned (Myers and Pepin 1990). Even when the log-normal distribution can be assumed appropriate, its efficiency is inversely related to the proportion of zero observations in the data (Aitchinson and Brown 1957 in Myers and Pepin 1990). Stefánsson (1996) presented a method to model both the probability of a non-zero catch and the mean of positive values, by combining two Generalized Linear Models – GLM (McCullagh and Nelder 1989), using the binomial and the gamma density functions. Stefánsson's methodology belongs to a group of methods used to handle *zero-inflated data* (Tu 2002) that accommodate theoretical distributions other than the gamma and are emergent tools in biometrics (Ridout et al. 1998) and fisheries (e.g., Ye et al. 2001; Lemos and Gomes 2004; Maunder and Punt 2004; Ortiz and Arocha 2004).

This work aims to understand the underlying determinants of the abundance of horse mackerel, blue whiting, and hake in the Portuguese continental margin using a model-based approach to the 22 demersal surveys conducted from 1989 to 1999 on the Portuguese shelf and upper slope. The approach incorporates the information on both the probability of occurrence of a positive catch and the amount of the positive catch and evaluates several predictor variables. Sousa et al. (2005) mapped and described five spatially distinct fish assemblages on the Portuguese shelf, i.e., groups of co-occurring species that are persistent in space and time, with geographical boundaries determined by depth and latitude (Fig. 1). They found that depth and latitude correlated with the major gradients of biological differentiation on the shelf. We believe that such knowledge on how fish populations distribute geographically is an important contribution to the understanding of this ecosystem and, therefore, was taken into account in the analyses.

2 Methods

2.1 Data

We have analysed an 11-year time series (1989–1999) of catch rates in weight (kg h^{-1}) of horse mackerel, blue whiting, and hake, from 22 surveys, conducted in the fall (11 surveys), summer (9) and winter (2) by IPIMAR. The sampling design consisted of a fixed grid of 97 sampling stations, spread throughout the shelf and upper slope between 36 and 710 meters deep, trawling speed did not vary substantially between surveys, and catch rates were standardized to 60 min of tow duration. The technical characteristics of sampling are fully described in Cardador et al. (1997) and ICES (2002) and thus will not be reported here.

In the period under analysis, the macrofauna available to bottom trawling on the Portuguese coast included more than 300 taxa, including fish, crustaceans, cephalopods and other groups. However, only a few species accounted for the vast majority of the catch in weight. Among these are the blue whiting, horse mackerel, and the European hake, respectively the second, fourth and fifth most important species in weight (1989–1999). Hake and horse mackerel have a high market price. Blue whiting has a low market price but plays a major

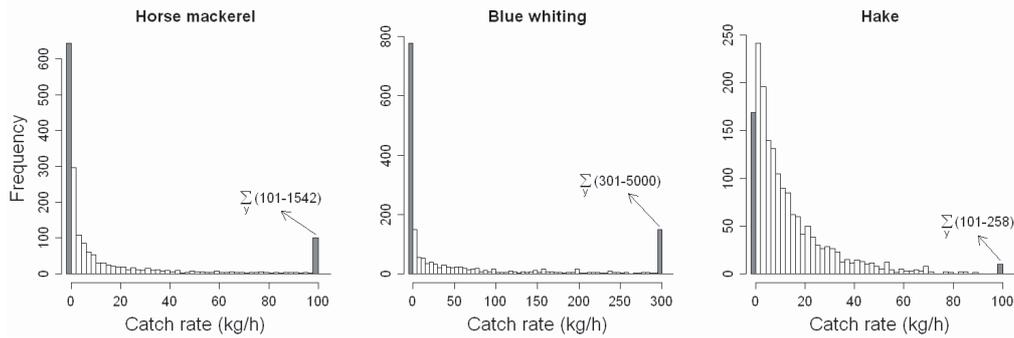


Fig. 2. Frequency distributions of catch rate of horse mackerel, blue whiting, and hake. In each graph, the first and last classes denote, respectively, zero catch rate and the cumulative frequency of catch rate within the range indicated by the summation.

role in the trophic chain, being a forage species for predators like hake and horse mackerel (Silva et al. 1997; Cabral and Murta 2002) and is used to produce high value fish derivatives such as surimi (Trondsen 1998). All three species are managed by a TAC system.

This same dataset was previously used by Sousa et al. (2005) to map and describe the demersal marine community inhabiting the continental margin off Portugal, how it organizes into fish assemblages (shallow northern – SN, intermediate northern – IN, deep – D, intermediate southern – IS, and shallow southern – SS), their spatial distribution, and the environmental factors that they are associated with. The areas inhabited by fish assemblages thus appeared as a natural choice to incorporate geography into the analyses. There is also additional information collected along with species catch in the Portuguese groundfish surveys, such as depth and trawling hour, which are likely to correlate with catch rates. We have regarded catch rate by species as a response variable to the explanatory categorical variables *year* (1989–1999), *season* (summer, autumn, winter), *assemblage* (SN, IN, D, IS, SS), and to the continuous variables *latitude* (°N), *trawling hour* (from 6 am to 9 pm) and *depth* (m).

Exploratory data analysis showed that catch varied with the time of the day, a finding previously reported by other authors (Bailey 1982; Gordo and Macpherson 1991; Papaconstantinou and Stergiou 1995). Accordingly, the circular variable “trawling hour” was first converted to a numerical (0–1) scale and then transformed by the sinusoidal functions $\sin(2\pi \text{ hour})$ and $\cos(2\pi \text{ hour})$. By such transformation we force catch rates to have absolute maximum and minimum values within the day cycle.

2.2 Modelling

Prior examination of catch rate frequency distributions by species revealed high positive skewness (Fig. 2), with a considerable proportion of stations with zero catch, namely, 10% (hake), 38% (horse mackerel) and 46% (blue whiting). In order to account for both the probability of occurrence and the amount of catch in weight by sampling station, modelling was conducted in three steps: (1) estimate the probability of positive catch, (2) estimate the value of catch rates conditional to positive catch (hereafter referred to as *positive catch rates*),

(3) combine the two estimates to get the overall estimate of catch rates unconditioned to whether the probability of catch is zero or greater than zero, to which we refer hereafter as *abundance*.

It is assumed that presence/absence of catch follows a binomial distribution (1)

$$f(y|\pi) = \binom{n}{y} \pi^y (1 - \pi)^{n-y} \quad (1)$$

where n is the number of Bernoulli trials, π the probability of a positive catch, and y the number of successes. It is further assumed that the probability of a positive catch at the sampling station i , $P(Y_i = 1) = \pi_i$, depends on the p -dimensional vector, z_i , of predictor variables, through the logistic regression model with the logit link (Hosmer and Lemeshow 1989), hence,

$$\pi_i = \frac{\exp(z_i^T \beta)}{1 + \exp(z_i^T \beta)} \quad (2)$$

where β is a p -dimensional vector of regression coefficients. Exploratory data analysis (EDA) showed that the variance of positive catch rates was approximately proportional to the square of the mean response (Fig. 3), which implies a constant coefficient of variation (Brynjarsdóttir and Stefánsson 2004). Accordingly, to estimate the value of positive catch rates (step 2), it was assumed a gamma density with shape, ν , and scale, ν/η , parameters (3).

$$f(y|\nu, \eta) = \frac{1}{\Gamma(\nu)} \left(\frac{\nu}{\eta}\right)^\nu y^{\nu-1} \exp\left(-\frac{\nu}{\eta} y\right). \quad (3)$$

Assuming that the predictors interact in a multiplicative way, the gamma regression model with a log link (4) (McCullagh and Nelder 1989) was used to estimate the expected value (η) of positive catch rates.

$$\eta_i = \exp(z_i^T \beta). \quad (4)$$

While not substantially altering the results from the EDA a square-root transformation of positive catch rates was found necessary to improve the gamma model’s goodness-of-fit. This procedure was applied for the three species and was prompted by the extreme skewness of the original positive catch rates

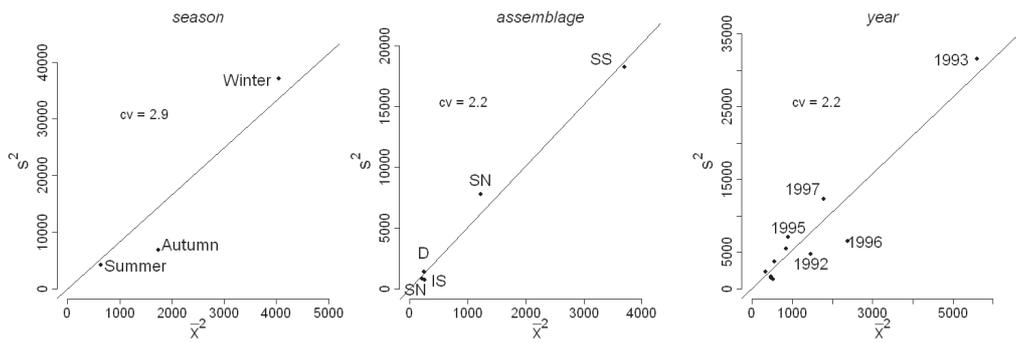


Fig. 3. Scatterplots of sample variance ($s^2 - \text{kg h}^{-2}$) versus squared mean catch rate ($\bar{x}^2 - \text{kg h}^{-2}$) of horse mackerel by season, assemblage and year.

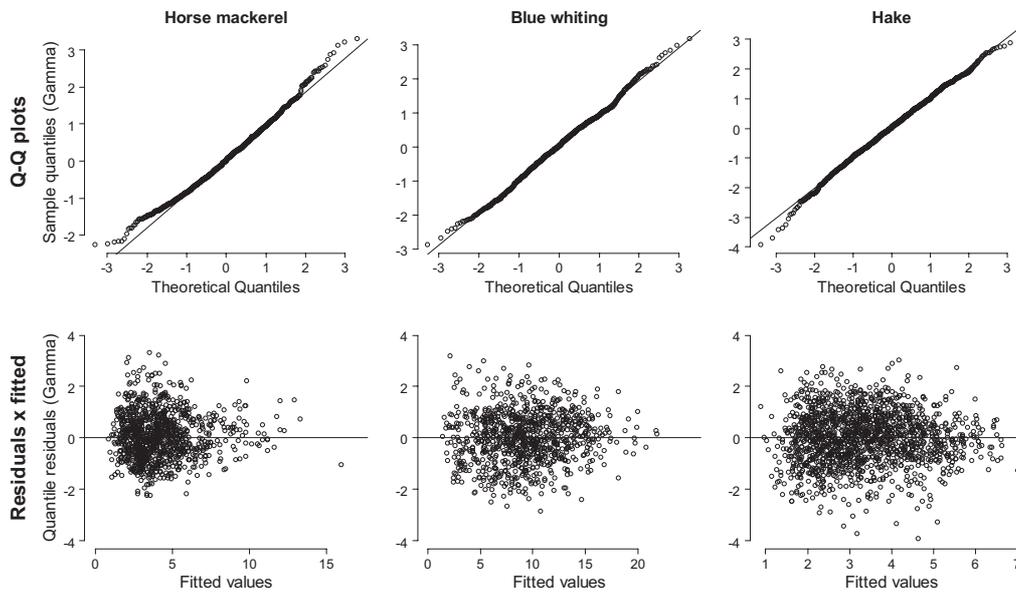


Fig. 4. Analysis of residuals of gamma models fitted to square-root-transformed catch rate of horse mackerel, blue whiting, and hake: qq-plots and plots of residuals versus fitted values.

(Fig. 2). Finally, abundance (predicted unconditional catch rates, $\hat{\mu}$) were computed from the product of separate estimates of probability of positive catch and squared positive catch rates, i.e., $\hat{\mu} = \hat{\pi} \times \hat{\eta}^2$, where the square is due to the previous square-root transformation of the response. The estimates of abundance are thus the combination of two separate GLMs. The modelling strategy consists of a stepwise procedure that starts by testing the significance ($\alpha = 0.05$) of predictor variables (main effects) and is followed by the inclusion of first order interactions that seemed ecologically possible at first place. The significance of the difference in the deviance between two models due to an additional factor was assessed through a chi-square test ($\alpha = 0.05$) (McCullagh and Nelder 1989). Modelling was conducted in R environment (R development core team 2006).

The proper transformation and use of raw residuals in diagnostic analysis of GLMs has been the subject of previous attention in the literature (e.g., Pierce and Schafer 1986; McCullagh and Nelder 1989). For gamma models, the most commonly used residuals have problems of non-Normality (Pearson residuals), and have biased expectations or heteroscedasticity

(deviance residuals) (Dunn and Smyth 1996; Turkman and Silva 2000). Here we have used quantile residuals for the gamma model (R package *statmod*), which are obtained from inverting the fitted gamma function for each response value and finding the equivalent standard normal quantile (Dunn and Smyth 1996).

3 Results

3.1 Fitted models

The analysis of (randomized quantile) residuals for the gamma regression models fitted with qq-plots (top plots) and plots of observed *versus* fitted values (bottom plots), for the three species (columns) is presented in Figure 4. Goodness-of-fit analyses of the gamma model revealed minor violations of its assumptions, including very moderate deviations from the expected standard normal distribution of quantile residuals (Fig. 4, qq-plots, first row). The models that best explained the probability of positive catch (π) and the amount of positive

Table 1. Deviance tables for horse mackerel, blue whiting, and hake logistic models (probability of positive catch). Significances of terms are marked as “****” ($p < 0.001$), “***” ($p < 0.01$), and “**” ($p < 0.05$); “depth⁰” denote quadratic terms of order “0” of the depth covariate.

Source of variation	D.f.	Deviance	% explained	Resid. d.f.	Resid. Deviance	
Horse mackerel						
Null				1703	2260.6	
factor (year)	10	81.0	3.6%	1693	2179.6	***
factor (season)	2	19.6	0.9%	1691	2160.0	***
factor (assemblage)	4	565.5	25.0%	1687	1594.5	***
depth	1	147.1	6.5%	1686	1447.5	***
cosin (hour)	1	15.3	0.7%	1685	1432.2	***
Total explained	18	828.5	36.6%			
Blue whiting						
Null				1703	2349.7	
factor (year)	10	38.1	1.6%	1693	2311.6	***
factor (season)	2	9.4	0.4%	1691	2302.2	**
factor (assemblage)	4	1014.7	43.2%	1687	1287.5	***
depth	1	48.5	2.1%	1686	1238.9	***
latitude	1	28.6	1.2%	1685	1210.3	***
cosin (hour)	1	7.2	0.3%	1684	1203.2	**
depth: latitude	1	22.1	0.9%	1683	1181.1	***
Total explained	20	1168.7	49.7%			
Hake						
Null				1703	1101.7	
factor (year)	10	24.9	2.3%	1693	1076.8	**
factor (assemblage)	4	24.4	2.2%	1689	1052.4	***
depth	1	0.4	< 0.1%	1688	1052.0	
depth ²	1	90.8	8.2%	1687	961.2	***
depth ³	1	45.6	4.1%	1686	915.7	***
depth ⁴	1	53.7	4.9%	1685	861.9	***
Total explained	18	239.8	21.8%			

catch rates (η) differed slightly among species (Tables 1 – logistic models, and 2 – gamma models), although the covariates *year*, *assemblage* and *depth* have been significant in all models. A brief description of the models fitted is given below by species avoiding exhaustive details on the exact formulation of the linear predictors (Eqs. (2) and (4)).

• HORSE MACKEREL

(i) $\pi_{ijkdlh} \sim \beta_0 + Y_i + S_j + A_k + D_d + \cosin(H)_h + \varepsilon_{(.)}$

(ii) $\eta_{ijkdhl} \sim \beta_0 + Y_i + S_j + A_k + D_d + \cosin(H)_h + L_l + S_j \times L_l + \varepsilon_{(.)}$

where β_0 is the intercept, Y_i ($i = 1$ to 11) is the year effect from 1989 to 1999; S_j is the season effect [$j = 1$ (summer), 2 (autumn), 3 (winter)]; A_k is the assemblage effect [$k = 1$ (SN), 2 (IN), 3 (D), 4 (IS), 5 (SS)]; D_d is the effect of depth (m); $\cosin(H)_h$ is the effect of trawling hour; L_l is the effect of latitude (degrees) and $\varepsilon_{(.)}$ is the error term.

The logistic model fitted to presence/absence of horse mackerel explained about 37% of total variability (Table 1). The greatest contribution was due to the assemblage effect with 25% of the deviance explained. Depth and year explained, respectively, 6.5 and 3.6% of the total variability. The horse mackerel gamma model included the main effect term of latitude and the interaction term of this covariate with the season (Table 2), in addition to the same main effects found significant in the binomial model for this species. The major contributors to explaining a total of about 21% of the overall variability

in the data were due to the assemblage (9.1%), year (5.6%), and depth (2.2%) and also to the first-order interaction term of latitude and season (2.4%).

• BLUE WHITING

(i) $\pi_{ijkdlh} \sim \beta_0 + Y_i + S_j + A_k + D_d + L_l + \cosin(H)_h + D_d \times L_l + \varepsilon_{(.)}$

(ii) $\eta_{ijkdhl} \sim \beta_0 + Y_i + A_k + D_d + \cosin(H)_h + L_l + (D_d)^2 + A_k \times \cosin(H)_h + \varepsilon_{(.)}$

where the meaning of summands is as described for horse mackerel models.

About 50% of the total variability in the presence/absence of blue whiting was explained by the logistic model (Table 1). The assemblage explained a major proportion (43.2%), followed by depth (2.1%) and year (1.6%). These terms were all highly significant (Table 1). This model included the significant first order interaction term of *depth* and *latitude*. While *year* and *assemblage* were also significant in the gamma model such was not the case of the season term (Table 2). In the gamma model depth was included as a second order polynomial to account for the rise and fall of positive catch rates of blue whiting with depth, as detected previously by EDA. In combination, depth terms accounted for the greatest amount of explained variability in the gamma model (10.3%). The interaction between hour and assemblage was significant in the gamma model and explained about 2% of the total variability (Table 2).

Table 2. Deviance tables for horse mackerel, blue whiting, and hake gamma models (amount of positive catch). The estimates of the dispersion parameters are 0.86 (horse mackerel), 0.58 (blue whiting), and 0.25 (hake). Significances of terms are marked as “****” ($p < 0.001$), “***” ($p < 0.01$), and “**” ($p < 0.05$); “depth⁰” and “latitude⁰” denote quadratic terms of order “0” of the depth and latitude covariates.

Source of variation	D.f.	Deviance	% explained	Resid. d.f.	Resid. Deviance	
Horse mackerel						
Null				1057	1039.7	
factor (year)	10	58.1	5.6%	1047	981.6	***
factor (assemblage)	4	94.3	9.1%	1043	887.3	***
factor (season)	2	9.6	0.9%	1041	877.7	**
depth	1	22.9	2.2%	1040	854.8	***
latitude	1	5.2	0.5%	1039	849.6	***
cosin (hour)	1	5.5	0.5%	1038	844.1	*
factor (season): latitude	2	25.1	2.4%	1036	818.9	***
Total explained	21	220.8	21.2%			
Blue whiting						
Null				920	749.3	
factor (year)	10	32.9	4.4%	910	716.5	***
factor (assemblage)	4	42.2	5.6%	906	674.3	***
depth	1	26.9	3.6%	905	647.4	***
latitude	1	10.4	1.4%	904	637.1	***
cosin (hour)	1	5.7	0.8%	902	581.4	**
depth ²	1	50.0	6.7%	903	587.1	***
factor (assemblage): cosin (hour)	4	14.6	1.9%	898	566.8	***
Total explained	22	182.5	24.4%			
Hake						
Null				1534	585.2	
factor (year)	10	16.2	2.8%	1524	568.9	***
factor (assemblage)	4	67.9	11.6%	1520	501.0	***
factor (season)	2	2.5	0.4%	1518	498.5	**
depth	1	10.7	1.8%	1517	487.8	***
depth ²	1	17.8	3.0%	1515	470.0	***
depth ³	1	29.2	5.0%	1514	440.8	***
depth ⁴	1	18.8	3.2%	1513	422.0	***
latitude	1	0.1	< 0.1%	1516	487.7	
latitude ²	1	12.5	2.1%	1512	409.5	***
Total explained	22	175.7	30.0%			

• HAKE

$$(i) \pi_{ikd} \sim \beta_0 + Y_i + A_k + D_d + (D_d)^2 + (D_d)^3 + (D_d)^4 + \varepsilon_{(i)}$$

$$(ii) \eta_{ikjdl} \sim \beta_0 + Y_i + A_k + S_j + D_d + (D_d)^2 + (D_d)^3 + (D_d)^4 + L_l + (L_l)^2 + \varepsilon_{(i)}$$

where the meaning of summands is as described for horse mackerel models.

The amount of total variability explained by hake models were 22% (logistic, Table 1) and 30% (gamma, Table 2). The EDA showed that both the observed proportion of positive catch and the amount of positive catch rates of hake varied non-linearly with *depth* with two peaks within the observed depth range. Thus the depth effect was modeled as a high-order polynomial in the logistic and gamma models. In fact, *depth* (and its power terms, in aggregate) was the most important factor in the binomial model, explaining 17.2% of the total variability (Table 1), and in the gamma model (13%; Table 2). The factor *season* was only significant in the gamma model, accounting for a small proportion of the deviance explained (Table 2).

3.2 Patterns of abundance

The models fitted were used to make predictions and examine abundance patterns after first controlling for effects. As the seasonal effect was significant for both logistic and gamma horse mackerel models (Tables 1 and 2), while not for the other two species, horse mackerel abundance was compared between seasons. The seasonal effect is presented in Figure 5 where the remaining covariates were pooled by season. Mean predicted abundance (kg h^{-1}) of horse mackerel was significantly different between seasons. In the winter (28.2 ± 6.8) it was almost three times higher than in the summer (10.1 ± 1.0) and about two times higher than in autumn (13.3 ± 1.2).

Predicted temporal patterns of abundance are presented (Fig. 6 a- horse mackerel, b- blue whiting, c- hake). Predictions were pooled in a similar manner as for season, only now this factor was set to autumn, the only season always sampled along the 11-year series of surveys, and to which groundfish research surveys conducted in the Portuguese margin are most focused (Cardador et al. 1997).

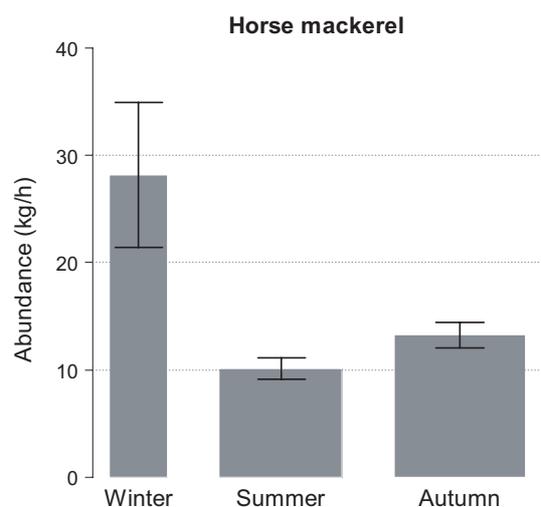


Fig. 5. Horse mackerel abundance estimated by season. Each point is the mean (kg h^{-1}), for the overall Portuguese margin, of the fitted values using the integrated logistic-gamma model. Vertical lines denote 95% confidence intervals for mean values. Bar width is proportional to the number of observations on each season.

Horse mackerel abundance hit its peak in 1993 ($38.0 \pm 8.1 \text{ kg h}^{-1}$) and was one order of magnitude lower in 1999 ($3.8 \pm 0.9 \text{ kg h}^{-1}$) (Fig. 6a). The year of 1992 provided the second highest abundance index of horse mackerel ($23.4 \pm 5.4 \text{ kg h}^{-1}$), although not significantly different than 1996 ($20.3 \pm 5.0 \text{ kg h}^{-1}$) and 1997 ($18.9 \pm 4.1 \text{ kg h}^{-1}$), as confidence limits overlap. Following the 1992–1993 and 1996–1997 peaks, abundance decreased steadily in subsequent years (Fig. 6a).

The highest abundance of blue whiting was estimated in 1991 ($96.6 \text{ kg h}^{-1} \pm 20.0 \text{ kg h}^{-1}$), yet not significantly different from 1990 ($89.0 \pm 19.8 \text{ kg h}^{-1}$), 1989 ($70.2 \pm 19.9 \text{ kg h}^{-1}$), 1995 ($65.3 \pm 14.8 \text{ kg h}^{-1}$) and 1998 ($72.7 \pm 16.6 \text{ kg h}^{-1}$) (Fig. 6b). The lowest abundances in the 11-year series were estimated for 1996 (22.4 ± 7.2) and 1997 ($21.9 \pm 7.2 \text{ kg h}^{-1}$).

Hake abundance was much less variable in time, compared to the former two species, ranging from a minimum of $6.8 \text{ kg h}^{-1} (\pm 1.2)$ in 1993 to a maximum of $15.9 \text{ kg h}^{-1} (\pm 2.8)$ in 1997 (Fig. 6c). The abundance peak of hake in 1997 was not significantly different than 1991 ($13.7 \pm 2.0 \text{ kg h}^{-1}$) and 1995 ($12.2 \pm 1.8 \text{ kg h}^{-1}$). The lowest abundance of hake was estimated in 1993 ($6.8 \pm 1.2 \text{ kg h}^{-1}$).

With the exception of 1993, in which year horse mackerel was the most abundant species, blue whiting presented the highest abundance indices, especially in 1989, 1990 and 1991 where it reached about ten and five times the relative abundance of hake and horse mackerel, respectively (Figs. 6a–c). The trends of horse mackerel and blue whiting are consistently opposed between 1991 and 1994, when the former species peaked. As for the second half of the nineties, no clear trends are discernible for blue whiting, and the same applies for hake throughout the entire series.

The individual effects of *assemblage*, *season*, *trawling hour* and *depth* upon the probability of positive catch (π), amount of positive catch rates (η^2) and abundance (μ), were analysed through plots of π against η^2 , where lines of constant $\hat{\mu} = \hat{\pi} \times \hat{\eta}^2$ are superimposed. Each predictor was allowed to

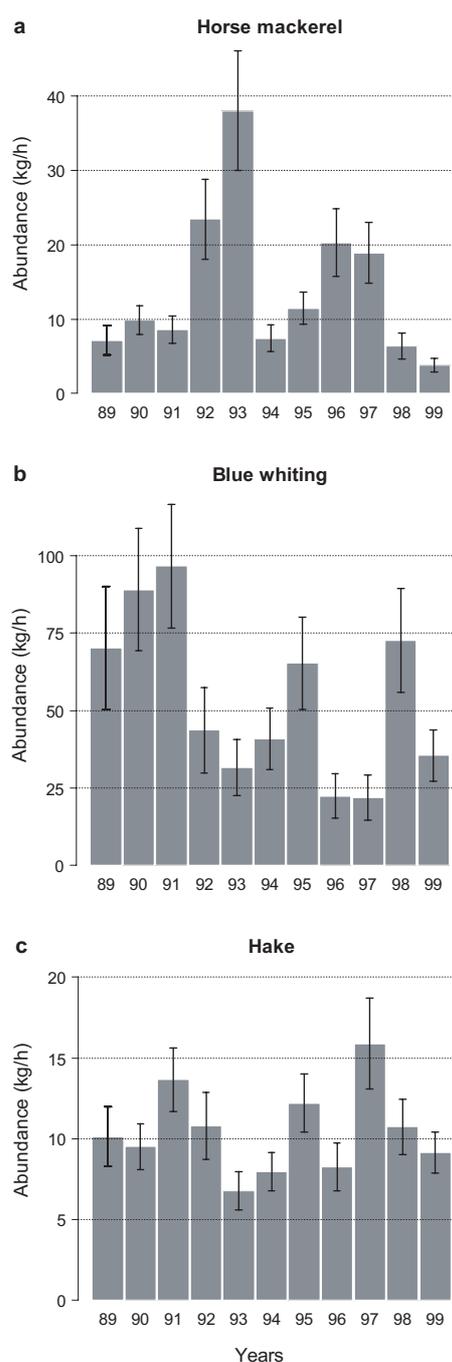


Fig. 6. Annual abundances estimated for the autumn season. Each point is the mean (kg h^{-1}), for the overall Portuguese margin, of the fitted values using the integrated logistic-gamma model. Vertical lines denote 95% confidence intervals for mean values. a) horse mackerel; b) blue whiting; c) hake.

vary while keeping the other predictors fixed. Most estimated probabilities of catching hake were close to 1 and overlapped among assemblages. Furthermore, hake trends along the η^2 axis (positive catch rates) did not vary substantially for some predictors; the plots for this species were not informative and, therefore, are not presented.

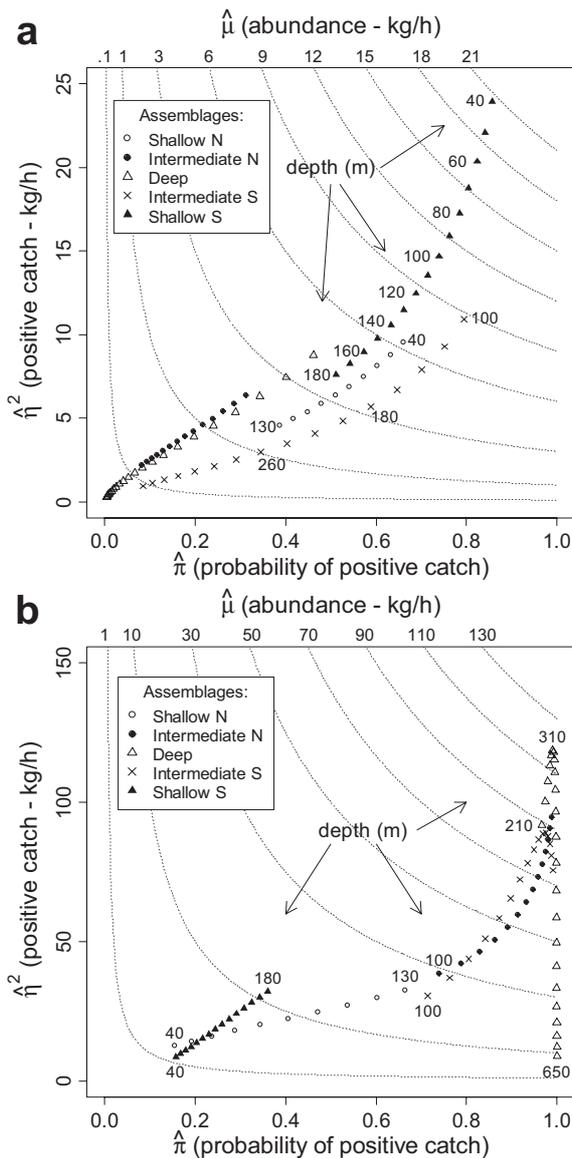


Fig. 7. Estimated effects of depth upon the probability of positive catch (π), amount of positive catch rates in weight (η^2) and abundance (μ), shown as contour lines whose values are on the top scale, by assemblage (different dot marks). The remaining predictors are fixed as follows: year = 1999; hour = 12 am; latitude = mean latitude of each assemblage. The numbers inside the plot denote the depth in meters at which estimates are obtained. a) horse mackerel; b) blue whiting.

The estimated effects of depth and assemblage are presented (Fig. 7 a- horse mackerel; b- blue whiting). The year was set to 1999, trawling hour to 12 am and the latitude to the mean latitude of each assemblage (SN and IN: 41°N, D and IS: 38°N, SS: 37°N). Depth varied according to the bathymetry of the assemblages (Sousa et al. 2005), namely, 40–130 m (SN), 100–230 m (IN), 210–650 m (deep), 100–400 m (IS) and 40–180 m (SS), by 10-m intervals in the shallow and intermediate northern assemblages and by 20-m intervals in the intermediate southern and deep assemblages, and season was set to autumn.

Horse mackerel is most abundant in the shallow southern assemblage but is also relatively abundant in the shallow northern and intermediate southern assemblages (Fig. 7a). Both the probability of catch and the amount of positive catch are negatively associated with depth in all assemblages; regarding the shallow southern assemblage, as depth increases (by 10-m depth intervals) from shallow grounds (40 m) to the lower depth boundary of the assemblage (180 m), the probability of catch reduces from about 0.82 to about 0.5. As the amount of positive catch also reduces, the abundance of horse mackerel decreases from about 21 kg h⁻¹ (40 m) to about 4 kg h⁻¹ (180 m) (Fig. 7a). This same reduction pattern also applies to the other assemblages. In the shallow northern assemblage abundance reduces from about 6 kg h⁻¹ at 40 m depth to 2 kg h⁻¹ at 130 m, and in the intermediate southern assemblage from 9 kg h⁻¹ at 100 m depth to 0.1 kg h⁻¹ at 400 m (Fig. 7a). The probability of catching horse mackerel is high (0.8) in the upper depth limit (100 m) of this latter assemblage with, however, lower positive catches comparing to the shallow southern assemblage.

Blue whiting is most abundant in the deeper assemblages (deep, intermediate northern and southern) and much less abundant in shallow (northern and southern) assemblages (Fig. 7b). In the deep assemblage, where abundance vary by one order of magnitude (10 kg h⁻¹ at about 650 m to 120 kg h⁻¹ at 310 m), the probability of catch remains near 1. In the intermediate southern assemblage the probability of catch varies from about 0.7 at the upper depth limit of the assemblage (100 m) to about 0.95 from 300 m depth on (Fig. 7b). With the exception of the deep and intermediate southern assemblages, both probabilities of positive catch and the amount of positive catch rates are expected to be higher at greater depths. Such is the case of the intermediate northern assemblage where the estimates increase steadily from the upper depth limit of the assemblage at 100 m (probability = 0.7 and abundance = 30 kg h⁻¹) down to 240 m (probability ~ 1 and abundance = 90 kg h⁻¹). However, in the deep and intermediate southern assemblages, abundance increases from lower depths to about 300 m deep, where it peaks for both assemblages, decreasing at greater depths (Fig. 7b). Being much less abundant in shallow assemblages, the probability of catching blue whiting at ~100 m depth is about twice as high in the SN assemblage (0.5), compared to the SS assemblage (~0.25), although positive catch rates remain similar (Fig. 7b). This suggests that near shore, blue whiting has a greater tendency to school to the south than to the north.

The effect of trawling hour, assemblage and season on horse mackerel estimates is presented (Fig. 8 a- winter and b- autumn). As trends in the summer plot did not differentiate substantially from those in the autumn, the former plot was omitted. The year was set to 1993 because there were only winter surveys in 1992 and 1993, and the latitude and depth are means by assemblage (SN: mean depth is 72 m; IN: 167 m; deep: 467 m; IS: 210 m; SS: 95 m). Trawling hour was set to vary from 6 am to 9 pm at 1-hour intervals.

The maximum estimates of abundance are obtained at 12 am in all assemblages and seasons. This translates to a significant negative correlation between the cosine of trawling hour and abundance, as the cosine function equals -1 (its

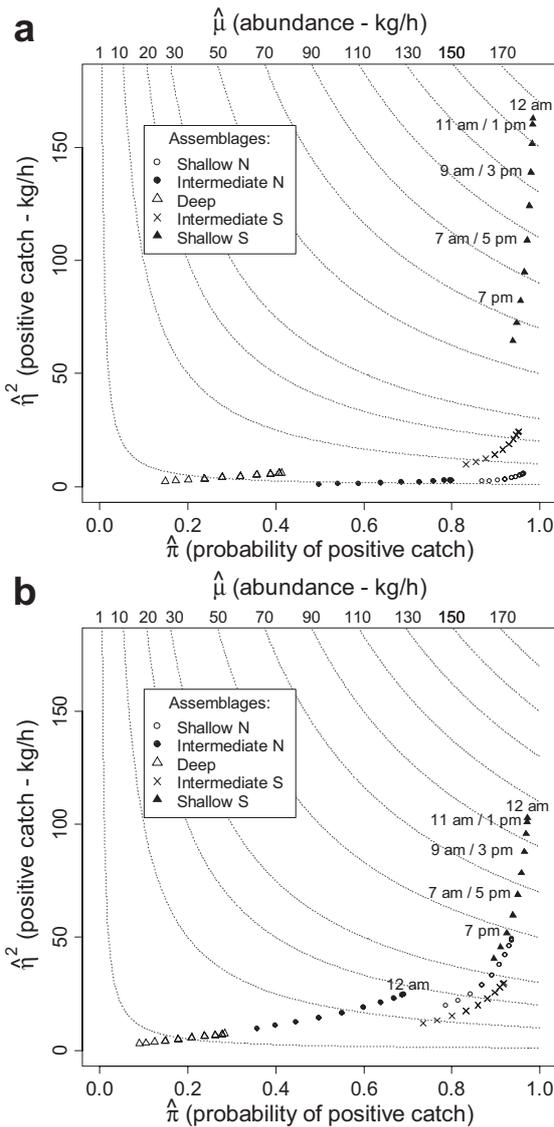


Fig. 8. Estimated effects of the trawling hour upon π , η^2 and μ of horse mackerel, by assemblage and season: a) winter; b) autumn. The remaining predictors are fixed as follows: year = 1993; depth = mean depth of each assemblage; latitude = mean latitude of each assemblage. The information inside the plot denote the trawling time at which estimates are obtained; trends are similar to all assemblages with the daily maximum at 12 am, as pointed up for the shallow southern assemblage (a, b).

minimum) at half a complete cycle (coincident with 12 am). Abundance estimates then decrease symmetrically around noon, with the estimate at 11 am equalling the one at 1 pm and so on (Fig. 8a).

The abundance of horse mackerel is significantly higher in the winter compared to autumn (Fig. 5). This difference seems to be mostly accounted by variation in the shallow southern assemblage, where maximum abundance at 12 am reduces from about 160 kg h⁻¹ in the winter (Fig. 8a) to about 100 kg h⁻¹ in the autumn (Fig. 8b). In fact, in the winter, horse mackerel is almost absent from assemblages other than the shallow southern (Fig. 8a). In the northern assemblages (shallow and

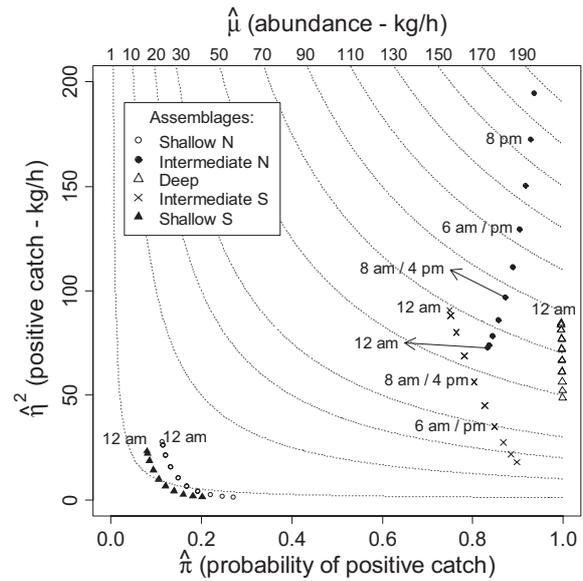


Fig. 9. Estimated effects of the trawling hour upon π , η^2 and μ of blue whiting, by assemblage. The remaining predictors are fixed as follows: year = 1993; depth = mean depth of each assemblage; latitude = mean latitude of each assemblage, season = autumn. The information inside the plot denote the trawling time at which estimates are obtained; trends are similar to all assemblages with the daily maximum at 12 am, as pointed up for the intermediate southern assemblage, with the exception of the intermediate northern assemblage where an opposite trend is detected.

intermediate) an opposite trend takes place, with higher abundance in the autumn. In the shallow northern assemblage, the maximum abundance, at 12 am in the winter, is about 5 kg h⁻¹ (Fig. 8a) whereas in the autumn, it reaches almost 50 kg h⁻¹ (Fig. 8b), one order of magnitude higher. As for the intermediate northern assemblage, maximum abundance increases from about 1 kg h⁻¹ in the winter (Fig. 8a) to almost 20 kg h⁻¹ in the autumn (Fig. 8b). The probability of positive catch remains similar between seasons in the intermediate northern assemblage, while in the shallow northern assemblage its range is wider in the autumn (Fig. 8a) compared to the winter (Fig. 8b).

The effect of trawling hour and assemblage on blue whiting estimates is presented in Figure 9. The remaining covariates were controlled as in Figure 8b. Blue whiting is much more abundant in deeper assemblages, especially in the intermediate northern assemblage, where abundance ranges from about 60 kg h⁻¹ at 12 am to 180 kg h⁻¹ at 9 pm, and is almost absent from shallow assemblages (Fig. 9). The probability of positive catch does not change much in the deeper assemblages, remaining quite high (>0.7), in particular in the deep assemblage (~1). In all assemblages, to the exception of the IN assemblage, maximum estimates are obtained at 12 am. In the IN assemblage, the peak takes place at 9 pm, as the overall trend is shifted compared to the other assemblages (Fig. 9).

4 Discussion

Traditionally, zero values have been a problem when analysing marine survey data. In our data set, for example,

about half the observations for blue whiting was zero. The integrated methodology applied here, however, proved to address this question properly. The amount of deviance explained by the models lies within the range of values obtained in similar studies. Gamma models fitted to the catch rates of the Mediterranean swordfish, accounted for 15 to 35% of total variability (Tserpes et al. 2004). In another example, Ye et al. (2001), using data from the eighties and nineties from the Kuwait driftnet fishery, accounted for 23.6 to 29.5% of variability concerning presence / absence of pelagic fish species and 36 to 46% for the positive catch rates of the same species.

The assemblage factor explained most of the variability in catch rates, especially for horse mackerel and blue whiting. Although these two species contributed themselves to define the assemblages, it should be kept in mind that such definition was based upon data matrices containing tens of different species, usually 40 to 50, and that the data were previously log-transformed in order to reduce the influence of the most abundant species (Sousa et al. 2005, 2006). Uncertainty may arise at a first glance by stating that the assemblages are simultaneously a function of geography and depth and that this could cause overspecification in the model. However, it should be noted that depth and latitude also vary within assemblages. In addition, overspecification would only occur if, in a given model, the factor “assemblage” could be expressed exactly as a combination of latitude and/or depth, or other predictors, which is not the case. Regarding main effects, the analysis shows that depth was the most important factor to account for presence and biomass of hake and the second most important for horse mackerel and blue whiting.

In the northeast Atlantic, horse mackerel commonly occurs over the continental shelf (Abaunza et al. 2003), and the distribution of this species on the Portuguese continental margin is no exception. It is by far most abundant close to shore, in the shallow (northern and southern) assemblages, which themselves comprise a major proportion of the Portuguese shelf. The probability of positive catch, amount of positive catch, and abundance of horse mackerel, decrease with increasing depth. Ontogenetic migrations of horse mackerel are well documented with eggs and larvae occupying the first 50 m of the water column (Coombs et al. 2001) and fish moving deeper as they grow (Sousa et al. 2005) as a result of changes in feeding habits (Sánchez 1993; Silva et al. 1997; Cabral and Murta 2002).

Horse mackerel estimates were highest in 1992 and 1993, years when winter surveys took place. Such peaks probably resulted from a favourable combination of both season and year. Horse mackerel spawns in the wintertime (Santos et al. 2001), forming dense schools near the bottom which are available to the bottom trawl. Similar findings concerning higher aggregation in the winter had also been previously reported in the Eastern Atlantic by Polonsky (1965 in Abaunza et al. 2003). Furthermore, a relatively strong recruitment was reported in 1991 (Santos et al. 2001), initiating a cohort that in 1993 was two years old, in agreement with an estimated mean length of about 15 cm for horse mackerels caught in the shallow southern assemblage, in the same year and season (Sousa et al. 2005).

From the winter of 1993 to the autumn of the same year, the models estimated a decrease in abundance of horse

mackerel in the shallow southern assemblage, quite the opposite of what happened in the shallow and intermediate northern assemblages. As the northern and southern parts of the Portuguese continental margin have different upwelling conditions (Sousa et al. 2006) this might suggest a northward migration of individuals over the shelf in response to the rather abnormal water cooling conditions reported by Santos et al. (2001), due to strong upwelling between 1992 and 1995. Migration of horse mackerel is well documented (e.g., Macer 1977; Rückert et al. 2002) in relation to water temperature (Abaunza et al. 2003), among other factors.

Horse mackerel seems to migrate downwards at daytime, becoming more available to bottom trawling, and then moving upwards at dawn. As there was no sampling by night, one cannot be sure that the fish remained high in the water column then, although this is a likely possibility. Previous findings on vertical migrations of horse mackerel have been described (Macer 1977), in response to prey displacements which horse mackerel feed upon. Jardas et al. (2004) have reported higher feeding intensity of horse mackerel by nighttime, supporting the trophic nature of these migrations.

Blue whiting is both more abundant and more likely to be caught in the deep and intermediate assemblages, being absent from shallow assemblages. Such preference for deeper grounds is in agreement with previous reports by Bailey (1982), Silva et al. (1996) and Sousa et al. (2005). The unique curvature of blue whiting abundance with depth (Fig. 7b), in the deep and intermediate southern assemblages, is most probably related to the fact that in these assemblages depth varies within a range that accommodates a rise and fall in abundance: the empirical distribution of blue whiting catch rates observed in these surveys shows that it reaches a peak at about 300–400 m being, however, always present down to much greater depths.

Schools of blue whiting gather near the bottom by day when abundance is maximum and keep away from the bottom in the early morning and late afternoon. Such daily vertical displacements, common to several primary consumers including horse mackerel, were also reported for blue whiting by Bailey (1982). Acoustic surveys carried out on the Portuguese margin in the summer of 1983 (Silva et al. 1996), provided evidence of pelagic schools of blue whiting in deep layers (200–400 m) during daytime, moving close to the surface at night and returning to the bottom at sunrise. These vertical displacements appear to be related to the vertical migration of macrozooplankton deep scattering layers (DSL) (Silva et al. 1996). Acoustic surveys carried out in the spring of 1998, also showed similar vertical activity of blue whiting associated with the DSL (IPIMAR 2000). The trophic interaction with zooplankton was further confirmed by analyses of stomach contents (IPIMAR 2000). An exception to this pattern was detected in the intermediate northern assemblage where blue whiting leaves the bottom layers early in the morning up until about midday, gradually returning to the bottom before the late afternoon. We are not aware of any straightforward factors which might explain this behaviour. However, there are substantial differences in productivity between the northern and southern parts of the Portuguese margin. To the north, the upwelling is more intense and persistent and the shelf morphology is much more

regular compared to the south which has shorter food chains composed by different organisms (Cunha 2001). These differences are likely to be influential to a zooplankton feeder such as blue whiting.

According to Reid (2001), the warmer and more saline waters of the Iberian Peninsula are nursery grounds for blue whiting, accounting for its higher abundance there, compared to the whole NE Atlantic. At the smaller scale of the Portuguese margin, located at the lower limit of the species distribution, the model suggests that blue whiting is slightly more abundant to the north than to the south, as its abundance is especially high in the intermediate northern assemblage. The relationship between such regional differences and overall migrations is unclear. In the North Atlantic, blue whiting is known to have important seasonal feeding and spawning migrations ranging over a much wider latitude than the Portuguese shelf (Bailey 1982; Carrera et al. 2001). However, no clear relationship has been reported between blue whiting movements at the southern limits of its distribution and post-spawning migrations (Carrera et al. 2001).

The ubiquity of hake on the Portuguese margin, previously reported by Sousa et al. (2005), was probably the reason why models for this species were somewhat less parsimonious and informative than those for horse mackerel and blue whiting, including significant quadratic terms that are difficult to interpret from an ecological point of view. Still, the inclusion of nonlinearity in the models was based on empirical knowledge of the distribution of the species; peaks of both presence and positive catch of hake were observed at about 120 and 280 meters deep, with a local minimum in between and decreasing after the second peak, in good agreement with a similar description by Cardador (1995). Hake catch rates increase to the north until 38°45' (Lisbon latitude) and decrease afterwards. This could be explained by reports (Cardador et al. 2000) that hake juveniles tend to concentrate at the mouth of the Tejo river (Lisbon latitude). Nonlinearity in covariates can be dealt with by our approach, although it has been suggested (Maunder and Punt 2004) that discretizing the respective covariate may be preferred. Still, we find it difficult to define discrete boundaries for depth, as artificial categories may cover up underlying trends in the data. Since hake is known to migrate to deeper grounds as it grows (Macpherson and Duarte 1991; Sousa et al. 2005) future studies should include information on age as an additional predictor to improve models parsimony, and thus reduce the confounding effect caused by the species ubiquity.

Research surveys conducted by IPIMAR on the Portuguese margin for more than 25 years, have been the most powerful tool to understand the underlying determinants of the distribution and abundance of the most important demersal species in the area. The adoption of a fixed survey sampling design in the beginning of the nineties, however, has not been matched by the adoption of appropriate statistical estimation procedures.

We present an innovative model-based approach to estimate species abundance that addresses the sparse nature of the data and is based upon environmental variables regularly collected during the surveys. This methodology provides estimates of abundance trends and insight into species distribution and behaviour in response to the environment.

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