

Alternative usage of common feeding grounds by large predators: the case of two hakes (*Merluccius hubbsi* and *M. australis*) in the southwest Atlantic

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Abstract

Monthly variations in spatial and depth distributions, sex ratios, and maturity status in two species of hakes, *Merluccius hubbsi* and *M. australis*, were analysed in an area where their ranges overlap spatially on the shelf and slope around the Falkland Islands, and in international waters at 45–47° S (High Seas), using data collected by scientific observers on commercial fishing vessels. A variety of exploratory analyses were carried out on the raw data before patterns were quantified using generalised additive models. Both species use the areas studied as their feeding grounds. *M. australis* occur mainly on the Falkland shelf south of 51° S, whereas *M. hubbsi* is widely distributed throughout both the Falkland and High Seas shelf areas. Preliminary schemes of the seasonal migrations of both hakes in Falkland waters and on the High Seas are suggested and discussed. *M. hubbsi* and *M. australis* are found to be strongly segregated, both spatially and temporally, on their common feeding grounds, thus avoiding potential inter-specific competition for food resources.

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Résumé

Usage alterné des zones de nutrition par de grands prédateurs : le cas de deux merlus (*Merluccius hubbsi* et *Merluccius australis*) en Atlantique Sud-Ouest. Les variations mensuelles de la répartition spatiale, et en fonction de la profondeur, ont été étudiées chez deux espèces de merlus *Merluccius hubbsi* et *Merluccius australis*, ainsi que celles du sex-ratio, et du stade de maturité sexuelle, là où leurs zones de distribution se chevauchent sur le plateau et le talus continental autour des îles Malouines, et dans les eaux internationales à 45–47° S (Hautes Mers), en utilisant des données collectées par des observateurs scientifiques sur des bateaux de pêche commerciale. Une grande variété d'analyses exploratoires a été menée sur les données brutes, avant que des schémas puissent être déterminés au moyen de modèles additifs généralisés. Les deux espèces utilisent ces zones comme zones de nutrition. *M. australis* se trouve principalement sur le plateau des Malouines, au sud du 51° S, tandis que *M. hubbsi* est largement réparti sur les zones du plateau continental des Malouines et de Hautes Mers. Des schémas préliminaires de migration saisonnière des deux merlus sont proposés et discutés. *M. hubbsi* et *M. australis* seraient fortement séparés, à la fois dans l'espace et dans le temps sur leur commune zone de nutrition, évitant ainsi une compétition interspécifique potentielle, en ce qui concerne les ressources alimentaires.

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Keywords: Distribution; Hakes; *Merluccius hubbsi*; *Merluccius australis*; Southwest Atlantic

1. Introduction

Hakes (Merlucciidae) are abundant nektonic fishes inhabiting shelf and continental slope waters of the Atlantic Ocean,

eastern Pacific, and south-western Pacific off New Zealand (Cohen et al., 1990). These voracious predators make diurnal vertical migrations concentrating near the bottom during the daytime and ascending into pelagic layers at night (Inada, 1981). Most hake species make seasonal spatial migrations moving inshore, and to lower latitudes, to spawn in summer

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and moving back offshore, and to higher latitudes, to their feeding grounds in winter (Pitcher and Alheit, 1995).

Two hake species occur on the shelf and slope of the southwest Atlantic: southern hake *Merluccius australis* (Hutton, 1872) and common hake *Merluccius hubbsi* (Marini, 1933). Both hakes are subject to traditional trawling and longline fisheries in Chile, Argentina, Uruguay and the Falkland Islands (Csirke, 1987). Southern hake occur along the Chilean coast in the eastern Pacific south of 40° S, around Cape Horn, and on the Patagonian Shelf north to 49° S. Common hake, in contrast, inhabit only Atlantic waters off South America: the Patagonian and Argentine Shelves between 28° and 54° S (Cohen et al., 1990). Little information is available on the variation in population structure across the species' range and on the seasonal migrations undertaken by hakes. Direct studies of migrations have proven to be difficult: tagging experiments have resulted in high mortality of tagged fish (Jones, 1974). Migrations have, therefore, only been studied indirectly by analyses of the seasonal distribution of the catch and effort of the hake fleet that target hake throughout the year and follow the seasonal movements of hake schools on the shelf (Podesta, 1990).

The patterns of seasonal migration in the common hake, *M. hubbsi*, have only been studied in detail in its northern populations (Podesta, 1990; Aubone et al., 2000), which move in autumn from their spawning grounds (inshore waters between the San Matias and San Jorge Gulfs) northwards to their feeding grounds on the shelf edge near the frontal zone between the Brazil and Falkland Currents. Here, they over-winter before returning to the spawning grounds in spring (Podesta, 1990). Movements of the southern populations of common hake are much less clear. It is assumed that they migrate, from spawning grounds in the San Jorge Gulf, offshore to the east and south-east and over-winter on the southern part of the Patagonian Shelf (Otero, 1986).

Based on studies of parasitological markers and morphometry, George-Nascimento and Arancibia (1994) proposed that southern hake, *M. australis*, migrate from their inshore spawning grounds at 49° S in the Pacific along the Chilean coast to the south-east, negotiate Cape Horn, and enter feeding grounds on the southern part of the Patagonian shelf. Thus, the shelf and continental slope waters around the Falkland Islands are used as feeding grounds by both *M. hubbsi* and *M. australis*.

The primary aim of this study is to investigate spatial and temporal patterns, in the distributions of the two hake species, on their common feeding grounds on the shelf around the Falkland Islands and in international waters at 45–47° S, and to develop a conceptual model of their seasonal movements. Catch data from commercial vessels are used to investigate the species, distributions, whilst data on changes in the biological status help to clarify the reasons for observed changes in distribution.

2. Materials and methods

2.1. Data sources

Since the introduction of regulated fisheries around the Falklands in 1987, all licensed vessels fishing in the Falkland Islands Interim Conservation and Management Zone (FICZ) and Falklands Outer Conservation Zone (FOCZ) have submitted daily catch reports to the Falkland Islands Fisheries Department (FIFD). In addition, Falklands registered vessels report their catches when they are working outside the Falklands zones. Historically, trawlers fishing in the FICZ have reported just the total catch of both hakes together making it impossible to separate by species (Tingley et al., 1995). Reporting of pooled catches is a common practice in hake fisheries in regions where two (*M. capensis* and *M. paradoxus*, South Africa) or three (*M. merluccius*, *M. senegalensis* and *M. polli*, northwest Africa) hake species are encountered in catches (Punt, 1992; Martos and Peralta, 1995). As a result of this pooled reporting of the total catch of hakes by commercial trawlers, only data collected by scientific observers placed on board commercial fishing vessels have been used in this study. Data from two observer programmes were available. FIFD places observers on a subset of commercial fishing vessels licensed to fish in the Falklands zones. The Instituto Español de Oceanografía (IEO) places observers on a subset of Spanish flagged vessels fishing in the southwest Atlantic.

Data from FIFD observers were available from January 1988 to February 2002. During this period, data were collected from 12 489 demersal trawls. *M. hubbsi* was recorded in 5625 of these hauls and *M. australis* in 2150. The IEO data set comprised 5537 demersal trawls with hake catches in the period February 1989–December 1999. *M. hubbsi* was recorded in 5469 trawls and *M. australis* in 818.

M. australis and *M. hubbsi* can be difficult to distinguish (Cousseau and Cotrina, 1980). Preliminary analysis of the length data suggested that a significant proportion of identifications of *M. australis* by IEO observers may be doubtful. Although this issue has been addressed recently by the IEO observer programme, the analyses of *M. australis* presented here use only data from FIFD observers. Furthermore, records of *M. australis* from 102 trawls analysed by FIFD observers were also excluded due to uncertainties in identification. Two sets of data on common hake *M. hubbsi* (FIFD and IEO) were used in the present study as they covered different localities: Falkland Zones (mainly FIFD) and international waters (mainly IEO).

The trawl fishery for hakes, both in the FICZ and in the High Seas region (i.e. in international waters between 45° and 47°30' S), takes place throughout the year. Trawls are usually several hours in duration. The stretched mesh size in the trawl codend for vessels working within the FICZ is restricted to 90 mm by license conditions (FIFD, 2001).

Both FIFD and IEO observers typically sampled two trawls a day, recording catch weight by species together with

the trawl start position and average trawling depth. Length-frequency samples were taken when possible comprising a random sample of about 100 specimens (or the total catch if there were less than 100 fish in a given trawl). Each individual was measured (total length, to the nearest 1 cm below) and its sex recorded. FIFD observers also recorded the maturity of specimens in length-frequency samples using an eight-stage maturity scale modified from the seven-stage Nikolsky (1963) scale with stage III split into two stages (early and late maturation). IEO observers used a five-stage maturity scale and recorded maturities during size stratified sampling only. Analysis of maturity presented here used only FIFD observer data, as it was impossible to match the two sets of maturity data.

The vessels on which observers are placed may be subject to license conditions that restrict the species that may be targeted. Within the Falklands zones there are fisheries for the longfin squid *Loligo gahi*, shortfin squid *Illex argentinus*, skates and rays, and finfish. Some finfish licensed boats are restricted from targeting hakes, and certain areas are closed to certain license types. We have considered only demersal trawls, as the gear type used is broadly similar across the fleets. In the analyses of spatial and depth distributions we have used data from all demersal trawls irrespective of license type. Data from research trawls carried out by the FIFD were also included.

2.2. Analyses of hake distributions

A variety of visualisation techniques were used to investigate the raw data. Maps were constructed by plotting trawl-by-trawl CPUE. This was chosen in preference to presenting gridded data for a number of reasons. More precise location of catches allows better comparison with features such as bathymetry, and both the average catch levels, and catch variability, can be assessed from the same maps. The location of trawls without hake catches recorded by FIFD observers were included to show the overall sampling effort in a particular month. Preliminary analyses showed little inter-annual variation in seasonal distributions, and it was decided to pool the data gathered over the study period.

To allow a quantitative comparison of monthly trends in the relative abundance of the two species in different regions the data were split geographically. For *M. australis* data were restricted to the Falklands zones south of 47.5° S and were split into quadrants, north and south of 51° S, and east and west of 60° W. For *M. hubbsi* three regions were considered: the High Seas region (44.5–47.5° S), and the northern (47.5–51° S) and southern (south of 51° S) parts of the Falklands zones. For all trawls where hake were present the natural logarithm of CPUE (kg h^{-1}) was plotted for each month using notched boxplots: where the notches do not overlap, there is a significant difference in the medians at the 95% level (McGill et al., 1978).

The depth distribution of the two hakes was assessed using the FIFD data. The proportion of all observed trawls with a

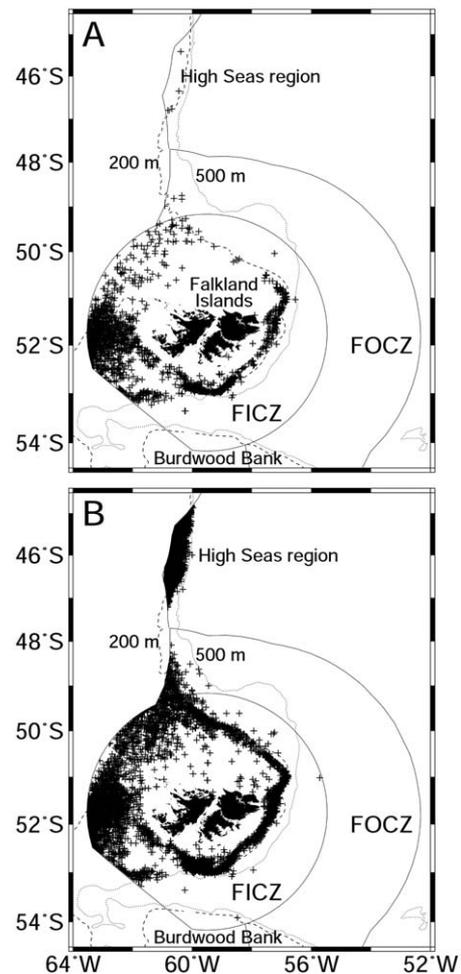


Fig. 1. Trawl locations with non-zero catches of southern hake *M. australis* (A, FIFD data only) and common hake *M. hubbsi* (B, FIFD and IEO data combined).

non-zero catch of each hake species was calculated for 50-m depth classes. The mean CPUE of each species was calculated for the same 50-m depth classes including both zero and non-zero hake catches. The co-occurrence of the two hake species was assessed by calculating the proportion of all trawls where both species were taken.

Following these exploratory analyses, generalised additive models (GAMs) were used to quantify the presence and abundance of the two hakes. The two-stage Delta-Gamma or Delta-Lognormal approach (Stefánsson, 1996 and references therein) was employed. This involves first fitting a model with a binomial response to describe the presence/absence of each species of hake in the trawls, then fitting a second model, with a Gamma or Lognormal response, to model the CPUE of hake in those trawls where they occurred. The GAMs included the following explanatory variables: smooth functions of spatial position and depth, and factors for year, month and license type. As license type was only applicable to trawls from the Falklands zones, a pseudo-license type was assigned to research and high seas trawls. We consider spatial position to be a two-dimensional smooth function of latitude and longitude, following Bowman and Azzalini (1997).

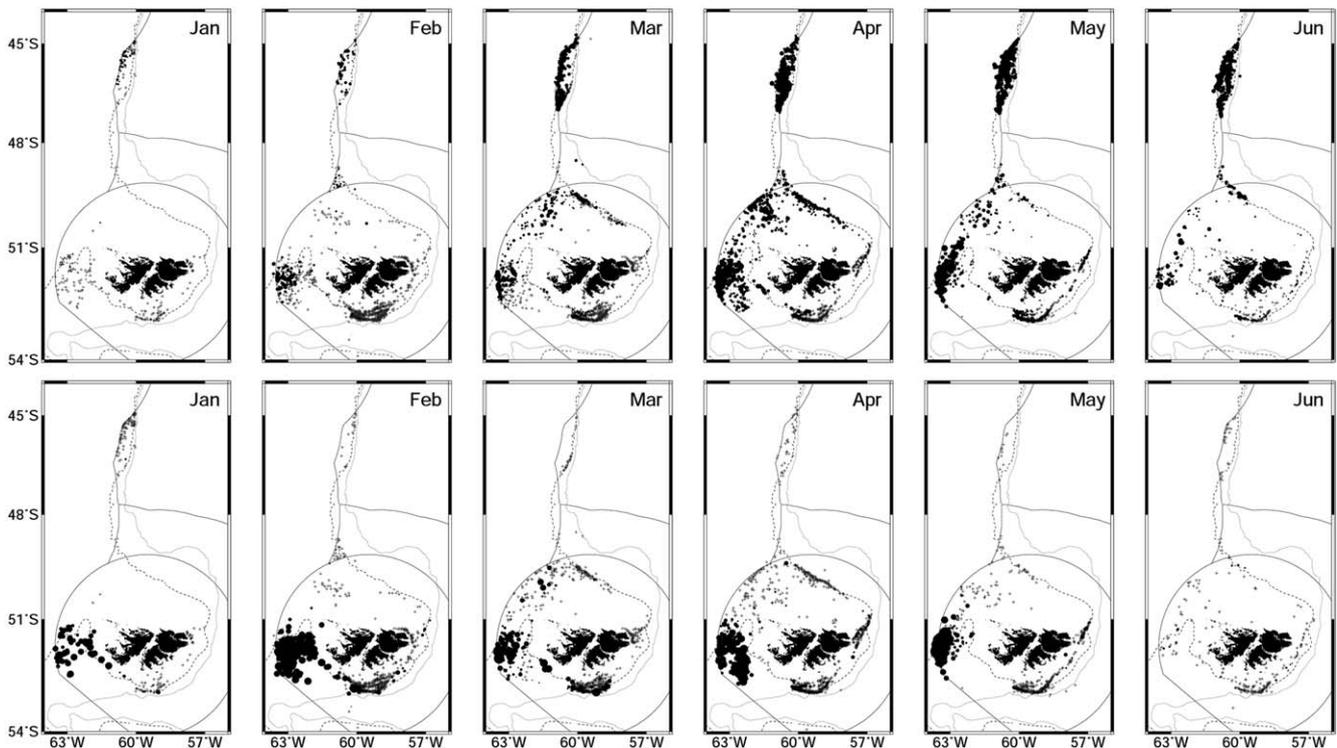


Fig. 2. Monthly distributions of haul-by-haul CPUE (catch per unit effort) of *M. hubbsi* (above) and *M. australis* (below) using FIFD observer data aggregated over the period 1988–2002 (black circles). The circle diameter is proportional to the cube root of CPUE (kg h^{-1}), the scaling factor is three times larger for *M. australis* than *M. hubbsi*. Trawls without catches of hakes are shown as crosses.

GAMs were fitted using the version 0.8.6 of the mGCV package (Wood, 2000) in the version 1.6.1 of the R statistical environment (Ihaka and Gentleman, 1996). This package fits the GAMs using Generalised Cross Validation (GCV) or an Un-Biased Risk Estimator (UBRE), and the decision, on whether to retain a particular explanatory variable in the model, was made on the basis of comparing the GCV/UBRE score with and without the variable. Parametric, rather than smooth, forms of some variables were also considered.

2.3. Analyses of biological trends

Overall length-frequency distributions were constructed using data pooled over all years. For *M. australis* only the FIFD observer data were used: length-frequency samples were available from 329 trawls with a total of 9479 individuals sampled. FIFD and IEO data were pooled to construct separate distributions for *M. hubbsi* in the FICZ (1430 trawls/94 683 individuals sampled) and in the High Seas region (1038 trawls/109 396 individuals sampled). GAMs were used to investigate differences in size by sex, area, and year.

Sex ratios were estimated on a monthly basis. For trawls where more than 20 individuals were sexed, GAMs were again used to explore the trawl-by-trawl variation in sex ratio in relation to month, year, and trawl depth. The proportion of females in a trawl sample was modelled, using a logit link function.

The monthly distribution of maturity stages was calculated, using the FIFD random samples only, for both *M. australis* and *M. hubbsi*.

3. Results

3.1. *Merluccius australis*

3.1.1. Distribution

M. australis occurred in all areas sampled by FIFD observers over the period 1988–2001, with the majority of records coming from the deeper shelf (200–500 m) in the southwest of the FICZ (Fig. 1a). *M. australis* was also sometimes encountered over the shallower shelf in the north-west of the FICZ and around the 200-m contour, including some recorded occurrences in international waters as far north as 45° S.

The monthly pattern of CPUE demonstrates that the distribution of *M. australis* within the FICZ varies through the year (Figs. 2 and 3). Trawlers in January found *M. australis* mainly to the west of the Falkland Islands at depths greater than 200 m. In February, CPUE increased in the southwestern part of the FICZ and *M. australis* also appeared as by-catch in south-eastern region where the fishery for *L. gahi* takes place, along the 200-m depth contour to the south and east of the Islands, and on the shelf in the north-west of FICZ. The highest CPUEs in March and April were found in trawls south of the 200-m contour in the west of FICZ. In May,

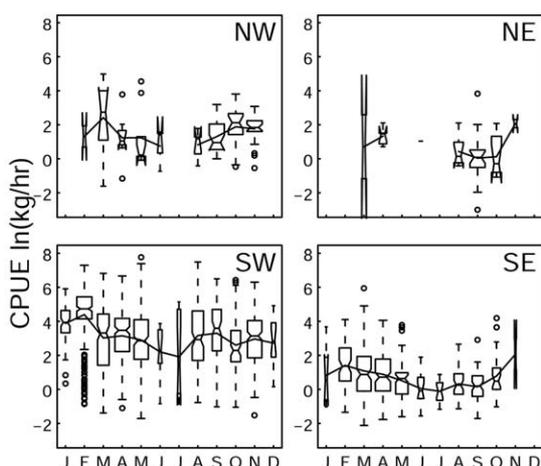


Fig. 3. Boxplots of monthly haul-by-haul CPUE ($\ln[\text{kg h}^{-1}]$) in trawls with non-zero catches) for *M. australis* in four regions of the Falklands zones: north/south of 51° S, and east/west of 60° W. The superimposed line indicates the monthly mean log CPUE.

catches were concentrated on the western edge of FICZ. *M. australis* was largely absent from trawls carried out in Falkland waters in June and July. It appeared again in trawls within FICZ in August and September with high CPUEs being recorded in the southwest of the FICZ at 53° S close to the 500-m depth contour. In October and November, CPUEs were relatively high over the deeper shelf area (>200 m) in the southwest and west of the FICZ, and CPUE also increased to the south-east and north-west of the Islands. In spite of a relatively small number of sampled trawls in December, it is apparent that *M. australis* still occurred in the western part of FICZ at this time (Fig. 2).

The distribution of *M. australis* catches by depth is bimodal with the greatest occurrence, and highest average CPUE, in trawls between 400 and 500 m depths. Southern hake occurred only rarely in trawls in shallow waters, but was fairly common in trawls at 300–350 m depths (Fig. 4a).

A series of generalised additive models were constructed for the presence of *M. australis* in trawls and its CPUE in trawls when present (Table 1). In models for the presence of *M. australis* the UBRE score indicated that license type could be eliminated and the effect of year included simply as a linear parametric term. The smooth terms in this model (Fig. 5a) demonstrate that *M. australis* is much more likely to be encountered in trawls in the southern, and particularly the south-western, part of the region, and that it is more likely to occur in deeper trawls. The effect of month is less strong, indicating a decreased likelihood of occurrence in trawls after mid-April, and only a slight increase in the latter part of the year.

All explanatory variables were retained in the model of CPUE in trawls where *M. australis* occurred. Use of lognormal distribution proved more satisfactory than a gamma distribution for the CPUE data. The effect of position and depth on *M. australis* CPUE was similar to the effect on its presence (Fig. 6a). CPUEs are higher in the south-western part of the region studied and at depths around 450 m. The

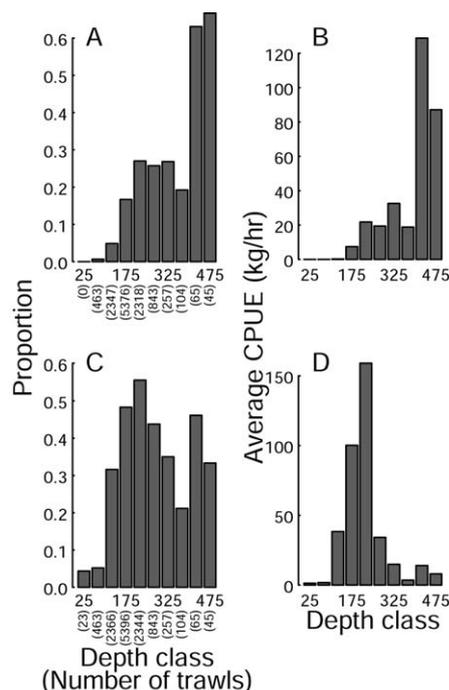


Fig. 4. Proportion of all bottom trawls recorded by FIFD observers with catches of southern hake *M. australis* (A) and common hake *M. hubbsi* (C). Trawls are grouped in 50 m depth classes labelled at the class midpoint. The total number of trawls in each depth class is given in parenthesis. The depth distribution of average CPUE of *M. australis* and *M. hubbsi* over all observed trawls is given in (B) and (D), respectively.

smooth fit representing the effect of month suggests a general decrease in CPUE through the year, whilst the effect of year suggests a slight overall decrease in abundance over the period 1998–2002.

3.1.2. Length-frequency composition

The length distribution of both sexes of southern hake from the pooled samples was essentially unimodal with a slight left skew (Fig. 7a). The modal size of sampled females was slightly larger than that of males (73 and 71 cm, respectively). A small mode of 42 cm was evident in the male length distribution. No fish smaller than 38 cm were caught. A GAM expressing length in terms of sex and a smooth function of year accounted for 15.5% of the null deviance in size and demonstrated that the difference between the size of male and female *M. australis* in the Falklands data were not significant ($P = 0.82$). Inter-annual variation in the size of fish was apparent ($P < 0.0001$), though there was no dominant trend over the period.

3.1.3. Sex ratio

Females predominated in catches throughout the year (Fig. 8a). They made up between 73% and 83% of sexed individuals in January–May. The peak proportion of females observed in August (81%), dropped to 64% in September, then trended upwards to 73% in December. No samples were available in June and July. A GAM model incorporating smooth functions of month, year and depth accounted for

Table 1

GCV/UBRE scores and percent of null deviance explained in a sequence of generalised additive models of the presence of *M. australis* and *M. hubbsi* in trawls and CPUE in trawls where the species was present. The full suite of explanatory variables was position (2D smooth of latitude and longitude), depth, month, year and license type. In all cases the full model containing all explanatory variables was compared with models where each variable was eliminated in turn. The final models considered are indicated by bold type

Model	Explanatory variables	GCV/UBRE ^a score	Deviance explained (%)
Presence of <i>M. australis</i> —binomial	All	0.255	38.7
	Position	0.183	28.5
	Depth	0.287	37.1
	Month	0.219	37.8
	Year	0.083	35.4
	License type	0.073	36.4
	License year	0.019	32.2
	License type year parametric	0.008	34.4
CPUE of <i>M. australis</i> —lognormal	Full	1.242	70.2
	Position	1.432	65.0
	Depth	1.268	69.5
	Month	1.331	68.0
	Year	1.346	67.6
	License type	1.396	66.1
Presence of <i>M. hubbsi</i> —binomial	All	0.057	35.1
	Position	0.035	24.7
	Depth	0.090	34.1
	Month	0.091	25.1
	Year	0.034	33.7
	License type	0.019	33.6
	License year	0.011	32.3
	License type year parametric	0.013	32.4
CPUE of <i>M. hubbsi</i> —lognormal	Full	1.778	66.2
	Position	2.302	55.9
	Depth	1.807	65.6
	Month	2.290	56.4
	Year	1.982	62.2
	License type	1.865	64.3

^a The mGCV package uses UBRE in cases in which the scale parameter is assumed known, i.e. in the binomial model for presence/absence.

55.7% of the null deviance in the proportion of females in the trawl-by-trawl data. The fitted smooth functions are illustrated in Fig. 9a. The increase in the proportion of females present in August is reflected in a peak in the monthly component for the proportion of females, although the lack of samples from June and July implies some caution is required in interpreting this fit. There are indications of an upward trend in the proportion of females from 1993 onwards. However, the confidence intervals are wide and only limited samples are available from the late 1990s. In contrast, samples are well spread over the 150–500 m depth range and it is clear that the proportion of females generally reduces with increased depth.

3.1.4. Maturity

Immature (maturity stage I) fish, when present, occurred only in very small proportions (Fig. 10a). In spring (August–November) post-spawning adult fish, both males and females, were present. In December–January only resting or early-developing females were present, although several mature males were recorded in these months. From February to

May, a general increase in the maturity of both females and males was apparent. Mature females were detected in very small proportions in catches from the Falklands zones. Mature males were recorded, albeit as a generally small proportion of the catch, throughout the year.

3.2. *Merluccius hubbsi*

3.2.1. Distribution

M. hubbsi was widespread at depths between 150 and 300 m over the shelf and shelf edge around the Falkland Islands and in the High Seas region (Fig. 1b). It was present in a significant number of trawls in the area to the south-east of the Islands where the *L. gahi* fishery takes place (Figs. 2 and 11). The occurrence in catches and CPUE by depth showed that this species was most abundant in trawls at 150–250 m depths (Fig. 4c,d). *M. hubbsi* was also recorded in trawls in shallower (<150 m) waters near the Falklands.

Only about 20% of trawls with hake yielded a simultaneous catch of both species in any month and, where they did

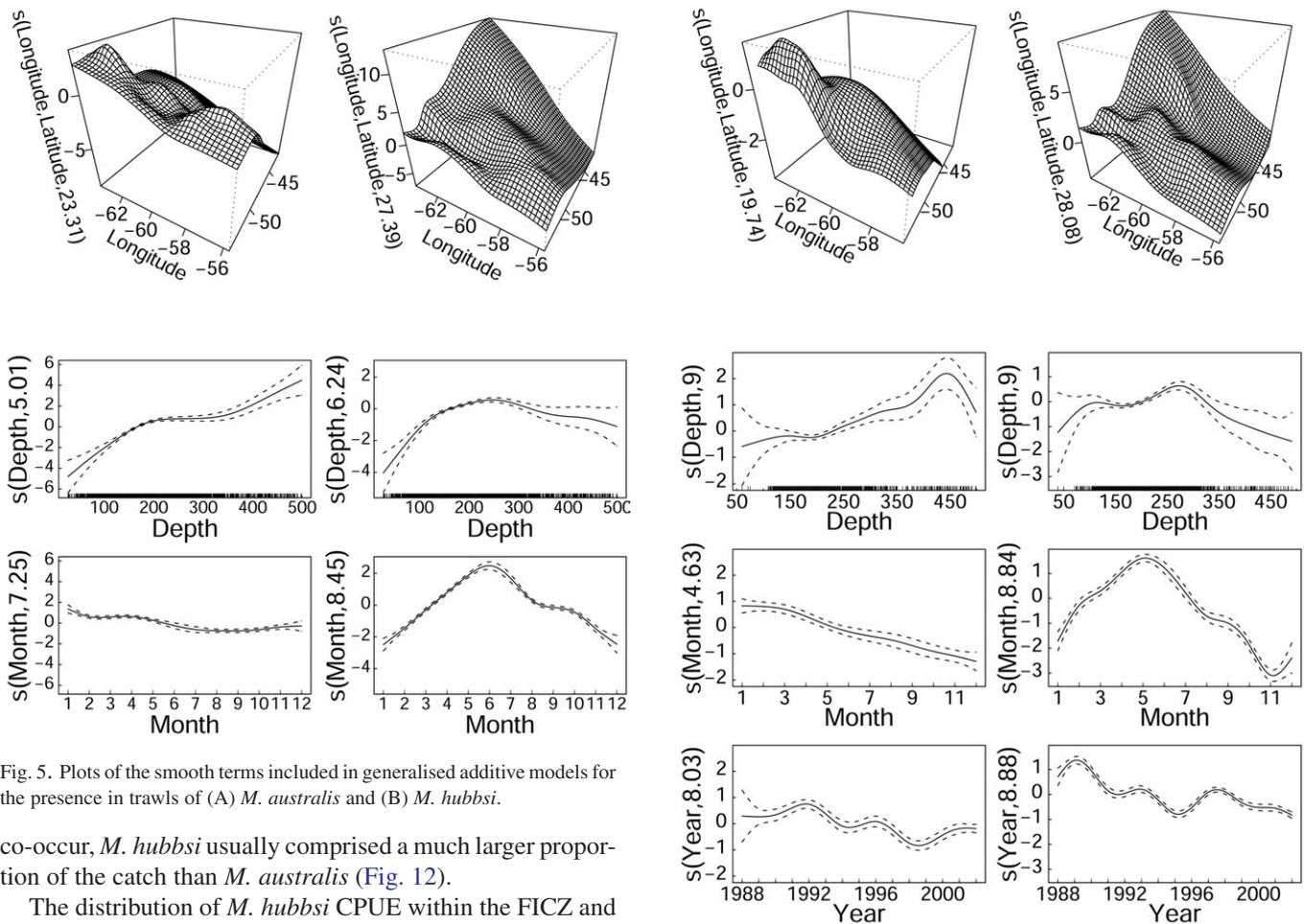


Fig. 5. Plots of the smooth terms included in generalised additive models for the presence in trawls of (A) *M. australis* and (B) *M. hubbsi*.

co-occur, *M. hubbsi* usually comprised a much larger proportion of the catch than *M. australis* (Fig. 12).

The distribution of *M. hubbsi* CPUE within the FICZ and in the High Seas region varied substantially through the year (Figs. 2 and 11). In January, *M. hubbsi* was essentially absent from trawls in Falkland waters and only small catches (mean CPUE of 144 kg h^{-1} in trawls with *M. hubbsi*) were taken in the shallower waters of the northern part of the High Seas region. In February, common hake appeared in catches in the southern (deeper water) part of the High Seas region and also occurred further south (to $47^{\circ}30' \text{ S}$). In Falkland waters, they were first encountered in the western part of FICZ, and the north of the FOCZ, near the 200-m depth contour. In March, *M. hubbsi* occurred widely in trawls in the northern part of the FICZ and mean CPUE in the High Seas region increased to 488 kg h^{-1} . The highest catches in April and May occurred south of the 200-m contour in the west of the FICZ and on the High Seas. *M. hubbsi* was present around the Falkland Islands in winter (June–August), but the highest winter catches were observed on the High Seas. In August–September, *M. hubbsi* was still caught widely in the west and north of the FICZ, but was largely absent from the south-eastern area of FICZ. In October, CPUEs were relatively low over the entire Falkland shelf, but high CPUEs were still observed on the High Seas. In November–December, in spite of a significant number of trawls, *M. hubbsi* was not recorded around the Islands and mean CPUE at $45\text{--}46^{\circ} \text{ S}$ decreased to 350 kg h^{-1} in trawls with *M. hubbsi* from the peak of 713 kg h^{-1} observed in April–August.

Fig. 6. Plots of the smooth terms included in generalised additive models for the CPUE of (A) *M. australis* and (B) *M. hubbsi* in the subset of trawls where the species was present.

The most satisfactory GAM model for the presence of *M. hubbsi* omits year and license type as explanatory variables (Table 1). The likelihood of *M. hubbsi* occurring in a trawl is highest in the north-west of the region and peaks at around 250 m depth (Fig. 5b). There is a strong seasonal relationship, with the highest likelihood of occurrence in June. A GAM with a lognormal distribution again proved more satisfactory than a gamma distribution in describing the CPUE of *M. hubbsi* in trawls where it was present. All explanatory variables proved useful. Plots of the smooth variables (Fig. 6b) show a similar pattern to those in the model for the presence of *M. hubbsi*, namely higher CPUE in the north-west of the region and at intermediate depths (250–300 m). CPUEs are also strongly seasonal, peaking in May–June. As with *M. australis*, there is a generally decreasing trend in CPUE from 1988 to 2002, although the peaks and troughs in the smoothed year effect are out of phase with those in *M. australis*.

3.2.2. Length-frequency composition

The pooled length distribution of *M. hubbsi* was unimodal for both sexes, both in the FICZ and on the High Seas. The

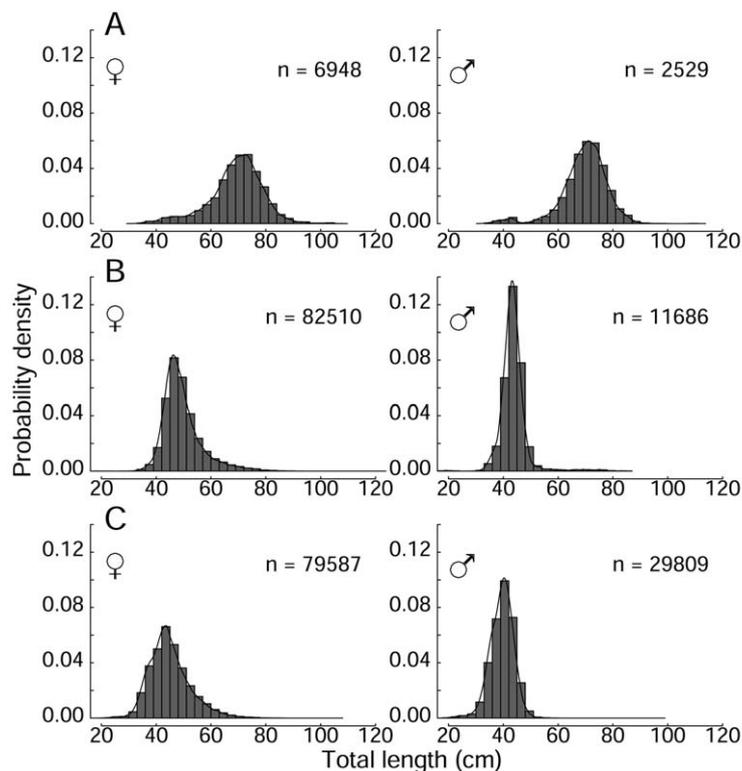


Fig. 7. Overall length-frequency distributions for *M. australis* (A, FIFD data) and common hake *M. hubbsi* in the FICZ (B, FIFD and IEO data) and in the High Seas region (C, FIFD and IEO data) using pooled samples from 1988 to 2002. Distributions for females are given in the left column and males in the right. The line gives kernel density estimates of the distributions from which the position of the modes were estimated.

modal size of both males and females was about 3 cm larger in the FICZ than on the High Seas. Common hake were sexually dimorphic in size. The modal size of females in both regions was 4–5 cm larger than that of males (Fig. 7b,c). A GAM expressing length in terms of sex, region (Falklands zones vs. High Seas) and a smooth of year confirmed a significant difference in the size of male and female *M. hubbsi* ($P < 0.0001$). The two regions also showed a significant ($P < 0.0001$) difference in fish length with larger fish occurring in the Falklands zones. For both sexes in both regions there were again significant ($P < 0.0001$) inter-annual variations in mean size, but as in *M. australis* there was no particular trend in size over the period.

3.2.3. Sex ratio

In the Falkland waters, females predominated in catches of common hake throughout the year. Their proportion decreased from almost complete dominance in January (95%) to 80–85% in February–May, followed by a gradual increase from 90% in June to almost 100% in November (Fig. 8b). On the High Seas, the overall proportion of females was lower than that in Falkland waters. The proportion of females peaked in March and then again in October–November (Fig. 8c). Exploratory GAM models were fitted to the data from the Falklands zones and High Seas region separately. The sex ratio in the Falkland waters is heavily female biased and 16.9% of trawls sampled yielded exclusively females, in contrast to just 1.9% in the High Seas region. In Falkland

waters (Fig. 9b) the smooth components fitted in the GAM models suggest there is rather little variation in sex ratio from month to month, in contrast with the High Seas region (Fig. 9c) where the proportion of females peaks in September/October. In both areas, there are indications of a slight upward trend in the proportion of females through the 1990s; however, this is variable and confidence intervals are large. In Falkland waters, the model fit suggests a decrease in the proportion of females in deeper water, whilst the opposite is the case in the High Seas region. In both cases, however, the vast majority of samples are from shallower trawls (<250 m in Falkland waters, <150 m in the High Seas region). Consequently, confidence intervals are large and the trends cannot be considered clear.

3.2.4. Maturity

In Falkland waters, immature fish (maturity stage I) were found to be present in very small proportions throughout the year. In summer (January–February) from 10% to 25% of both males and females were in spawning condition, whereas about a half had resting gonads (Fig. 10b). In March–May, spawning animals disappeared from catches, followed by post-spawning females and males. A high proportion of preparatory females (stage IV) and preparatory and spawning males were observed in July and August, followed by a prevalence of fishes with resting gonads (stages II and III) in September–November. On the High Seas, the occurrence of immature fishes was much higher than in Falkland waters

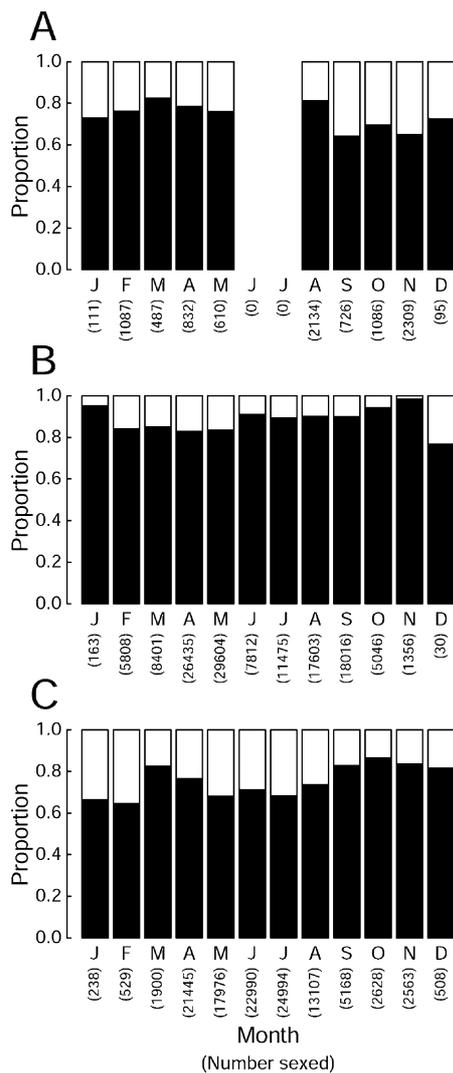


Fig. 8. Proportions of females (black bars) and males (white bars) in all sexed individuals of *M. australis* (A, FIFD data) and *M. hubbsi* in the FICZ (B, FIFD and IEO data) and in the High Seas region (C, FIFD and IEO data) on a monthly basis, using pooled length-frequency samples from 1988 to 2002. The number of individuals is given in parenthesis beneath the abscissa.

(Fig. 10c). A high proportion of females was in resting condition from January through June. In July–September, most females were maturing. Trends in the maturities of males were similar to those of females, but with a higher occurrence of maturing animals. Unlike females, about half of the males sampled were mature in June. Unfortunately, the small number of animals sampled in December in Falkland waters, with none from the High Seas, prevented the gaining of a clear picture of the maturity status of *M. hubbsi* at the end of the year.

Taking into account the high abundance of females, it was possible to distinguish three periods in the maturity status of *M. hubbsi* both in Falkland waters and on the High Seas. The post-spawning period ran from March to June while the resting/feeding period occurred from July to November. The spawning period, when the majority of fish were absent from Falkland waters and the High Seas, was from December to

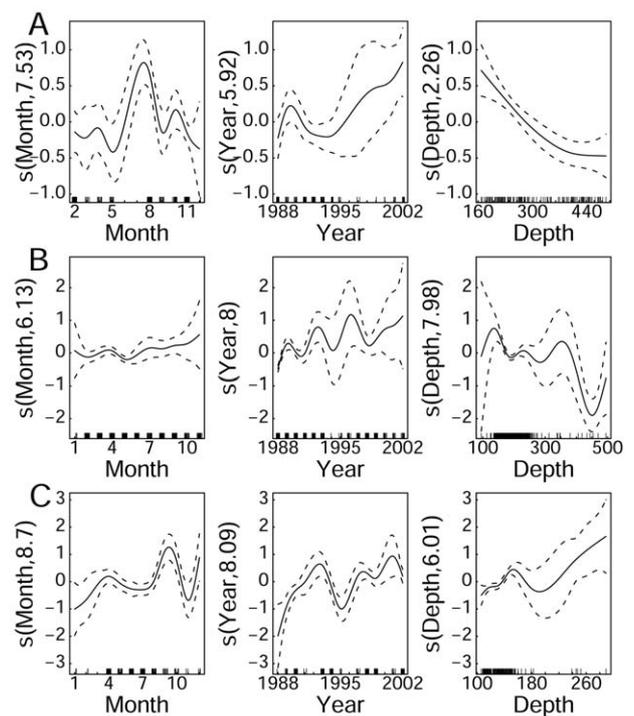


Fig. 9. Plots of the smooth functions of month, year and depth in generalised additive models fitted to the proportion of females in trawls for more than 20 individuals were sexed. (A) *M. australis* (FIFD data); (B) *M. hubbsi* in the Falklands zones (FIFD and IEO data); (C) *M. hubbsi* in the High Seas region (FIFD and IEO data).

February. However, this picture was not as clear as with *M. australis*, because quite significant numbers of fish were either preparatory (mainly females) or even spawning (mainly males) in austral winter.

4. Discussion

The spatial overlap in the ranges of the hakes *M. hubbsi* and *M. australis* on the Patagonian shelf is well documented (Inada, 1981). Data obtained in the early 1980s suggested, however, that the southern (Patagonian) hake *M. australis* should dominate around the Falkland Islands (Csirke, 1987). After the establishment of the FICZ in 1987, it was recognised that the bulk of the hake catch in Falkland waters consisted of the common hake *M. hubbsi* (mean 91% in 1987–1991) (Tingley et al., 1995). Our data show that the spatial overlap, in the distributions of the two hakes, is largely limited to the shelf and continental slope areas south of 51° S whilst shelf and slope areas north of 51° S, are occupied almost exclusively by common hake.

Only a very small proportion of *M. australis* and a small proportion of *M. hubbsi* females have been found with gonads in spawning condition. This confirms that neither species spawns around the Falkland Islands, as assumed by Tingley et al. (1995). Although a larger proportion of mature males than females were observed in some months within the FICZ in both species, this does not necessarily imply the

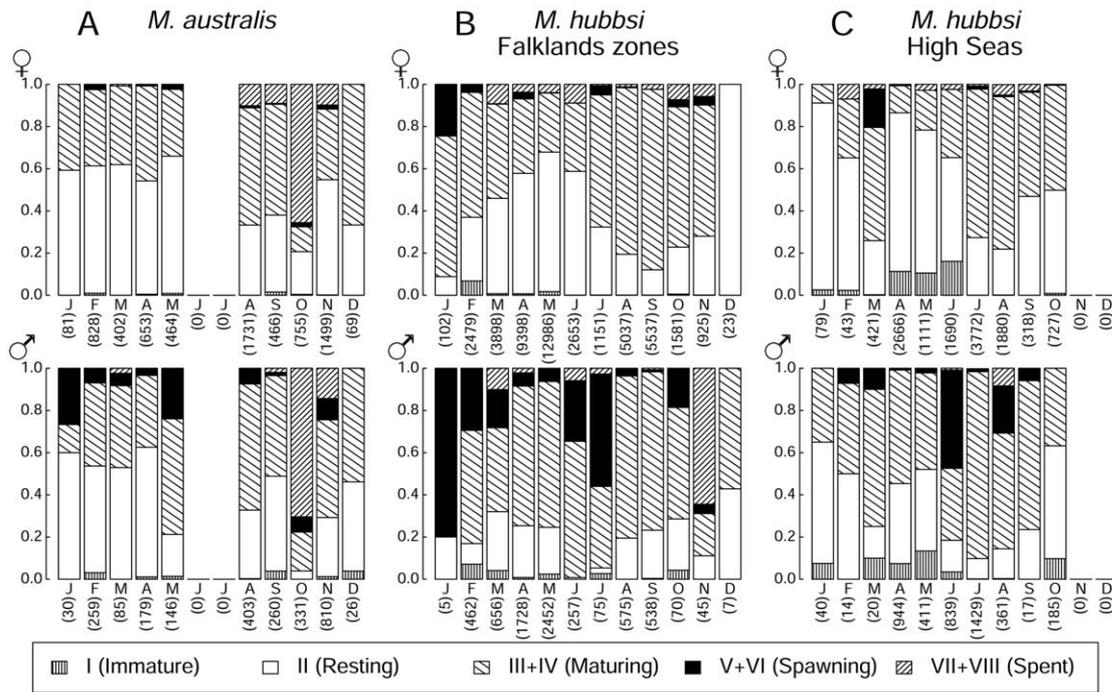


Fig. 10. Monthly maturity status for (A) female and male southern hake *M. australis* (FIFD data) and common hake *M. hubbsi* (FIFD data), separately for the FICZ (B) and High Seas (C) regions, using random samples pooled over the period 1988–2002.

occurrence of spawning. Males start maturing earlier than females, sometimes at the end of their time on the feeding grounds (i.e. *M. australis* from New Zealand waters; Colman, 1995). Thus, waters around the Falkland Islands represent the feeding ground of both hake species.

The use of trawl data from two observer programs, spanning a 15 year period and a variety of fisheries, provides considerably wider spatial and temporal coverage than is normally the case with scientific survey data. However, the inference of distribution patterns from commercial data, rather than scientific survey data, obviously requires some caution. The location of commercial trawls is influenced by a variety of considerations including license conditions (restricted species and closed areas), vessel capabilities, commercial priorities and the knowledge and experience of the crew. Within a particular locality, fish behaviour (e.g. schooling leading to distinctive acoustic traces) may allow the targeting of particular species. This has implications for the comparability of catch rates as the resulting hake catches include by-catch in addition to targeted trawls. GAMs can provide a useful means of standardising commercial CPUE data for these differing vessel effects (e.g. Denis et al., 2002) quantifying the patterns found the exploratory analyses of spatial and temporal trends in the raw distribution data. Standardisation for the varying commercial priorities and restrictions noted above is via the incorporation of a factor representing the license type held by the vessel. In fact, license type was retained as a useful explanatory variable only in the models of CPUE of the two hakes, not in the models of presence/absence. This suggests that different fishing practices can affect the catch rate of hakes, but not to

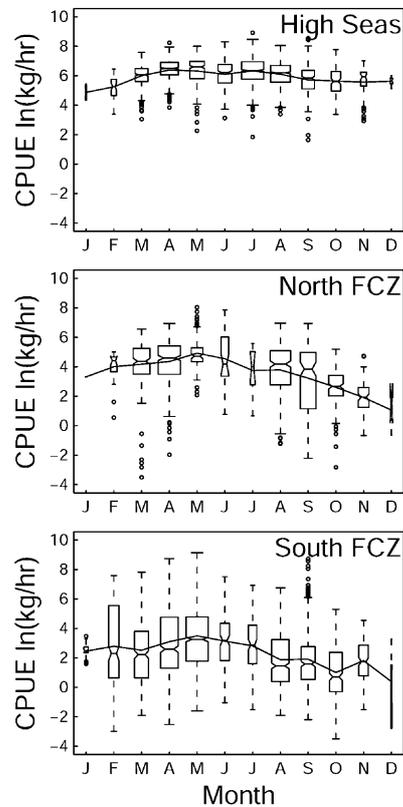


Fig. 11. Boxplots of monthly haul-by-haul CPUE ($\ln[\text{kg h}^{-1}]$) in trawls with non-zero catches for *M. hubbsi* in three regions: the High Seas (44.5–47.5° S), and the northern (47.5–51° S) and southern (south of 51° S) parts of the Falklands zones. The superimposed line indicates the monthly mean log CPUE.

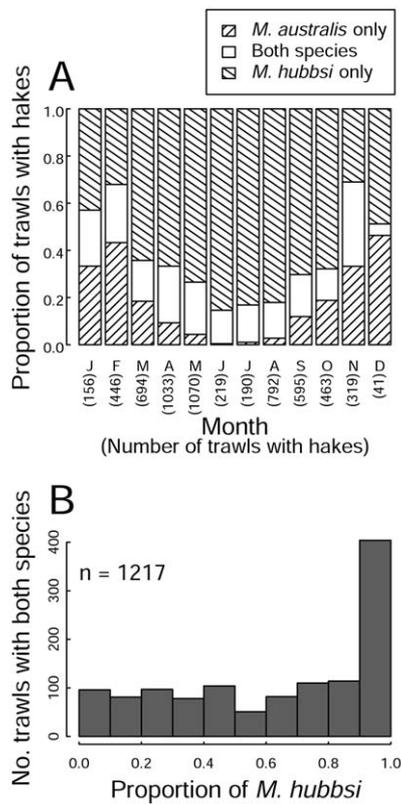


Fig. 12. The proportion of all trawls with catches of hakes where only *M. australis* or *M. hubbsi* was caught and where both species were caught (A), and the distribution of the proportion of *M. hubbsi* in trawls where both hake species were caught (B). FIFD data only.

the extent of total avoidance. This is intuitively reasonable for fish dispersed on their feeding grounds rather than aggregated in easily identified schools.

When carrying out statistical standardisation of CPUE data it is, of course, necessary to be aware of the limitations of that data. For example, the shelf area to the south-east of the Falklands is only open to trawlers targeting *L. gahi*. There is only a limited overlap between the fleets targeting *L. gahi* in the south-east and that targeting finfish in the western part of the Falklands zones so complete separation of the effects of fleet and area cannot be expected. Visualisation and basic analyses of the raw data thus remain important precursors to the use of generalised additive modelling.

The GAM terms, representing the overall effect of spatial position and depth on the presence and abundance of *M. australis* and *M. hubbsi*, provide a clear confirmation of the spatial separation of the two species. The presence/abundance of *M. hubbsi* are highest in the north-west of the region and peaks at depths of 200–300 m, whilst both presence and abundance of *M. australis* are greatest in the south-west of the study region and at depths of 400–500 m. The temporal pattern in the presence and abundance of *M. hubbsi*, which peaks in austral winter, is clearly demonstrated by the GAM smooth of month, while that of *M. australis* is rather less clear. Examination of the raw data suggests a noticeable drop in the abundance of *M. australis* in the region in June

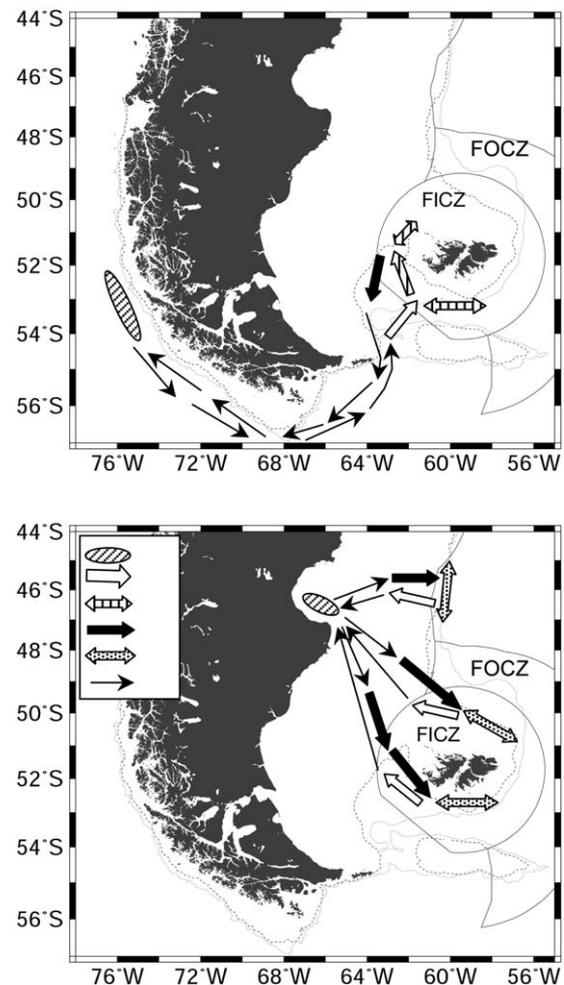


Fig. 13. Scheme of possible seasonal migrations by *M. australis* and *M. hubbsi* in Falkland waters. Supposed spawning grounds of *M. australis* (after Aguayo-Hernandez, 1995) and *M. hubbsi* (after Aubone et al., 2000) (1); spring (2); summer (3); autumn (4) and winter (5) migrations on the feeding grounds; supposed migrations to and from the spawning grounds (6).

and July. However, this effect is only weakly represented by the smooth term for the effect of month on the presence of *M. australis* whilst the monthly term, in the GAM for abundance, suggests a simple decrease through the year. The limited data available from the southwest of the FICZ in June, July and December are certainly partly responsible for this paradox and fact that the seasonal pattern the presence and abundance of *M. australis* remains rather less clear than that of *M. hubbsi* at present.

By supplementing the analyses of the spatial and temporal patterns, in the distributions of the two hakes with information on their biological status through the year, it has been possible to formulate preliminary schemes of their seasonal migrations in Falkland waters and the High Seas region (Fig. 13). In spring, post-spawning *M. australis* first arrive in the southwest of the FICZ concentrating initially in the deeper (400–500 m) waters around 53° S. Over the summer, the majority of *M. australis* are in resting condition and distributed over the deeper shelf in the south-western part of

FICZ, mainly at 200 and 500 m depths. It also disperses, to some extent, to the shallower shelf areas (~200 m) in the north-west of the zone and along the 200-m depth contour to the north-east and north of the Falkland Islands. In autumn, there is a slight increase in maturity and catch rates are the highest in the west of the FICZ just deeper than the 200-m contour. In May, animals are concentrated at the western edge of the FICZ around 52° S and our assumption is that they move out of Falkland waters at this time of year to spawn further to the south-west. To date, spawning grounds of *M. australis* are known only off the Pacific coast of Chile, where the main spawning area is located between 43° and 47° S and with secondary areas between 52° and 54° S (Aguayo-Hernandez, 1995). There spawning occurs from July to September, which coincides with the apparent absence of *M. australis* from Falkland waters. An analysis of individual morphometry and parasitological fauna, from fish caught near the Falklands and off southern Chile, suggested that fish from both regions belong to a single interbreeding population with several stock units (George-Nascimento and Arancibia, 1994).

Common hake *M. hubbsi* have a different migration pattern in Falkland waters than *M. australis*. In January, *M. hubbsi* is present in small numbers in the shallowest parts of the High Seas region and is absent from the FICZ. Fish migrate first into the western part of FICZ in February at depths around 200 m. In autumn (March–May), *M. hubbsi* is found in large numbers both on the High Seas and in the northern and western parts of FICZ. By May, it has penetrated to the southern and south-eastern parts of FICZ. *M. hubbsi* have their widest distribution in winter. In spring, they disappear first from the south-eastern parts of FICZ (in September) gradually moving in a north-westerly direction (in October). *M. hubbsi* disappear from the FICZ in November and from the High Seas region in December, presumably moving to their spawning grounds in inshore Argentinean waters. The period of common hake absence from Falkland waters and the High Seas, and their maturity cycle, coincides with the spawning period of *M. hubbsi* in the San Jorge Gulf (December–February; Aubone et al., 2000).

Both *M. australis*, in Chilean waters and *M. hubbsi* in Argentinean waters, have a substantial sexual dimorphism in growth rate with females growing faster, and attaining larger sizes, than males (Aguayo-Hernandez, 1995; Aubone et al., 2000). However, in waters around the Falkland Islands, this difference in size is not so pronounced, especially in *M. australis* where no significant difference in total size was detected. In hakes with long seasonal migrations, it is known that the larger fish usually migrate faster and farther than smaller fish (i.e. north Pacific hake *M. productus*) (Smith et al., 1990). Thus, a pronounced sexual dimorphism in fish size can affect the length compositions, sex ratios and age structure in different parts of the species' range. Near the periphery of range of *M. productus*, large females predominate while smaller fish are found near the centre of the range (=spawning grounds) (Smith et al., 1990; Dorn, 1992). This

is exactly the situation that occurs in both hake species in the southwest Atlantic. Near the spawning grounds of *M. hubbsi* smaller males predominate in catches (Bezzi et al., 1995). Only the larger males can migrate to the peripheries of the species range. As the proportion of large males in the overall length-frequency distribution is small, this leads to a prevalence of females, and to similar modal sizes of the sexes, in areas close to the peripheries of the species range. Thus, in the High Seas feeding grounds, *M. hubbsi* females are prevalent but the proportion of females, and the modal size of both sexes, are smaller than in the feeding grounds around the Falkland Islands which are more distant from the San Jorge Gulf spawning grounds. The same trend, in sex ratios and sizes of the sexes, is observed in *M. australis* on the Falkland shelf and slope. The increase in the proportion of females, in shallower waters in the Falklands zones, may represent another aspect of the differing migration ranges of the sexes—the shallow waters of the FICZ are further from the Pacific spawning grounds so may only be reached by the larger fish, which are mostly females. Females of another gadoid fish—Atlantic cod—also made feeding migrations farther from their spawning grounds than their male counterparts, creating female-dominated schools in the peripheries of their ranges, as demonstrated by the analysis of sex ratios (Morgan and Trippel, 1996) and acoustic tagging (Robichaud and Rose, 2003).

In spite of the recognised difficulty in distinguishing *M. australis* from *M. hubbsi* morphologically (Cousseau and Cotrina, 1980), it is clear that these species are segregated and occupy different spatial and temporal niches on their common feeding grounds on the shelf and slope around the Falkland Islands. They are segregated temporally, with different and non-overlapping spawning seasons—the austral winter in the case of *M. australis* and austral summer in *M. hubbsi*. During these periods, one species is absent, spawning outside Falkland waters, giving the other species the advantage of expanding its range to feed, without competition, on the feeding grounds of the Falklands shelf. In other seasons (spring and autumn), when both species are present on the Falklands shelf, they remain spatially segregated with *M. australis* occurring mainly in the south-western sector of the FICZ and *M. hubbsi* everywhere else. Where they do co-occur on the south-western part of the Falkland shelf, there is still a segregation by depth with *M. australis* occurring mainly on the shelf edge and slope deeper 300 m and *M. hubbsi* occurring on the shelf <250 m depth. The same depth segregation between two sympatric species of hakes is observed in South African waters between shallow water *M. capensis* and deep water *M. paradoxus* (Payne and Punt, 1995). The feeding spectrum of the two hakes on the Falkland Shelf is still unknown. However, studies of their feeding in other regions showed that *M. australis* is primarily a piscivorous predator, with southern blue whiting comprising a large part of their diet (Payá, 1992; Aguayo-Hernandez, 1995). Interestingly, the arrival of *M. australis* on the Falkland shelf coincides in time and space with the spawning

migrations of southern blue whiting, which aggregates to spawn on the shelf edge at 300–400 m on the slope south of Falklands in August–October (Shubnikov et al., 1969). After spawning, southern blue whiting disperses northwards in both directions along the shelf edge and southern hake again apparently follows some of these aggregations and, as a result, are encountered mainly in the deep-water area to the southwest of the Islands. In contrast, *M. hubbsi* is more opportunistic predator feeding on a variety of fishes and cephalopods (Angelescu and Prenske, 1987). *M. hubbsi* utilises the Falkland shelf more extensively than *M. australis* and is abundant everywhere including the south-eastern part of the Falkland Shelf up to 250 m depth. In winter, these areas of the Falkland Shelf are the main feeding grounds of the Patagonian longfin squid *L. gahi*, which aggregate in the warm intermediate water layer at 200–250 m depth at this time of the year. Here, they are targeted by a variety of nektonic predators and exploited by the fishing fleet (Arkhipkin et al., 2003; Hatfield and des Clers, 1998). Thus, it is likely that feeding spectra of both hakes around the Falklands are also different, further segregating their ecological niches. Studies of the diet of both hakes around the Islands are needed to clarify the ecological role they play in the ecosystem of the Patagonian and Falkland shelves.

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References

- Aguayo-Hernandez, M., 1995. Biology and fisheries of Chilean hakes (*M. gayi* and *M. australis*). In: Alheit, J., Pitcher, T.J. (Eds.), Hake: Biology, Fishery and Markets. Chapman and Hall, London, pp. 305–337.
- Angelescu, V., Prenske, L.B., 1987. Ecología trófica de la merluza común del Mar Argentino (*Merlucciidae*, *Merluccius merluccius hubbsi*). Parte 2. Dinámica de la alimentación analizada sobre la base de las condiciones ambientales, la estructura y las evaluaciones de los efectivos en su área de distribución. Ser. Contrib. INIDEP 561, Mar del Plata, Argentina.
- Arkhipkin, A., Grzebielec, R., Sirota, A.M., Remeslo, A.V., Polishchuk, I.A., Middleton, D.A.J., 2003. The influence of seasonal environmental changes on ontogenetic migrations of the squid *Loligo gahi* on the Falkland shelf. Fish. Oceanogr. 12.
- Aubone, A., Bezzi, S., Castrucci, R., Dato, C., Ibanez, P., Irusta, G., Perez, M., Renzi, M., Santos, B., Scarlato, N., Simonazzi, M., Tringali, L., Volliarino, F., 2000. Merluza (*Merluccius hubbsi*). In: Bezzi, S., Akselman, R., Boschi, E. (Eds.), Síntesis del estado de las pesquerías marítimas argentinas y de la Cuenca del Plata. Años 1997–1998, con una actualización de 1999. Publicaciones especiales, INIDEP, Mar del Plata, pp. 29–40.
- Bezzi, S.I., Verazay, G.A., Dato, C.V., 1995. Biology and fisheries of Argentine hakes (*M. hubbsi* and *M. australis*). In: Alheit, J., Pitcher, T.J. (Eds.), Hake: Biology, Fishery and Markets. Chapman and Hall, London, pp. 239–268.
- Bowman, A.W., Azzalini, A., 1997. Applied Smoothing Techniques for Data Analysis: the Kernel Approach with S-Plus Illustrations. Oxford University Press, Oxford.
- Cohen, D.M., Inada, T., Iwamoto, T., Scialabba, N., 1990. FAO species catalogue. Vol. 10. Gadiform fishes of the world (Order Gadiformes). An annotated and illustrated catalogue of cods, hakes, grenadiers and other gadiform fishes known to date. FAO Fisheries Synopsis, v. 10. FAO, Rome.
- Colman, J.A., 1995. Biology and fisheries of New Zealand hake (*M. australis*). In: Alheit, J., Pitcher, T.J. (Eds.), Hake: Biology, Fishery and Markets. Chapman and Hall, London, pp. 365–388.
- Cousseau, M.B., Cotrina, C.P., 1980. Observaciones sobre diferencias morfológicas entre la merluza común (*Merluccius hubbsi*) y la merluza austral (*Merluccius polylepis*). Rev. Inv. Des. Pesq. 2, 47–56.
- Csirke, J., 1987. The Patagonian fishery resources and the off-shore fisheries in the South-West Atlantic. FAO Fish. Tech. Pap. n° 286.
- Denis, V., Lejeune, J., Robin, J.P., 2002. Spatio-temporal analysis of commercial trawler data using General Additive models: patterns of Loliginid squid abundance in the north-east Atlantic. ICES J. Mar. Sci. 59, 633–648.
- Dorn, M.W., 1992. Detecting environmental covariates of Pacific whiting, *Merluccius productus*, growth using a growth-increment regression model. Fish. Bull. US 90, 260–275.
- FIFD, 2001. Fisheries Department fisheries statistics, 6. FIG Fisheries Department, Stanley.
- George-Nascimento, M., Arancibia, H., 1994. La fauna parasitaria y la morfometría de la merluza austral (*Merluccius australis* (Hutton)) como indicadores de unidades de stock. Biol. Pesq. 23, 31–47.
- Hatfield, E.M.C., des Clers, S., 1998. Fisheries management and research for *Loligo gahi* in the Falkland Islands. CalCOFI Rep. 39, 81–91.
- Ihaka, R., Gentleman, R., 1996. A language for data analysis and graphics. J. Comput. Graph. Stat. 5, 299–314.
- Inada, T., 1981. Studies of the merlucciid fishes. Far Seas Fish. Res. Lab. Bull. 18, 1–172.
- Jones, B.W., 1974. World resources of the genus *Merluccius*. In: Harden Jones, F.R. (Ed.), Sea Fisheries Research. John Wiley and Sons, New York, pp. 139–166.
- Martos, A.R., Peralta, L.F., 1995. Biology and fisheries of North-west African hakes (*M. merluccius*, *M. senegalensis* and *M. polli*). In: Alheit, J., Pitcher, T.J. (Eds.), Hake: Biology, Fishery and Markets. Chapman and Hall, London, pp. 89–124.
- McGill, R., Tukey, J.W., Larsen, W.A., 1978. Variations of box plots. Am. Stat. 32, 12–16.
- Morgan, M.J., Trippel, E.A., 1996. Skewed sex ratios in spawning shoals of Atlantic cod (*Gadus morhua*). ICES J. Mar. Sci. 53, 820–826.
- Nikolsky, G.V., 1963. The Ecology of Fishes. Academic Press, New York.
- Otero, H.O., 1986. Determinación del ciclo migratorio de la merluza común (*Merluccius hubbsi*) mediante el análisis de índices de densidad poblacional y concentración del esfuerzo de pesca. Publ. Com. Tec. Mix. Fr. Mar. 1, 75–92.
- Payá, I., 1992. The diet of Patagonian hake *Merluccius australis polylepis* and its daily ration of Patagonian grenadier *Macruronus magellanicus*. In: Payne, A.I.L., Brink, K.H., Mann, K.H., Hilborn, R. (Eds.), Benguela Trophic Functioning, S. Afr. J. Mar. Sci., 12, pp. 753–760.

- Payne, A.I.L., Punt, A.E., 1995. Biology and fisheries of South African Cape hakes (*M. capensis* and *M. paradoxus*). In: Alheit, J., Pitcher, T.J. (Eds.), *Hake: Biology, Fishery and Markets*. Chapman and Hall, London, pp. 15–47.
- Pitcher, T.J., Alheit, J., 1995. What makes a hake? A review of the critical biological features that sustain global hake fisheries. In: Alheit, J., Pitcher, T.J. (Eds.), *Hake: Biology, Fishery and Markets*. Chapman and Hall, London, pp. 1–14.
- Podesta, G.P., 1990. Migratory pattern of Argentine hake *Merluccius hubbsi* and oceanic processes in the Southwestern Atlantic Ocean. *Fish. Bull. US* 88, 167–177.
- Punt, A.E., 1992. Selecting management methodologies for marine resources, with an illustration for southern African hake. In: Payne, A.I.L., Brink, K.H., Mann, K.H., Hilborn, R. (Eds.), *Benguela Trophic Functioning*, 12, pp. 943–958. *S. Afr. J. Mar. Sci.*
- Robichaud, D., Rose, G.A., 2003. Sex differences in cod residency on a spawning ground. *Fish. Res.* 60, 33–43.
- Shubnikov, D.A., Permitin Yu, E., Voznyak, S.P., 1969. Biology of the pelagic gadoid fish *Micromesistius australis* Norman. *Trudy VNIRO* 66, 299–306.
- Smith, B.D., McFarlane, G.A., Saunders, M.W., 1990. Variation in Pacific hake (*Merluccius productus*) summer length-at-age near southern Vancouver Island and its relationship to fishing and oceanography. *Can. J. Fish. Aquat. Sci.* 47, 2195–2211.
- Stefánsson, G., 1996. Analysis of groundfish survey abundance data: combining the GLM and delta approaches. *ICES J. Mar. Sci.* 53, 577–588.
- Tingley, G.A., Purchase, L.V., Bravington, M.V., Holden, S.J., 1995. Biology and fisheries of hakes (*M. hubbsi* and *M. australis*) around the Falkland Islands. In: Alheit, J., Pitcher, T.J. (Eds.), *Hake: Biology, Fishery and Markets*. Chapman and Hall, London, pp. 269–304.
- Wood, S.N., 2000. Modelling and smoothing parameter estimation with multiple quadratic penalties. *J. R. Stat. Soc. B* 62, 413–428.