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Seasonal movements of veined squid *Loligo forbesi* in Scottish (UK) waters

Mafalda Viana[1,2,a], Graham J. Pierce[1,3], Janine Illian[1,5], Colin D. MacLeod[1], Nick Bailey[4], Jianjun Wang[1] and Lee C. Hastie[1]

[1] School of Biological Sciences, University of Aberdeen, Zoology Building, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK
[2] University of Algarve, Faculdade de Ciências do Mar e Ambiente (FCMA), Campus de Gambelas, 8000-117 Faro, Portugal
[3] Instituto Español de Oceanografia, Centro Oceanografico de Vigo, PO Box 1552, 36200 Vigo, Spain
[4] Fisheries Research Services Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, AB11 9DB, UK
[5] Centre for Research into Environmental and Ecological Modelling (CREEM), School of Mathematics and Statistics, University of St Andrews, The Observatory Buchanan Gardens, St Andrews, KY16 9LZ, UK

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Abstract – In order to protect and sustainably manage fishery resource species, it is essential to understand their movements and habitat use. To detect the hypothesised migration of maturing veined squid *Loligo forbesi* from the west coast of Scotland (UK) to the North Sea and identify possible inshore-offshore movements, we analysed seasonal, spatial and environmental patterns in abundance and size distribution, based on commercial fishery landings data and trawl survey data from Scottish coastal waters (International Council for the Exploration of the Sea, ICES areas IVa, IVb and VIa). A geographic information system (GIS) was used to build monthly contour maps of abundance. Generalised additive mixed models (GAMM) were used to quantify patterns in size distribution and abundance. In most years, there was no evidence of movement from the West to the East coast of Scotland. Evidence of inshore-offshore movements during the life-cycle of the cohort that recruits in autumn (winter breeders) was found instead. The winter breeding cohort appears to spawn in inshore waters and some evidence suggests that the spawning grounds of the summer breeders are also inshore. Across seasons, higher abundance of *L. forbesi* can generally be found in the north of Scotland at intermediate water depths and in warmer waters.

Key words: *Loligo forbesi* / Temporal and spatial distribution patterns / Migration / Life cycle

1 Introduction

To protect and sustainably manage fishery resources, it is essential to understand the temporal and spatial patterns of habitat utilization by exploited species (Arendt et al. 2001), including migration patterns. In the veined squid *Loligo forbesi* (Teuthoidea, Cephalopoda), such knowledge is important because squid fishing in UK waters is largely unrestricted (Pierce et al. 1998; Young et al. 2006a). *L. forbesi* is usually the only squid species caught in Scottish waters (Pierce et al. 1998), mostly as a by-catch from trawl and seine net fisheries targeting *Nephrops norvegicus* and demersal whitefish (Pierce et al. 1994; Pierce and Boyle 2003; Young et al. 2006a). Nevertheless, in recent years there has also been direct targeting of squid in summer in Scottish coastal waters, e.g. the Moray Firth (Young et al. 2006b).

Some loliginid squid species are known to move within their distribution range, as Hatfield and Rodhouse (1994) and Arkhipkin et al. (2004a) suggested for *Loligo gahi* around the Falkland Islands which, over the course of the annual life-cycle, move offshore to feed and inshore to spawn. *L. forbesi* occurs in coastal waters of the Northeast Atlantic from 20° to 60°N and, according to Holme (1974) and Sims et al. (2001), off the south-west of England, they perform seasonal migrations. This population hatches in the western English Channel during the winter (December-January) and migrates east towards southern North Sea. After a few months of rapid growth, they move back to the west area to spawn and die during the following December-January. In Scottish waters, previous analysis of month-to-month changes in the spatial pattern of fishery catches suggested that *L. forbesi* move from the west coast of Scotland into the North Sea to spawn in winter (Waluda and Pierce 1998), while the post-spawning adults move towards (or disappear last from) the northwest of Scotland. Following this scenario, the next generation of pre-recruit squid might be expected to migrate westwards in the spring. Bellido (2002) suggested that the west coast represents the main "reservoir" of squid abundance in Scottish waters,

[a] Corresponding author: mafaldaviana@gmail.com

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its distribution characterised by a more or less stable spatial structure, while the east coast is occupied seasonally (although with a widespread coverage in seasons of high abundance), by a population made up of small, fast moving aggregations. However, as reported in Young et al. (2006b), the summer directed fishery for *Loligo forbesi* in the Moray Firth, in the northern North Sea, takes very small squids, suggesting that recruitment may occur at several points along the coast and that, if present, a west-east migration is not the dominant pattern in all years. Therefore, the movement pattern proposed by Waluda and Pierce (1998), which was based on analysis of fishery data from a 5-year period, requires further investigation.

Several studies (e.g. Lum-Kong et al. 1992; Pierce et al. 2005) indicate a clear winter peak in maturation and spawning for *L. forbesi* in Scottish waters, which is consistent with the landings peak that occurs between October and December (Pierce et al. 1994; Bellido et al. 2001). However, as described for other loliginids such as *Loligo gahi* (Hatfield and Rodhouse 1994), there is evidence for winter and summer breeding cohorts - with the former tending to be the more important (Holme 1974; Collins et al. 1997, 1999). The relative importance of the two cohorts may have changed over the last few decades (Zuur and Pierce 2004; Pierce et al. 2005). Two distinct recruitment peaks are also reported, the main one in late summer and beginning of autumn, presumed to derive from winter spawners (Collins et al. 1997), and a second peak in spring, presumably derived from the summer breeding population. It is also possible that, despite the relatively clear and consistent seasonal patterns of landings, and distributions of size and maturity classes, individual squid may live 18 months or longer, so that the offspring of winter breeders become the summer spawners of the following year, as discussed by Boyle et al. (1995). Even the division into winter and summer breeders may be an oversimplification. Collins et al. (1999) identified three or four size modes in the Scottish population of *Loligo forbesi*, which could all represent separate micro-cohorts.

Evidence on squid distribution and abundance in Scottish waters is available from two main sources, commercial fishery catches (especially from demersal trawling) and research trawl surveys. Catch per unit effort (CPUE, kg per hour fishing, based on summed totals by ICES rectangle by month) from commercial demersal trawling, has previously been used as an abundance index for this species, justified by the facts that (a) most squid are taken as a by-catch and CPUE is not therefore biased due to fishermen selecting areas of high squid abundance, (b) the great majority of squid landings in Scotland are of *Loligo forbesi*, (c) most landings of squid derive from demersal gears, particularly single otter trawling, (d) the activity of the fleet extends over the whole continental shelf and is therefore thought to adequately sample the distribution of the species, (e) there are no quota on squid landings so there is little incentive to misreport catches and (f) discarding of *Loligo* is thought to be minimal, even when catches are small, so that landings can be assumed to a reflect catches (Pierce et al. 1994, 1998).

Length–frequency analysis has been used in several studies to establish geographic and temporal patterns of squid abundance (Hatfield and Cadrin 2001; Arkhipkin et al. 2006). There is no routine sampling for length frequency data on squid in the commercial fishery and previous project-based sampling has been restricted both geographically and in time, mostly focused on (then) important ports such as Kinlochbervie on the west coast (see Lum-Kong et al. 1992; Collins et al. 1997, 1999). However, FRS Marine Laboratory performs regular demersal trawling surveys in Scottish waters to estimate young fish abundance. These surveys are seasonal and cover the North Sea or west coast of Scotland or both. Although, squid are not the target of these surveys they have been recorded when present, including identification to species and measurement of mantle length. Occurrence of *Loligo forbesi* in the survey data tends to be spatially patchy, which is thought to indicate a patchy distribution (Pierce et al. 1998). Although length is only weakly related to age, with great variability in length-at-age (Challier et al. 2005), and there is evidence that animals can mature at different sizes (Boyle et al. 1995; Collins et al. 1999), and trends are likely to be complicated by the sequential recruitment of different microcohorts (Collins et al. 1999), nevertheless we would expect length to generally increase between recruitment and breeding periods. Results from Waluda and Pierce (1998) suggest that we should see evidence in the survey data of squid moving eastwards during the summer and autumn and increasing in size as they do so.

Pierce et al. (1998) found that the spatial pattern of catch rates for *Loligo* in trawl survey hauls in the North Sea in February could be related to sea bottom temperature (SBT). Subsequent analysis of fishery data showed that squid abundance in Scottish waters was positively correlated with winter sea surface temperature (SST), with higher abundance in areas with higher temperature, and negatively correlated with summer SST (Bellido et al. 2001; Pierce et al. 2001). In the present study, we are specifically interested in the relationship between body size (or abundance) and water depth or distance to shore, which could provide evidence for ontogenetic migration inshore-offshore. However, given the previously demonstrated importance of sea temperature in influencing local abundance, we also consider SST as an explanatory variable.

The main objectives of the present work were (1) to confirm whether Scottish *Loligo forbesi* performs migration movements from west coast to North Sea during winter time to spawn, and perhaps back again to west coast to recruit in Autumn, as suggested by Waluda and Pierce (1998), or whether an alternative explanation such as a west-east gradient in the timing of recruitment could better explain the data, and (2) to establish whether seasonal inshore-offshore movements occur, as has been documented in other *Loligo* species and, if these movements exist, to understand their relationship with the life-cycle and surrounding environment.

2 Material and methods

2.1 Datasets

The present study used two datasets held by Fisheries Research Services Marine Laboratory. The dominant seasonal cycle in *L. forbesi* (that of winter breeders) involves recruitment between July and November, spawning in December to March and disappearance from the fished population by June (Pierce et al. 1994; Boyle et al. 1995; Collins et al. 1997). Therefore, the time series for the present study all ran from July to June of the following year:

(a) Landings of squid in Scottish ports by all gears, 1980 to 2004, from International Council for the Exploration of the Sea (ICES) fisheries subdivisions IVa and IVb (North Sea - NS) and VIa (West Coast of Scotland - WC), and hours fishing for the fleet, in both cases summed by ICES rectangle and month of capture. However, FRS Marine Laboratory considers fishing effort (hours fishing) in demersal fisheries to be poorly reported since 1998. A visual comparison of the spatial distributions of squid catches and CPUE (summed catches divided by summed hours fishing by month, by ICES rectangle) showed similar patterns in both indices from 1980 to 1996, after which the patterns diverged. Therefore we regard total catches as an adequate abundance indicator and have used these data in all subsequent analysis.
(b) Length-frequency distributions for *Loligo forbesi* caught during trawling surveys in the same areas from 1987 until 2004. Prior to 1987, the survey series provided less complete coverage of the annual life cycle.

SST data were downloaded from the NCAR (National Center for Atmospheric Research, USA) web site, with a spatial resolution of 1 ° longitude by 1 ° latitude and re-sampled to the spatial resolution of 1 ° longitude by 0.5 ° latitude, the same as the ICES statistical rectangles. The data are monthly average model results from remotely sensed data, survey temperature data, and sea ice distribution (Reynolds and Smith, 1994). Sea depth data were downloaded from the website of the National Geographical Data Center, National Oceanic and Atmospheric Administration (NOAA, USA). The original data were gridded with 5′ by 5′ resolution; therefore the mean depth of single ICES rectangles was calculated.

2.2 West coast to North Sea migrations

Monthly sums of commercial trawl landings data (kg) from catches in each ICES rectangle were imported into a GIS system (ArcView 3.3, ESRI) to create contour maps of the spatial distribution of squid abundance of each month and each year. These maps were examined to detect month-to-month spatial shifts in the centres of high abundance.

From the survey data, we identified periods for which there was at least one sample of *L. forbesi* in most years in a given area: namely August and January/February in the North Sea, March and November/December on the west coast and assembled them to create (incomplete) time series from August to March the following year, the period during which a general increase in mantle length would be expected. Due to lack of sufficient data, series between 1993–1994 and 1995–1996 were not used. Mantle length was split into classes: $\leqslant$4.5 cm (Class 1), 5–9.5 cm (C2), 10–14 cm (C3), 15–19 cm (C4), 20–24.5 cm (C5), 25–29 cm (C6), 30–34 cm (C7), 35–44 cm (C8) and $\geqslant$45 cm (C9). Monthly length frequency distributions for each year (and for all years combined) were then examined for evidence of east-west movement over the course of post-recruit life. From summer to winter, winter breeding squid would be expected to increase in size. If a wide range of sizes is seen at any one time, consistent with the presence of a series of micro-cohorts, the eastward migration of maturing squid would tend to result in larger squid being found on the east coast than on the west coast during autumn and winter.

2.3 Inshore/Offshore migrations

The distance of the centre of each ICES rectangle, and of each survey haul (position when the net was shot), to the nearest land (distance to coast) was measured using the spatial join function of the geoprocessing extension in ArcView 3.3, using a British National Grid Projection and the coastline data from the GEBCO digital atlas. We included all islands and the Scandinavian coastline as well as the Scottish mainland coast in these calculations. For each month, the sum of monthly commercial catches (kg) from each ICES rectangle in each year (and average for all years combined), was plotted against the distance of the centre of each ICES square to the nearest coastal point. Plots were examined to identify any seasonal shifts in the distance from shore at which most squid were caught.

We also examined the monthly survey length-frequency data (again for single years and all years combined), in relation to distance from the coast, in this case focusing on three size classes, representative of small, medium and big squid: C2 (5–9.5 cm), C4 (15–19 cm) and C6 (25–29 cm). As in the previous length-frequency analysis, the annual series used data from August (North Sea), November/December (west coast), January/February (North Sea) and March (west coast). The number of animals of each length class caught in each haul was plotted against the distance of that haul from the nearest coastal point. Series from 1987-89 and 1994-1995 were not used due to lack of data in some months.

2.4 Generalised additive mixed modelling

To investigate the relationships of both size and abundance of *L. forbesi* caught with distance to the coast and environmental conditions, generalised additive mixed models (GAMM) were fitted, making use of the GAMM function available from R (version 2.4.0) mgcv/nlme library. The model selection was based on identifying which explanatory variables had significant effects and the absence of trend in residuals. To minimise the risk of accepting spurious relationships, significance was accepted only if $P < 0.01$. To avoid overfitting, the degrees of freedom for the smoothers were constrained to a maximum of 5 and to minimize the impact of between-year differences on the model, year was included as a random effect.

To model *L. forbesi* size distribution (model A), survey data was used, while fisheries data were used to model squid abundance distribution (model B and C). For model A, the mean mantle length (cm) of all squid in a haul is used as a response variable. However, in models B and C, the response variable is squid landings (kg). One characteristic of the *L. forbesi* fishery is that it is mostly by-catch and therefore

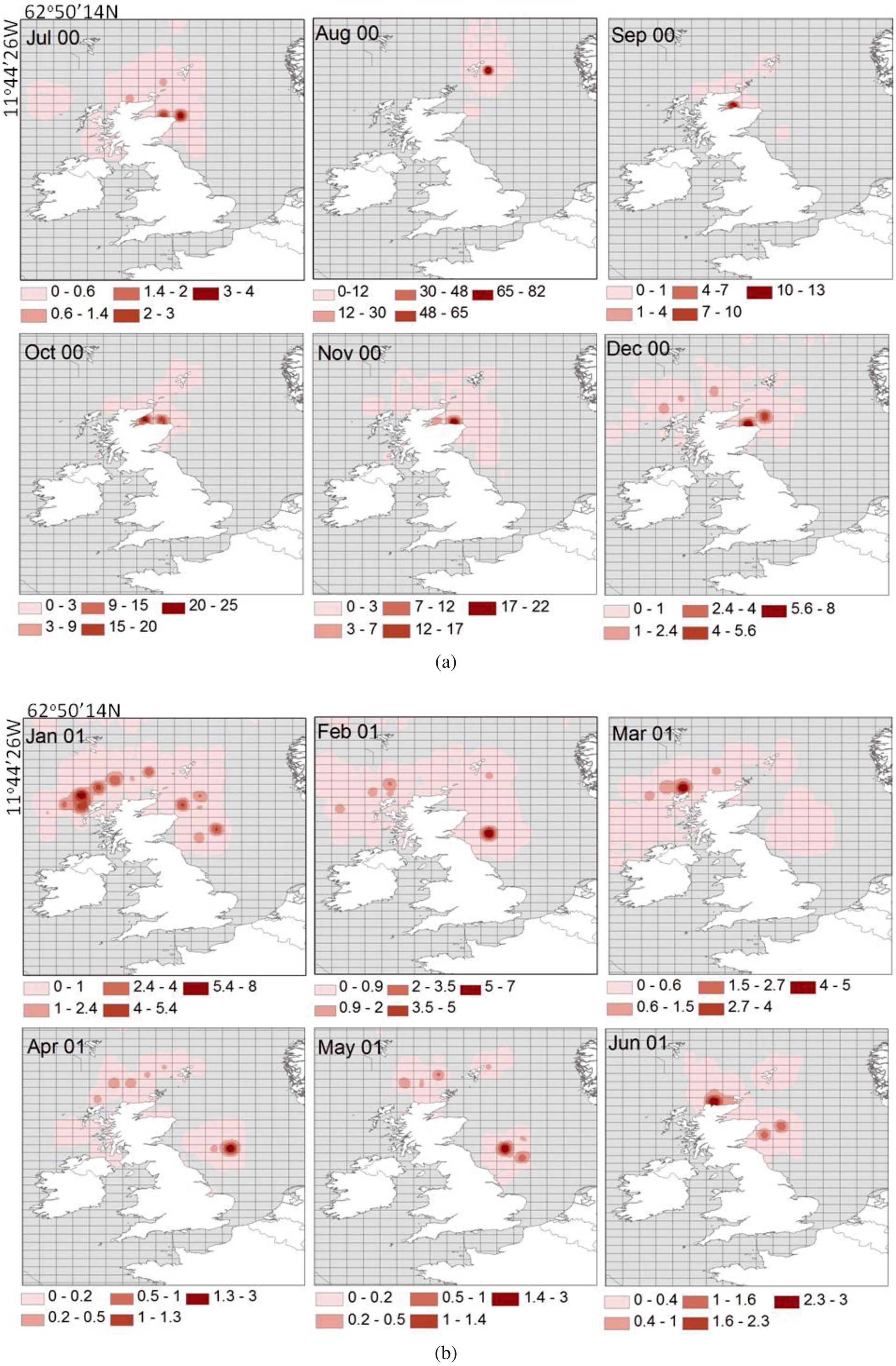


Fig. 1. Annual distribution of *Loligo forbesi* "fishery abundance" (landed catches, tons); (a) from July to December 2000; (b): from January to June 2001.

a large number of zero records of landings (by ICES rectangle by month) is common. As a consequence, squid abundance distribution was modelled in two steps. First, a binomial model (model B) was fitted to the presence/absence data. Secondly, the presence data, assuming a Gaussian distribution, was modelled (model C). Due to the existence of some very extreme values, landings data in model C were natural log transformed.

In every model, data from all years were combined, since there were very few observations in some years. Data were then divided into seasons: autumn/early winter (November and December), winter (January and February), spring (March to May) and summer (June to October). Finally, the GAMM was fitted using longitude (decimal degrees), distance to coast of the haul sampled (km), depth (m), and sea surface temperature (SST, °C) in which the haul was performed, as explanatory variables. To reduce the influence of the small number of very deep water samples, the variable depth was natural log transformed.

Before fitting the models, the auto-correlation of the data was estimated extracting series of consecutive hauls from individual cruises and running auto-correlation function in R statistic library on the average squid sizes. The results showed no auto-correlation.

3 Results

3.1 West coast to North Sea migrations

Loligo forbesi appears to be widely distributed around the Scottish coast. Although, commercial trawl hauls were performed all around Scotland, contour maps from fishery data reveal, in most of the studied years, a spatially restricted centre of abundance off North Scotland around May/June and an increase in abundance, with a spread in spatial distribution, towards the winter season. After this season, abundance begins to decrease and the spatial distribution contracts again. In certain years (e.g. 1989–1990 and 1995–1996), the GIS maps show a movement of the centre of abundance of *L. forbesi* from the west coast to the North Sea in winter and from the North Sea to the west coast in spring. However in some other years (e.g. 1981–1982 and 1994–1995), squid abundance peak appears mainly in one coast or shows a movement towards the west coast in winter and towards the North Sea in spring. Distinct abundance peaks can also be seen in different areas during the same month (e.g. October 1985).

In 2000-2001, these maps seem to provide evidence against a consistent migration of veined squid from the west coast of Scotland to the North Sea in winter and back again to west coast in spring as previously hypothesised (Fig. 1).

Based on survey data, the *L. forbesi* length frequency distribution, for the same area and month, is highly variable between years (Fig. 2). During August in the North Sea, there is a consistent dominance of small squid, especially length class 2, indicating that there is recruitment in this area. Small squid also tend to dominate on the west coast in autumn. However, it is difficult to distinguish clear or consistent patterns. In some years, size in November-December is larger than in summer of the same year, although smaller than in January-February of the following year, as expected, while differing from West to East. The occurrence of relatively small squid in the winter season, or even a mixture of class sizes, is also apparent. When approaching spring (March) on the west coast, in several of the years for which data were available, squid seem to be smaller than in the previous season, consistent with a second period of recruitment. Length frequency distributions neither completely support the idea of a dominant winter breeding population nor provide any clear evidence for migration of maturing animals from the west coast of Scotland to the North Sea.

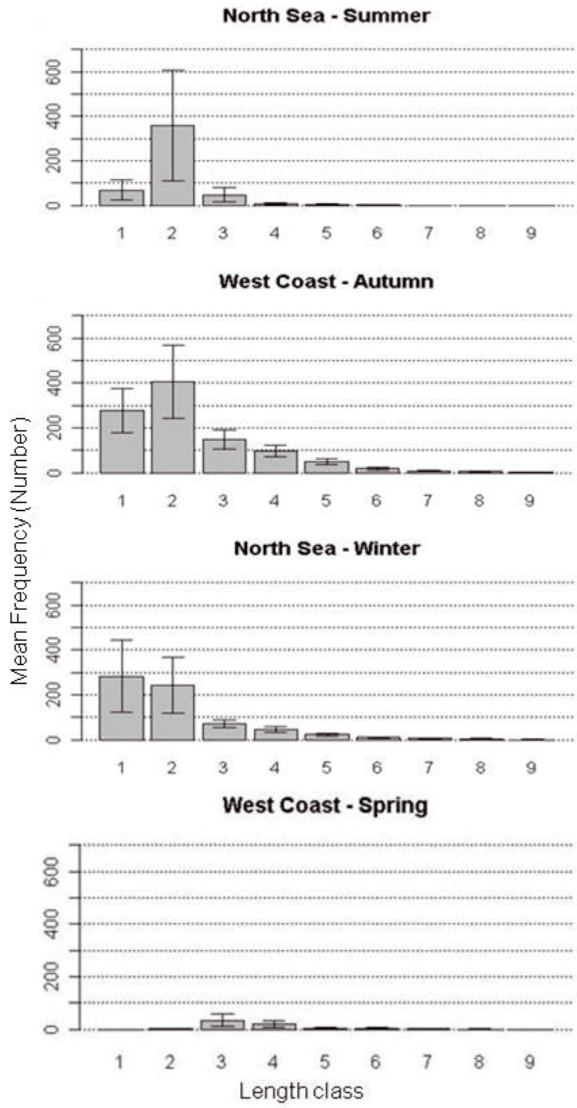


Fig. 2. *L. forbesi* length-frequency distributions, combined across all survey trawl hauls per season: mean ± standard deviations. The series starts in summer with data from the North Sea, then autumn from the west coast and continues to the winter with data from North Sea and spring from the west coast. The *x*-axis represents length class and the *y*-axis the mean frequency of squid occurrence (number).

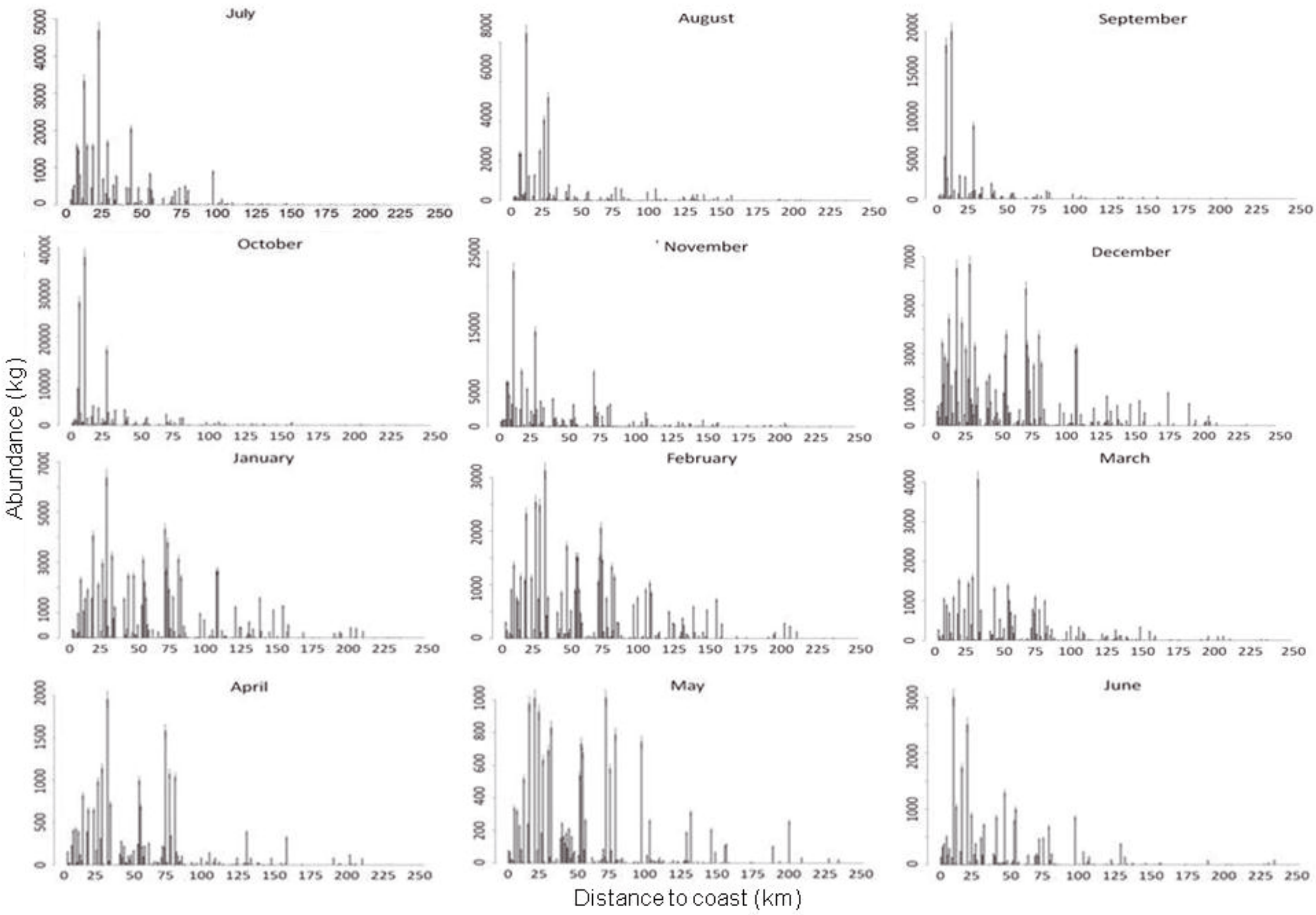


Fig. 3. Monthly *L. forbesi* fishery abundance (kg) in relation to distance to coast (km): combined data from the whole study area and all years: mean ± standard errors. The sequence starts in July and finishes in June.

3.2 Inshore/Offshore migrations

Based on fishery data, *L. forbesi* is caught both inshore and offshore, although abundance is never highest offshore and squid never completely disappear from inshore waters (Fig. 3). Between July and October (the main recruitment period), squid are mostly caught inshore, according to the distribution of squid abundance in relation to distance to coast. Between November and April of the following year, squid appear both in inshore and offshore grounds. The distribution appears to contract again, becoming more concentrated in inshore waters, in May and June. The distance from coast of the main centre of squid abundance in a given month varies somewhat from year to year, in that abundance peaks can appear in, or disappear from, offshore grounds one month earlier or later. Apart from this variation in timing, the appearance of *L. forbesi* in inshore and offshore grounds is clear and can be described as consistent. However, if there is movement from inshore waters to more offshore waters, it does not involve the whole population. It is not clear whether the contraction in range in May and June represents inshore movement or sequential disappearance (post-spawning mortality).

Squid from length classes 2, 4 and 6 all occur both in offshore and inshore grounds (Fig. 4). All three length classes tend to be found further offshore in February (winter) than in August (summer) or December (autumn) and show evidence of a shift towards the coast in March (end of winter), while the larger length classes also appear to occur further offshore in December than in August. The smallest squid are found closer inshore in December only. Individual squid are expected to increase in size over the period August to February so that the observed trends are partially consistent with an ontogenetic offshore migration. The abundance of large squid was very low in August.

3.3 Generalised additive mixed modelling

GAMM results were derived from (A) survey data using the average length from each haul as a data point and (B and C) fisheries data treating landings from one ICES rectangle in one month as a data point (Table 1). In model A, the explanatory variables "longitude", "distance to coast" and "depth" seem to be highly significant during all seasons, with exception of depth in autumn. However, the explanatory were variable SST, is significant only in summer. In both models B and C, all explanatory were variables revealed to be highly significant except for "distance to coast" during summer in model C.

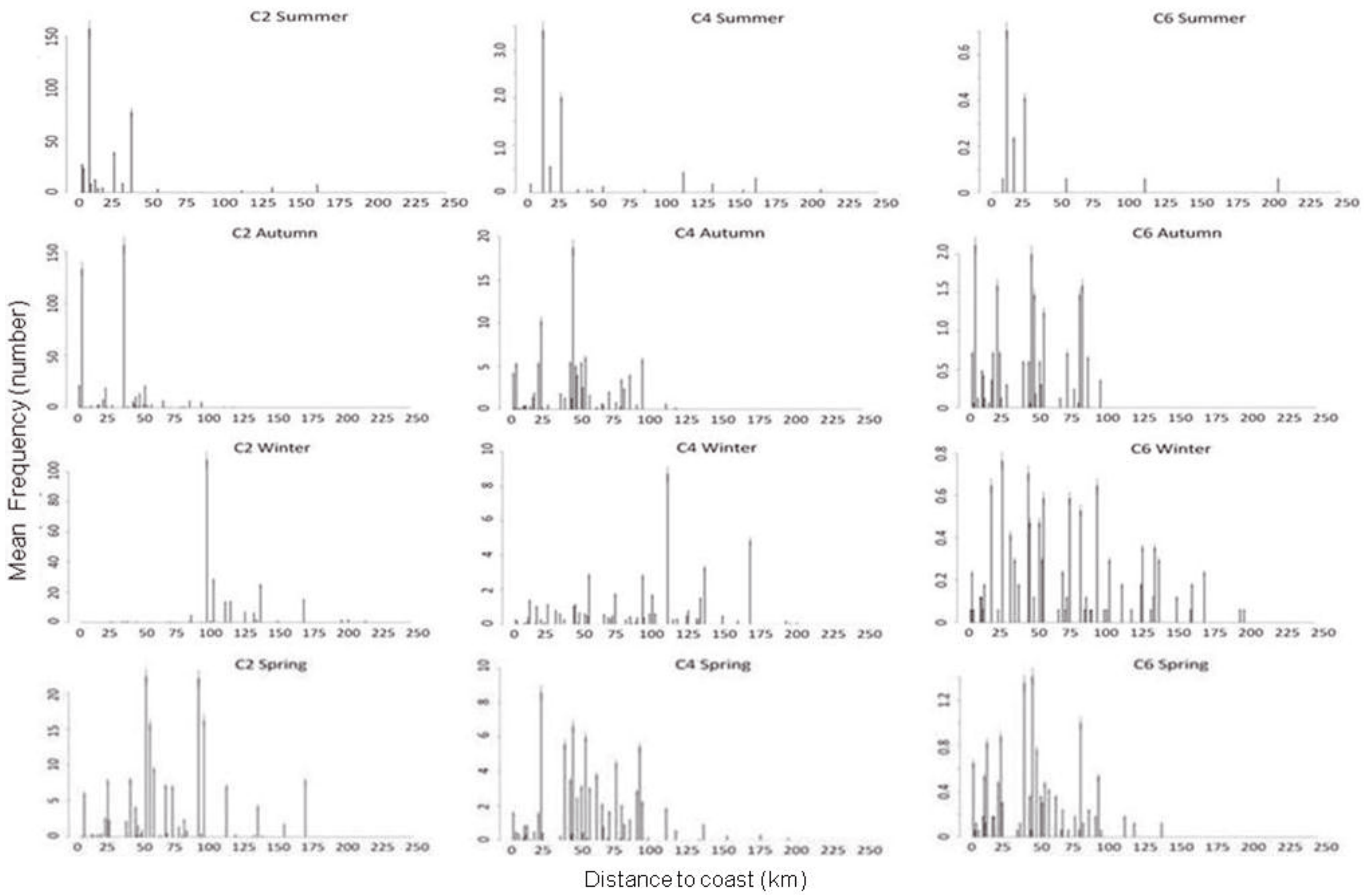


Fig. 4. Monthly *L. forbesi* survey abundance (kg) in relation to distance to coast (km): mean by size class and 95% confidence intervals. The series runs from summer to spring and data are presented for length classes C2, C4 and C6.

As a limit of 5 knots was fixed for all models, therefore the degrees of freedom of the smoothers vary between ∼1 and ∼4 in all seasons and for all explanatory variables.

The dispersion of standardised residuals, when plotted against the fitted values, was similar in all seasons within the same model. For that reason, here we show the residuals dispersion of the winter season as an example for model A and C (Fig. 5). No apparent pattern was detected in any of the models.

3.4 Generalised additive mixed modelling on squid size

The GAMM smooth curves for the variable "distance to coast" of model A (Fig. 6a) show that bigger squid appear closer to coast than smaller squid in winter and spring. However, in summer and autumn the opposite relationship is visible, bigger squid appear in waters further from the coast. In spring, summer and autumn, the shapes of the smoothers indicate that the trends may be reversed in waters most distant from the coast but confidence limits for this region are wide due to the low number of samples.

The results from the smoothing curve for longitude are very clear (Fig. 6a). In winter and spring, the squid length seems to increase from West to East. During summer and autumn, squid length seems to decrease from West to East. Although in autumn there were no available data for positive longitudes (east of 0°), the clear trend with tight confidence limits in this smooth curve indicates a negative relationship between "longitude" and squid length (bigger squid in the West).

The smooth curves for the effect of depth (Fig. 6b) show a similar relationship in summer, autumn and winter: bigger squid seem to be in deeper waters than small squid. However in spring, the relationship appeared to be more complex, with smaller squid also present at intermediate depths.

During spring, when temperature is a significant parameter for model A (Fig. 6b) the smooth curve for this effect shows that smaller squid occur in cooler waters than bigger squid.

3.5 Generalised additive mixed modelling on squid presence and abundance (given presence)

Models B (presence, Fig. 7) and C (abundance given presence, Fig. 8) showed quite similar results for most explanatory variables in most seasons. However, different results are apparent for the explanatory variables "distance to coast" in winter and SST in autumn and winter.

The smooth curves for the variable "distance to coast" (Figs. 7a and 8a) show that in autumn squid seem to be evenly distributed until a distance of approximately 150 km from the coast, where the abundance starts to decrease. This same relationship is seen in model B in winter, however in model C during winter, before this same pattern becomes visible, there is an increase in squid abundance until 50 km from the coast. The smooth curves for "distance to coast" in spring reveal an increase in squid abundance in waters further from the coast. Trends are least clear in summer.

In models B and C, across all seasons, the squid abundance seems to increase from West to East until approximately 3° W (Figs. 7a and 8a) where the abundance starts to decrease. This pattern reveals an abundance peak situated in the north of Scotland throughout the whole year.

The smooth curves for the effect of depth on abundance (Figs. 7b and 8b) show a similar relationship through all seasons. There seem to be an increase in squid abundance until intermediate depth waters and abundance then decreases in deeper waters.

The smooth curves for SST in models B and C (Figs. 7b and 8b) show that in summer, above 11 °C, squid abundance seems to decrease with increasing temperature up to 15 °C, where the confidence intervals become too wide to detect a relationship. In spring, squid seem to occur evenly distributed until water temperatures reach approximately 9 °C above which squid abundance seem to decrease with the increase of temperature. The SST smooth curves for winter and model B show that between 6 °C and 9 °C, squid presence is higher in warmer waters. However, above and below this temperature limits, abundance seems to decrease with the increase of temperature. In model C, the smooth curve for SST in winter clearly shows a positive relationship between squid abundance and temperature. For autumn, model B revealed that squid abundance occurs evenly distributed across all temperatures up to 11 °C where abundance starts to slightly decrease with the increase temperature. In model C, it a slight increase in squid abundance until approximately 11 °C is visible.

4 Discussion

Although there have been numerous previous studies on the biology and abundance of Loligo forbesi in Scottish waters, until now there has been no comprehensive evaluation of evidence for migration patterns.

4.1 West coast to North Sea migrations

The GIS maps generated in the present study indicate that *L. forbesi* does not routinely migrate from West to East coast of Scotland during winter or back towards the west coast in spring as had been suggested by Waluda and Pierce (1998). If such movement exists, the centre of abundance would expected to shift from the west coast of Scotland in late summer and autumn towards the North Sea in winter, where spawning may take place (Waluda and Pierce 1998; Pierce et al. 2001; Young et al. 2006a). The lack of this pattern in the data from most years analysed during the present study is evidence against such movement.

Different technical approaches were used by Waluda and Pierce (1998) and the present study. However, apart from small differences due to those divergent techniques, re-analysis of the five-year series used in Waluda and Pierce (1998) revealed no contradictory results, since for those few years the patterns are quite similar in both studies. In these years, a major abundance peak was registered for *L. forbesi* in Scottish waters (Zuur and Pierce 2004), possibly due to the mildest winter climate seen in the North Sea for 50 years (Becker and Pauly 1996), which could have influenced squid distribution in several ways. Squid may actively seek waters of a particular temperature (since they are poikilothermic) or may follow the distribution of their prey. Migration of squid into Scottish waters from further south, as Pierce and Boyle (2003) suggested, for example due to the strong coastal current flow along the west coast of Scotland that brings Atlantic water into the area and increases nutrient supplies, might also be a reason that led to the apparent migration pattern, described by Waluda and Pierce (1998). This inflow of Atlantic waters into the North Sea is higher in warmer years (Turrel et al. 1992)

The GIS maps of veined squid abundance, although not consist with the proposed East-West migration, are consistent with the alternative hypothesis that squid spread out from a rather localised area, which is more usually to the north. This spatially restricted peak of abundance in the North of Scotland usually appears around June and is followed by a spatial expansion of abundance when approaching the winter season. Although, the pattern is not evident in every year, *L. forbesi* seems to concentrate in the North of Scotland, which constitutes a possible spawning and/or recruitment site. Some maps also reveal two distinct abundance peaks, either in different coasts or one further south than the other. This could suggest that two cohorts or microcohorts exist (see Collins et al. 1997, 1999; Pierce et al. 2005), with different migratory behaviour – as Arkhipkin et al. (2004) discussed for the migratory squid *L. gahi*. However, these two abundance peaks are not visible in all years. One other possibility is the migration of *L. forbesi* from English or Irish waters into more northern waters in some years. Sims et al. (2001) reported that, according to environmental conditions, this species could vary the timing and range of its migration.

The length frequency analysis performed using survey data revealed no evidence of a consistent migration pattern from one coast to another. Since summer-autumn is thought to be the most important recruitment season (Collins et al. 1997), small to medium-sized animals are expected to be present. Squid length is expected to increase as the summer/autumn recruits mature prior to the (more important) winter spawning season (Collins et al. 1997). If squid migrate West to East and there are several microcohorts, the largest animals would tend to be found in the east. Peaks in the presence of small squid in the survey catches provide information on the timing of recruitment but clear evidence that growing squids move from west to east could not be identified in the present analysis.

According to Holme (1974), Collins et al. (1997, 1999), and Pierce et al. (2005), veined squid have two spawning seasons, in winter (around January) and in summer, although the latter is not as important as the first. Two recruitment seasons also occur in Scottish waters, the most important in late summer/autumn and the other in spring. The presence of almost exclusively length class 2 (5–9.5 cm) in August is evidence

Table 1. Approximate significance values of smooth terms, square R and number of observations used in the GAMM obtained from models A (squid average length in each haul), B (presence) and C (abundance given presence). The GAMM was fitted for summer (June to October), autumn (November and December), winter (January and February) and spring (March and April); $p < 0.0001$ except were indicated see subscripts below.

Model	Explanatory variable	df	F
Model A (length)			
summer $R^2 = 0.299$, $N = 1024$	Distance	2.12	13.73
	Longitude	1	14.13
	Depth	3.72	26.15
	SST (1)	3.72	5.75
autumn $R^2 = 0.073$, $N = 3102$	Distance	3.57	8.21
	Longitude	1	46.15
	Depth (2)	2.74	3.15
	SST (3)	2.75	1.33
winter $R^2 = 0.12$, $N = 1435$	Distance	1	86.24
	Longitude	2.06	6.87
	Depth	2.50	3.25
	SST (4)	2.28	2.33
spring $R^2 = 0.098$, $N = 2630$	Distance	2.38	7.46
	Longitude	3.31	12.29
	Depth	3.81	18.85
	SST	1.2	9.81
(1) p = 0.04, (2) p= 0.02; (3) p = 0.28, (4) p = 0.07			
Model B (presence)			
summer $R^2 = 0.188$, $N = 12434$	Distance	3.28	14.88
	Longitude	3.99	321.33
	Depth	3.96	198.26
	SST (1)	3.90	59.61
autumn $R^2 = 0.135$, $N = 4612$	Distance	3.51	14.53
	Longitude	3.77	79.65
	Depth	3.87	81.99
	SST	2.75	2.56
winter $R^2 = 0.235$, $N = 4761$	Distance	3.54	8.55
	Longitude	3.60	42.35
	Depth	3.94	88.48
	SST	3.88	49.28
Spring $R^2 = 0.146$, $N = 7629$	Distance	3.66	32.81
	Longitude	3.94	147.71
	Depth	3.96	179.77
	SST	3.52	37.65
(1) p = 0.05			
Model C (abundance given presence)			
summer $R^2 = 0.174$, $N = 4727$	Distance (1)	3.91	1.95
	Longitude	3.81	64.18
	Depth	3.83	23.29
	SST	3.67	14.56
autumn $R^2 = 0.232$, $N = 3252$	Distance	3.89	47.43
	Longitude	3.45	132.89
	Depth	3.89	67.22
	SST	2.4	6.19
winter $R^2 = 0.257$, $N = 2953$	Distance	3.83	10.46
	Longitude	3.84	84.77
	Depth	3.96	83.72
	SST	2.99	37.22
spring $R^2 = 0.169$, $N = 3247$	Distance	2.73	25.08
	Longitude	3.79	51.75
	Depth	3.86	34.94
	SST	2.91	22.78

(1) p = 0.13.

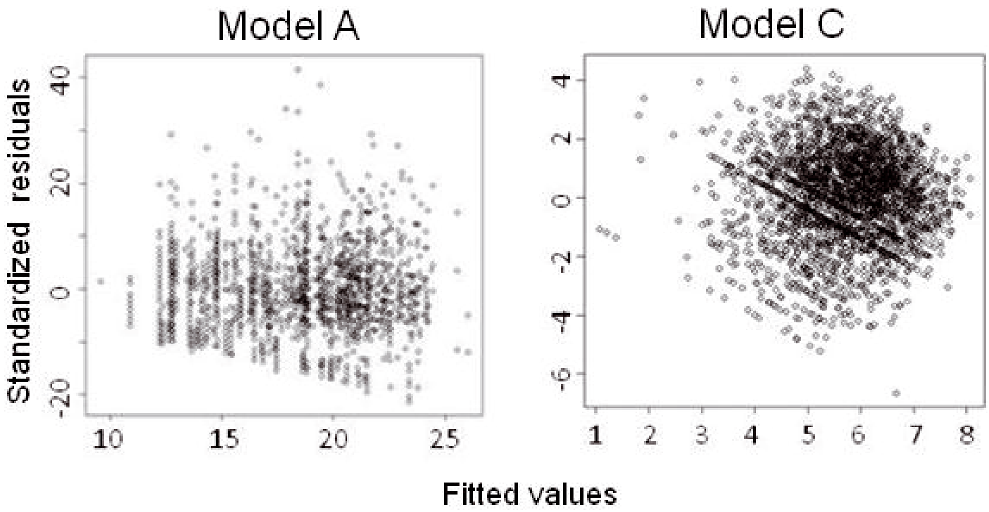


Fig. 5. GAMM residuals dispersion. Standardized residuals (y-axis) for datasets. Model A: average length in each haul; Model C: fisheries abundance as a response variable, against the fitted values (x-axis) of the models.

of the (dominant) summer recruitment season, these animals being future winter spawners (Pierce et al. 2005). Full recruitment to the main commercial (by-catch) fishery occurs at a mantle length of approximately 15 cm (Pierce et al. 1994) although finer mesh nets are used for directed fishing in the Moray Firth (Young et al. 2006b), which will effectively result in a smaller size at (fishery) recruitment. In spring (April), a second wave of recruitment (i.e. smaller animals) is expected to appear on the west coast (Pierce et al. 1994). The present length frequency analysis reinforces the suggestion of a second recruitment season in that length class 1 or 2 animals were also present in other seasons. However, there was no other peak of recruitment that was as clearly defined as in autumn, which can also indicate that recruitment season is extended for several months as suggested by Lum-Kong et al. (1992).

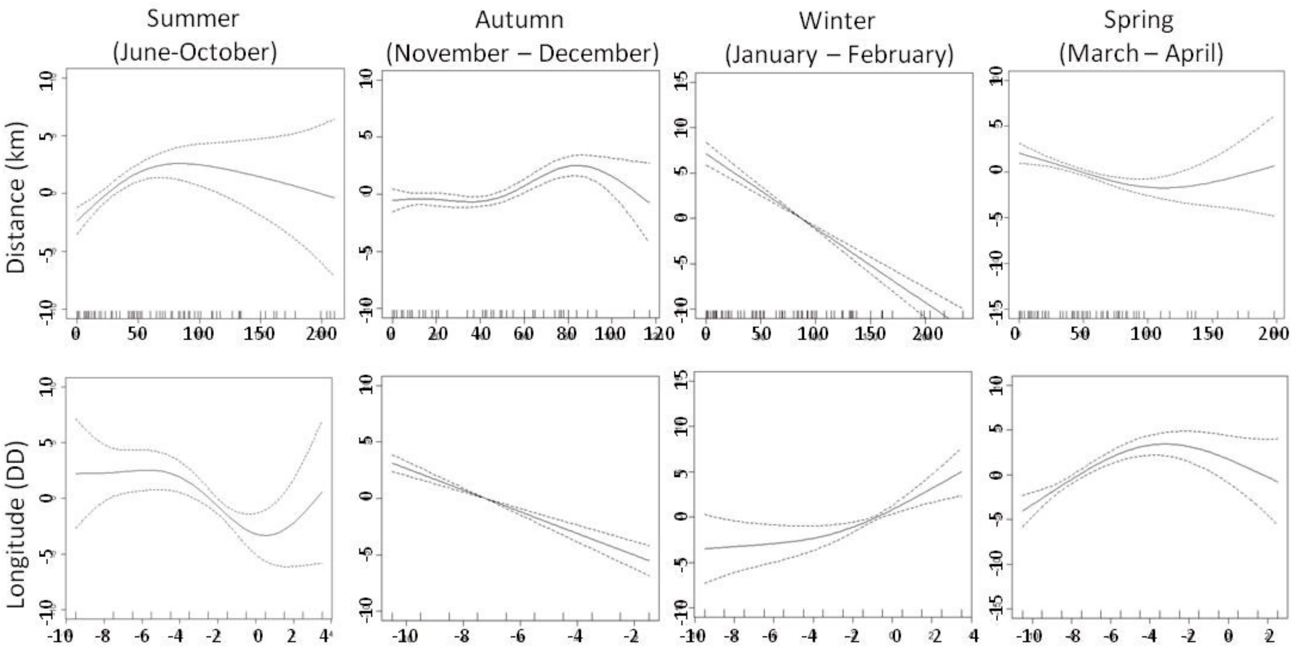
The existence of two (or more) cohorts (or micro-cohorts) would result in at least two different sizes in the same sampling area which may hide possible size distribution patterns within cohorts. Other concerns regarding the interpretation of the length-frequency analysis arise from the apparent reduction of average female size during the winter spawning season (possibly due to earlier breeding and hence post-breeding mortality in larger animals) (Collins et al. 1997), the highly variable growth rates (Pierce et al. 1994), and the possibility of incorrect identification of small squid (e.g. if *Alloteuthis* are sometimes mistaken for small *Loligo*, as discussed in Pierce et al. 2005).

4.2 Inshore/Offshore migrations

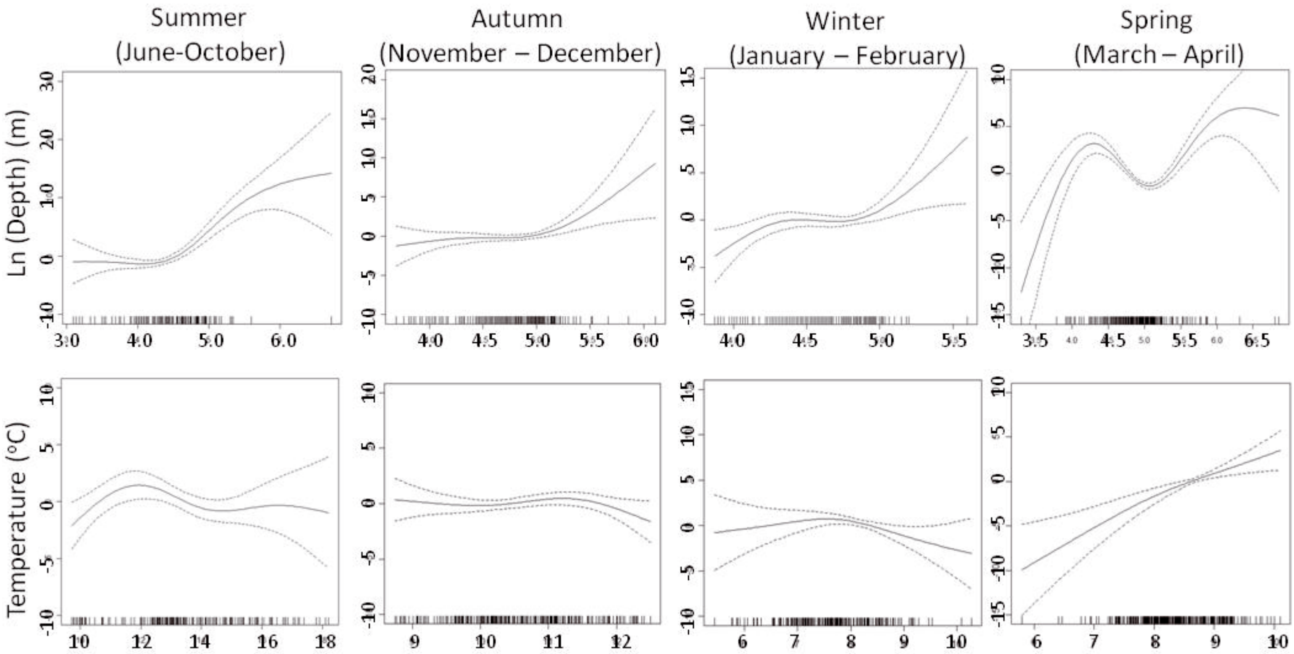
Studies on other loliginid squid species, such as *L. pealeii* from the northern United States (Hatfield and Cadrin 2001) or *L. gahi* from the SW Atlantic, suggest a movement of young squid from their nurseries in shallow inshore waters to feeding grounds in deeper waters (Hatfield and Rodhouse 1994). The hypothesis of an inshore-offshore migration in Scottish *L. forbesi* was first considered in the present study, analysing the monthly distance of centres of fishery abundance to the coast. Between May and October (spring and summer), squid appear almost exclusively close to the coast, suggesting that summer spawning and possibly spring recruitment take place in inshore grounds. This period also encompasses the start of the autumn recruitment period, and data from the commercial fishery in the Moray Firth suggests that small squid first appear close inshore in July and August (Young et al. 2006b). Between November and April (from late autumn to early spring) squid also appear in offshore waters but never completely disappear from the inshore grounds: therefore where winter breeders spawn or where late autumn recruitment occurs is not clear from these data. In some years, high squid abundance appears in offshore grounds one month earlier or later than usual, but otherwise the pattern described above is rather consistent between years.

Arkhipkin and Middleton (2002) discussed possible distinct migratory behaviour around the Falkland waters between two different cohorts of *L. gahi*: when one cohort is in offshore areas to feed the other is in inshore waters to spawn and this arrangement changes when the maturity season of the offshore cohort arrives (Arkhipkin et al. 2004). In the present study, since *L. forbesi* is present close to the coast all year around, and very few squid are recorded offshore in spring and summer, it is possible that one cohort is resident in inshore waters. Because in autumn and winter squid also appear far from the coast, it may be inferred that a distinct cohort (or part of the inshore cohort) migrates to offshore grounds. This hypothetical migratory cohort may derive from Scottish coastal waters, interacting with the hypothetical non-migratory cohort between May and October, or could migrate to offshore areas from the south as Pierce and Boyle (2003) discussed, or elsewhere.

According to Zuur and Pierce (2004) the mismatch, in abundance trends for autumn recruits and winter breeders in Scottish waters, could indicate that part of the adult spawning population migrates into Scottish waters from elsewhere in winter rather than arriving as immature animals in the autumn. Holme (1974) reported that the main spawning season of *L. forbesi* in the English Channel occurs during winter in



(a)



(b)

Fig. 6. GAMM results for model A. Squid average length is represented as a function of the smooth terms; (a) distance to coast and longitude; (b) ln (depth) and SST for each season. Dashed lines represent standard error boundaries around the main affects.

offshore grounds, and Lordan and Casey (1999) described the appearance of *L. forbesi* egg masses in offshore areas of Irish waters suggesting that spawning should occur in waters distant from the coast. Squid of intermediate length (classes C4 and C6) do not reveal any consistent distribution pattern but they seem to disappear from offshore waters in August and in some years in March. This may suggest that both summer spawning and spring recruitment occurs in inshore grounds, as Collins et al. (1995) and Lum-Kong et al. (1992) suggested for Ireland and Scotland, based on finding some egg masses on static fishing gear during summer. We observed *Loligo* eggs attached to creels in Stonehaven (near Aberdeen, North Sea) in July 2007.

Some of the apparent variability in seasonality of the life cycle of *L. forbesi* could reflect variation in the relative strength of summer and winter breeding populations (Zuur and Pierce 2004).

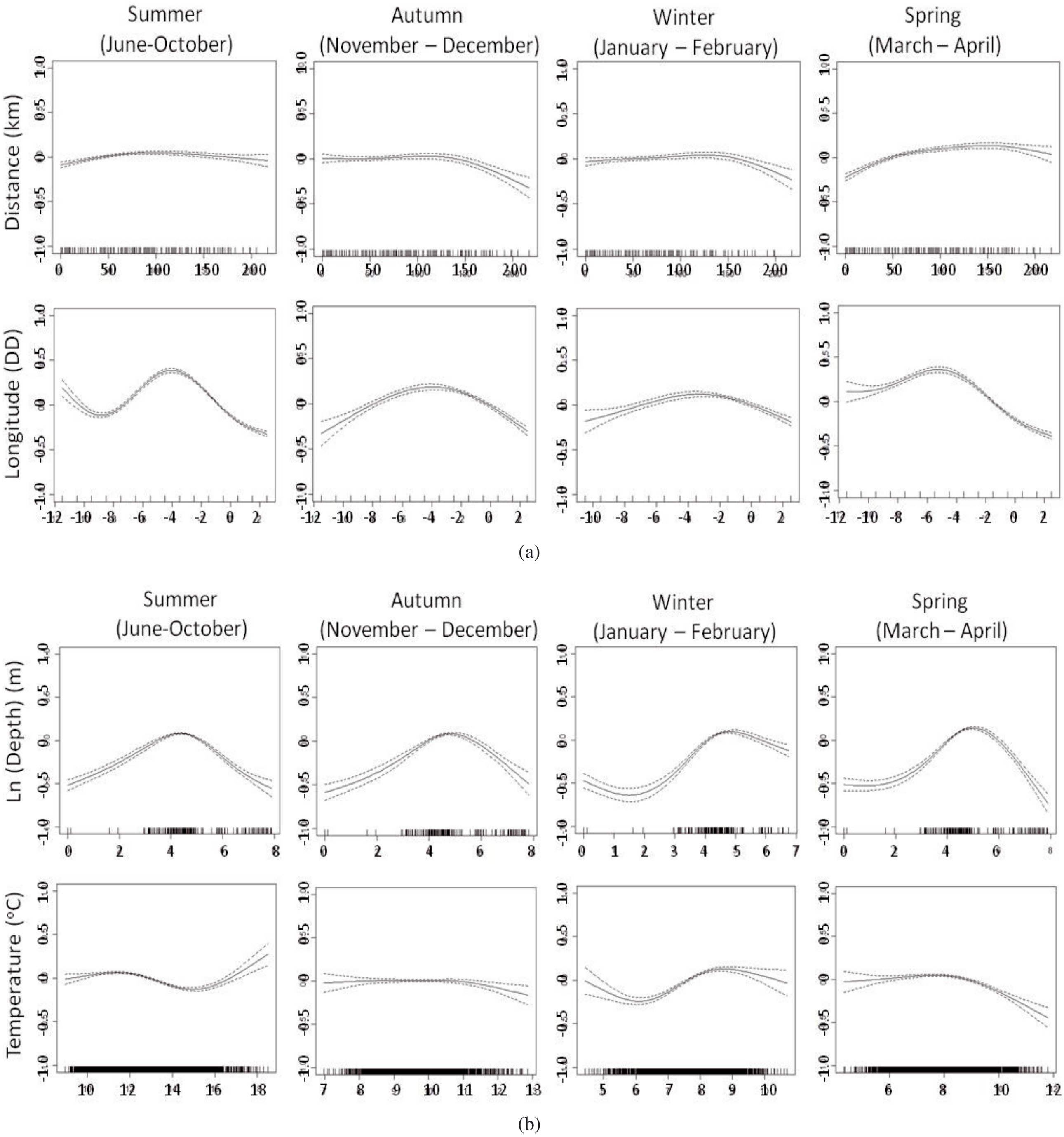


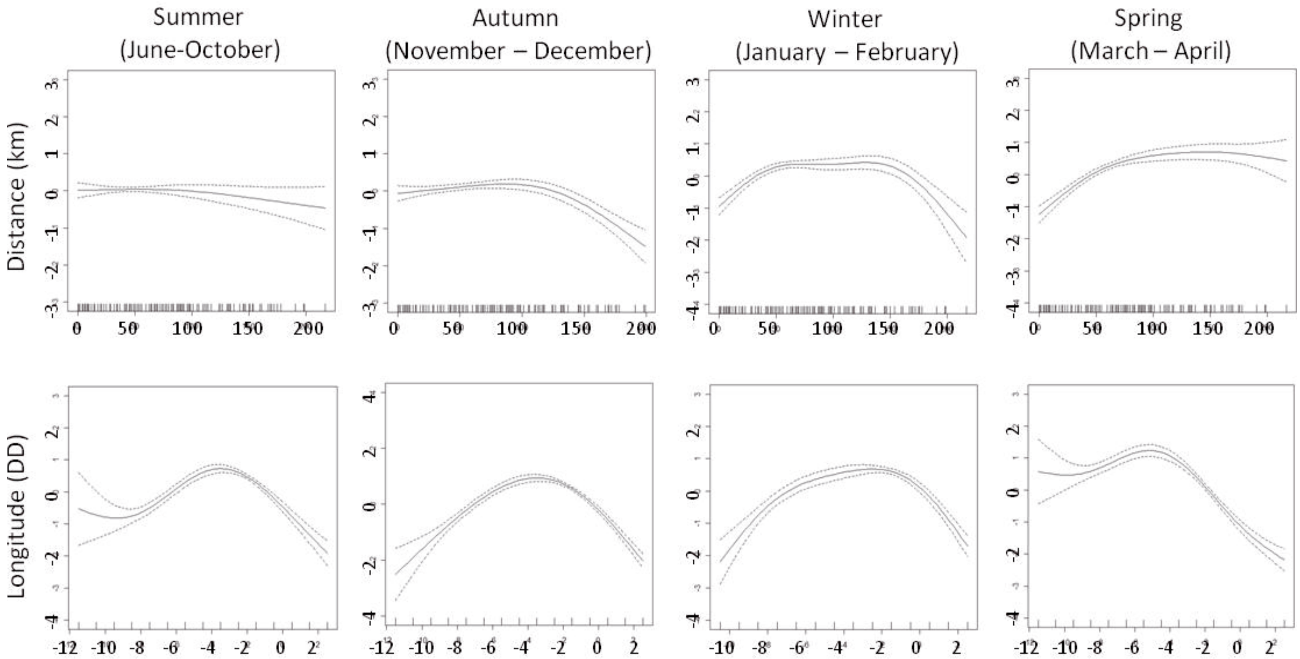
Fig. 7. GAMM results for Model B. Squid presence/absence are represented as a function of the smooth terms; (a) longitude (DD) and distance from coast (km) for each season; (b) SST (°C) and ln (depth) (m) for each season. Dashed lines represent 95% confidence limits around the main effects.

4.3 GAMM results

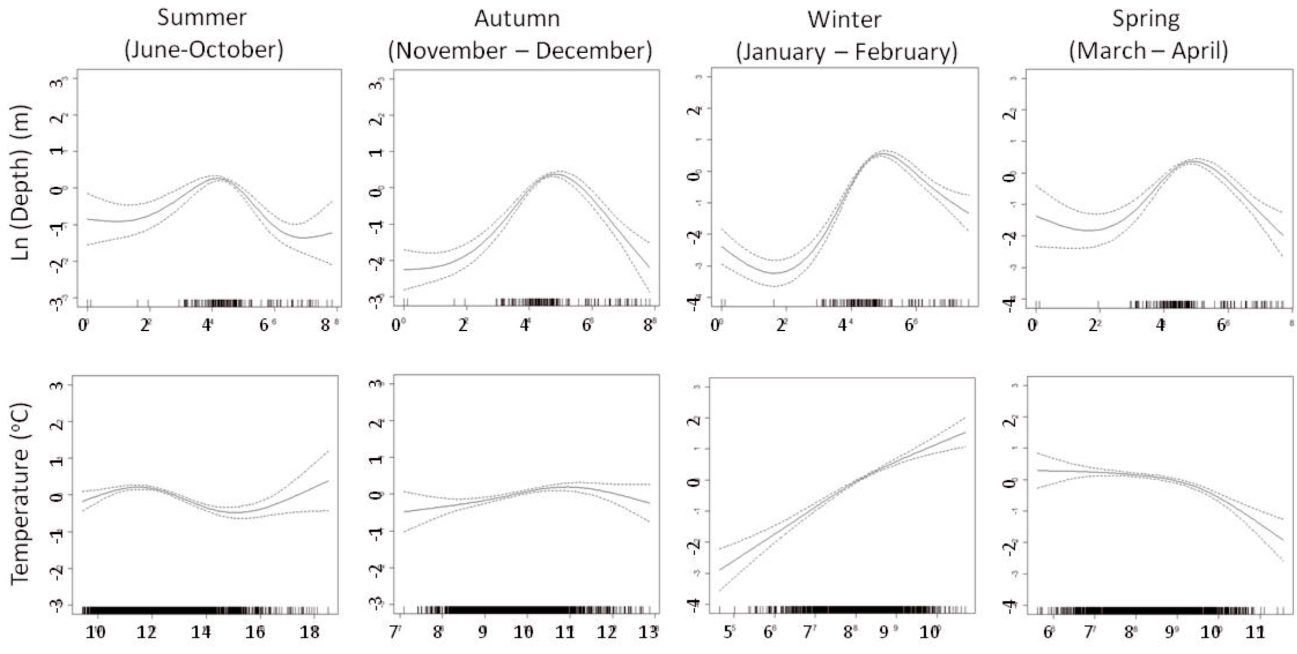
The residual distribution in all season of models A and C (Fig. 5), taken together with the significance values, suggests that the GAMM approach was appropriate, and models were adequate. Many of the smooth curves show complex relationships (i.e. neither simple linear trends nor single peaks or troughs), possibly reflecting the presence of more than one cohort of squid.

4.4 GAMM results on squid size

Several studies have been carried out on how environmental conditions affect squid movements and distribution,



(a)



(b)

Fig. 8. GAMM results for Model C. Squid landings are represented as a function of the smooth terms; (a) longitude (DD) and distance (km) for each season; (b) ln(depth) and SST (°C) for each season. Dashed lines represent 95% confidence limits around the main affects.

in particular the effect of sea surface temperature (SST) e.g. Arkhipkin et al. (2004a).

Distance of the haul from the coast and water depth were significant parameters in almost all seasons, which can indicate depth-related size segregation, perhaps reflecting inshore-offshore movements. The main trend visible in the smoothers representing the effect of distance to coast is an increase in squid length with proximity to coast in winter and spring, and a decrease in squid length in summer and autumn. Considering that depth increases with distance to coast, the smooth curves for the "distance to coast" variable in summer and autumn are consistent with findings by Arkhipkin et al. (2004a) for *L. gahi* from the Falkland Islands. The authors suggest that *L. gahi* juveniles move from spawning grounds located in shallow, inshore waters to feeding grounds near the shelf edge. Immature squid feed and grow in these offshore feeding grounds and, upon maturation, migrate back to inshore waters to spawn. Evidence from the GAMM, assuming that larger squid are breeding animals, suggests that breeding *L. forbesi* are present in inshore waters in winter. In summer the apparent trend is for larger squid to be found further offshore. However, most squid were found close to the coast in summer and this is also the main recruitment period, so that strong recruitment close inshore may dominate the relationship between average size and distance to coast regardless of where breeding takes place. Nevertheless, almost all *L. forbesi* spawning records come from inshore areas, e.g. Lum-Kong et al. (1992) found egg masses attached to inshore creel lines in Scotland. However, Lordan and Casey (1999) reported egg masses from this species in trawls at water depths of 135, 302 and 507 m.

Squid mantle length also tends to increase from West to East in winter and spring as far as 3° W (mid-way along the northern Scottish coast and also the western part of the Moray Firth). The concentration of the largest animals in this zone could signify that larger animals migrate into this area, presumably to breed, or that the life-cycle is more advanced in this zone and animals start to breed earlier. In summer and autumn there was an increase in size from east to west, which could represent a recruitment zone in the northeastern Scottish coast.

For summer, the smooth curve for SST reveals that bigger squid occur at SST around 12 °C. As evidence suggest that, in Scottish waters, squid from the winter cohort recruit during summer (Collins et al. 1995), this finding seems to be in agreement with Challier et al. (2005). The authors suggest that recruitment (therefore smaller squid) appears to be associated with low temperature in *L. forbesi* from the English Channel. Arkhipkin et al. (2004) however, suggests that, in summer, immature *L. gahi* prefer warmer waters. Nevertheless, *Loligo forbesi* is the most cold water *Loligo* species and it has been reported that juveniles and post-larval stages are highly sensitive to temperature (Challier et al. 2005).

Hatfield and Cadrin (2001) found that in *L. pealeii,* off the northeastern coast of United States, the body size generally increases with depth in all seasons. Similar patterns were found in the present study. Except for spring, the smoother for the effect of depth reveals that bigger squid tend to be in deeper waters than small squid.

4.5 GAMM results on squid abundance

Several studies on squid in UK waters have demonstrated empirical spatial relationships between the spatial distribution of *Loligo* abundance and environmental variables (Holme 1974; Pierce et al. 1998; Bellido et al. 2001).

In the present study, GAMM fitted to presence and abundance data revealed clearer trends for depth than for "distance to coast", with a peak in squid presence and abundance at intermediate depth in all seasons, but over shallower waters in summer than in the other seasons, consistent with an inshore-offshore migration. Previous studies (Hatfield and Cadrin 2001; Arkhipkin et al. 2004a) on loliginid squid reported movements between spawning and feeding grounds. Arkhipkin et al. (2004a) found that *L. gahi* from the Falkland Islands migrate inshore to spawn and offshore to feed.

Previous studies detected lower abundance of squid on the east of Scotland than the west coast (Waluda and Pierce 1998). The smoothing curve for longitude revealed that *L. forbesi* do increase in abundance from West to East until at approximately 3 °W after which the abundance starts to decrease. This pattern seemed to reveal an abundance peak situated in the north of Scotland throughout the whole year.

Waluda and Pierce (1998) showed that the spatial pattern of *L. forbesi* abundance in the North Sea in the winter is strongly related to water temperature and salinity, with higher abundance in areas with higher temperature and salinity. Although such a relationship is only visible between 6 °C and 9 °C in the presence-absence model, in model C (where abundance-given-presence data are used), the smooth curve for SST clearly indicates that squid abundance in Scottish waters increases with higher temperatures in winter. In summer and autumn, there seem to be an abundance peak at approximately 11 °C. Bellido et al. (2001) first used GAM to model fishery abundance of *L. forbesi* in the years 1983, 1988, 1989 and 1991 and found that, once seasonal variation was taken into account, high abundance was consistently restricted to a temperature range of 8–13 °C .

5 Conclusion

In conclusion, the present study provides evidence against the east-west migration of the veined squid in Scottish waters previously proposed by Waluda and Pierce (1998). Alternatively, we suggest a spreading out of veined squid abundance around June from a rather localised recruitment area, which usually occurs in the North of Scotland. Analysis of the veined squid abundance and length frequency against distance to coast allowed identify possible inshore-offshore movements. It seems that both *L. forbesi* cohorts have different migratory behaviour; e.g. while one is resident in inshore waters the other migrates to offshore waters during winter as Arkhipkin and Middleton (2002) discussed for *L. gahi* in the Falkland waters. Inshore waters are therefore likely to be the spawning ground for both veined squid cohorts. GAMM results show the possibility of depth-related size segregation in all seasons, perhaps reflecting inshore-offshore movements in Scottish waters. According to the GAMM analysis on fishery data, *L. forbesi* in Scottish waters can be found in higher abundance and bigger sizes at middle longitudes, intermediate depths and, depending on seasons, on water with approximately 11 °C. Nevertheless further studies considering prey abundance and squid maturity would allow for a better comprehension of *Loligo forbesi* movements in Scottish waters.

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