



## Habitat and distribution of post-recruit life stages of the squid *Loligo forbesii*



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### ABSTRACT

This study models habitat preferences of the squid *Loligo forbesii* through its post-recruitment life cycle in waters around Scotland (UK). Trawl survey and market sample data from 1985 to 2004 are used to model seasonal habitats of immature, maturing and mature squid (maturity being inferred from size and season). Squid presence–absence and catch rate in areas of presence were analysed using generalised additive models, relating spatiotemporal patterns of distribution and abundance to ecogeographic variables. For all maturity classes, higher abundance in winter and spring (i.e., quarters 1 and 2) was associated with deeper water while higher abundance in summer and autumn (quarters 3 and 4) was associated with shallower water, consistent with seasonal onshore–offshore migrations but suggesting that most spawning may take place in deeper waters. The preferred SST range was generally 8–8.75 °C while preferred salinity values were below 35‰ in winter and summer and above 35‰ in spring and autumn. Squid were positively associated with gravel substrate and negatively associated with mud. Seasonal changes in habitat use were more clearly evident than changes related to inferred maturity, although the two effects cannot be fully separated due to the annual life cycle. Habitat selection for this species can be satisfactorily modelled on a seasonal basis; predictions based on such models could be useful for fishers to target the species more effectively, and could assist managers wishing to protect spawning grounds. The extent to which this approach may be useful for other cephalopods is discussed.

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### 1. Introduction

Environmental conditions play an important role in the life cycles of cephalopods. High metabolic rates and high physiological sensitivity to changing environmental conditions result in high and variable growth rates and potentially high mortality if suitable food organisms are not sufficiently abundant, especially in early life stages. In addition, most species have short life cycles and non-overlapping generations, hence no buffering of population abundance against fluctuations in recruitment strength, resulting in marked environmentally driven between-year variation in distribution and abundance (see Pierce et al., 2008 for a review). Different life cycle stages are expected to show different environmental preferences.

Interannual variation in abundance has been shown to be linked to changing environmental conditions in many species. High SST within hatching areas of the Argentine shortfin squid *Illex argentinus* results in subsequent high abundance in the fishing grounds (Waluda et al., 2001). Interannual variation in abundance of the benthopelagic loliginid *Loligo forbesii* in UK waters is correlated with the North Atlantic Oscillation (NAO), sea surface temperature (SST) and sea bottom temperature (SBT) (Pierce et al., 1998; Bellido et al., 2001; Pierce and Boyle, 2003; Zuur and Pierce, 2004; Pierce et al., 2005). Robin and Denis (1999) found that the previous year's winter temperature could be used to predict fishery landings of this species in the English Channel. Georgakarakos et al. (2002) found a positive correlation between loliginid squid landings in Greek waters and SST in nutrient-rich areas. In the Falkland Islands, recruitment of *Loligo gahi* is related to the SST in October of the previous year (Agnew et al., 2002).

Ontogenetic migrations between feeding and spawning grounds are well-known in squid and cuttlefish, and again many

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studies highlight environmental links. Along the French Atlantic coast, cuttlefish (*Sepia officinalis*) distribution during the spawning season extends further north in warm years (Wang et al., 2003). Seasonal migratory movements of *L. forbesii* in UK waters are also temperature-dependent, with higher water temperatures resulting in earlier yearly migrations (Sims et al., 2001).

Although the mechanisms underlying interannual variation in abundance, seasonal movements and spatial distribution can be difficult to disentangle, studies focused on environmental correlates of spatial distribution are perhaps most relevant for identifying habitat preferences. Many studies link distribution to sea temperature. Thus, spawning zones of the squid *Ommastrephes bartramii* have been characterised in terms of SST (Ichii et al., 2009) and several studies have linked local abundance of *L. forbesii* to sea temperature (Waluda and Pierce, 1998; Bellido et al., 2001; Viana et al., 2009).

Cephalopod preferences for sediment type at different stages of the life cycle are less well documented. Sauer et al. (1992) found that *Loligo reynaudii* eggs off South Africa were mostly concentrated over either fine sand or flat reef, often in somewhat sheltered bay locations. In Scotland, a small directed fishery takes *L. forbesii* in inshore waters over rocky ground at the start of the season, and over sandy/muddy bottom later in the season (Young et al., 2006; Smith, 2011), possibly indicating a shift in habitat preference with maturity. Blanc et al. (1998) found cuttlefish nurseries in Morbihan Bay (France) on both heterogeneous (stone, shell-debris, sand and mud) and homogeneous (principally mud) bottom types.

Investigation of how environmental variables affect marine species throughout their life cycle can help identify habitat preferences and enable forecasting of distribution and abundance patterns, thus potentially contributing to responsible and sustainable fishery management (Valavanis et al., 2008). As fisheries are increasingly viewed within the wider context of marine spatial planning, identification of so-called “essential habitat” will also inform management of interactions between fishing and other human uses of the marine environment.

Statistical models of habitat preferences can be used to identify suitable sites for marine reserves. Cañadas et al. (2005) used models of cetacean habitat use in Spanish Mediterranean waters to define the boundaries of three proposed special areas of conservation (SACs). Most European cephalopod fisheries are largely or wholly unregulated, and the identification of important nursery, feeding and spawning habitats grounds could provide a basis for spatial management.

Valavanis et al. (2002) developed a marine information system for exploited cephalopods in the Eastern Mediterranean, which integrated life history data with a Geographic Information System (GIS). Information on limits of occurrence in relation to various environmental parameters was used to build composite maps indicating habitat suitability. Recent advances in statistical modelling, e.g., the development of generalised additive models (GAMs) and generalised linear models (GLMs) and the R language, coupled with the availability of satellite-derived oceanographic data, allow generation of more sophisticated models of species distribution and abundance. A GAM-based approach for *L. vulgaris* in the northwest Mediterranean showed that SST (with negative effects above 17.5 °C) and photosynthetically active radiation (PAR) were linked to fishery catch rates (Sanchez et al., 2008).

In Scotland, *L. forbesii* is routinely recorded during trawling surveys targeted at demersal fish, providing information on distribution and local abundance. The present study aims to relate the spatial pattern of *L. forbesii* abundance with ecogeographic variables (EGVs) describing characteristics of the water column and the seabed to quantify habitat usage at different stages of the life cycle. The selection of EGVs was guided both by informal hypotheses based on existing literature (which suggests, for example, that depth and SST may be important factors) and by practical

considerations (i.e., which data are readily available). This species is patchily distributed (see Pierce et al., 2008) and the statistical distribution of numbers of squid per haul includes a high number of zeros. To account for this in the present study, a two-stage approach was used, first modelling presence–absence and then numbers–given–presence. In addition, by subdividing the data by size class and season, we aim to determine habitat preferences at different stages of the life cycle.

## 2. Materials and methods

### 2.1. Catch data

Information on *L. forbesii* catches was obtained from trawl survey data, sourced from Marine Scotland Science Marine Laboratory in Aberdeen, Scotland, UK. The surveys were designed to estimate demersal fish abundance, but squid catches were routinely recorded. Squid were identified only to genus but in the majority of the surveyed area, only *L. forbesii* is common. It remains possible that some catches of *L. vulgaris* and *Alloteuthis subulata* were also included even though the former is rarely found in Scottish waters and the latter is separately recorded (see Pierce et al., 1998). Survey data were extracted for the period January 1985 to March 2004 within International Council for the Exploration of the Sea (ICES) subdivisions IVa, IVb, VIa, VIIa, VIIe, VIIf, VIIh and VIIj. The starting year for data extraction is when satellite SST data first became available. The surveys include some long-standing series, e.g., young fish surveys in spring. Two standard fishing nets were used: (1) the Grande Overture Verticale (GOV), with an internal liner of 20 mm stretched mesh size and headline height of 4 m, and fitted with 100 and 200 mm rubber discs to maintain ground contact) and (2) the Aberdeen trawl, 14.77 m in length, with a 75 mm cod-end mesh size, an external cover with a 35 mm stretched mesh size and a headline height of 2 m. Surveys within each series generally took place at a similar time each year and in the same area. During each survey, usually at least one haul was taken within each ICES rectangle along the established survey routes. The majority of these surveys were carried out using FRV “Scotia” although four other vessels (“Clupea”, “Clarkwood”, “GA Reay” and “Dawn Sky”) were each used for one or two surveys in the mid-1980s (see Pierce et al., 1998) and a new “Scotia” came into service in 1998. Although trawl selectivity is unlikely to be constant across nets (or vessels, Hastie, 1996) and will also depend on the ground-gear attached to the net, the same net was normally used within survey series and by analysing data for each quarter of the year separately, heterogeneity in gear selectivity within each analysis should be reduced.

Information extracted from the surveys included date, location, depth recorded during fishing, duration of haul (h) and length–frequency information on catch. Maturity stage was not recorded during the surveys, so in order to estimate the proportions of immature, maturing, and mature squid per haul, a maturity-length key was applied, in which maturity stage was inferred from body size and season, based on the monthly proportions of animals at each maturity stage in both sexes, and the sex ratio, in previous market samples and dedicated research cruises during 1990–2001 for which data on body length, sex, maturity stage (and date) were recorded (see Appendix A). ‘Immature’ corresponds to stages 1 and 2 on the scale reported by Pierce et al. (1994), ‘maturing’ corresponds to stage 3 and ‘mature’ corresponds to stages 4 and 5.

### 2.2. Environmental data

Environmental data were obtained from internet-based sources including NASA’s OceanColor website for SST and chlorophyll-a

(Chl-*a*) (4 km resolution MODISA (Moderate Resolution Imaging Spectroradiometer on Aqua satellite) data) and the International Research Institute for Climate and Society Data Library for salinity (model NOAA NCEP EMC CMB GODAS—Global Ocean Data Assimilation System). These data were processed using ESRI ArcGIS and converted into regular GIS grids using Arc Macro Language (AML). Buffer zones were created, using the ArcGIS <regionbuffer> command, around the haul locations, in each case centred on a point mid-way between the start and end points of the haul. Buffer zones were circular with a radius of 0.125 decimal degrees (3.4 km satellite pixels). The variables extracted were:

- (a) seabed topography metrics: aspect of the seabed (radians, from which cosine (measuring the tendency for the seabed to face north or south) and sine (the tendency for the seabed to face east or west) of aspect were calculated, seabed slope (degrees) and standard deviation of slope ('STD slope', calculated over a 9-cell area, measuring the 'bumpiness' of seabed topography);
- (b) oceanographic parameters: average salinity ('SAL') and sea surface temperature ('SST,' in °C) for the month in which the individual hauls were conducted.

Sediment composition data were extracted using ArcGIS from the British Geological Survey (BGS) database, determining the presence of mud, sand, gravel and rock categories as a proportion of the area of haul buffer zones. Only hauls from the original data set for which all of the above environmental data were available were used in the final analysis.

### 2.3. Analysis

All catch and environmental data were stored in MS Excel worksheets. Initial screening was carried out to remove (a) all 'foul' (incomplete) hauls, (b) hauls from deepwater locations (trawl depth > 400 m), (c) erroneous or implausible tow speeds and tow durations (all zero tow distances and speeds, also the top and bottom 2.5% of the remaining hauls when sorted by towing speed, and (d) hauls with SST values of < 4°C, likely due to haul buffer zones which were partially composed of land-based temperature values (i.e., where haul mid-points were near to the coastline).

All remaining records were coded by season (winter=January–March, spring=April–June, etc.) and for *Loligo* presence or absence (1, 0). For hauls in which squid were present, the numbers of immature, maturing and mature squid caught were estimated from the total number of squid caught in the haul, multiplied by the estimated proportions of immature, maturing and mature squid in each size class for the calendar month in which the haul was taken (Appendix A). These values were then divided by haul duration to produce the estimated numbers caught per hour.

We used a two-stage modelling process to overcome the issue of overdispersion in the response variable (squid catch rate), firstly modelling presence–absence and then catch rate (given-presence). Since we expected seasonal and maturity-related differences in habitat preferences, each analysis was broken down into twelve separate models (3 inferred maturity groups × 4 seasons). These analyses all necessarily include both sexes as the primary data set comprises only length–frequency data.

Although potentially continuous, in practice most sediment composition variables had relatively few unique values. Therefore, when smoothers could not be fitted, the proportions of sand, rock and mud (prop\_sand, prop\_rock, prop\_mud) were transformed into categorical variables (rounding values to the nearest 0.1 generally resulted in a suitable number of categories) or (in extreme cases, as with the variable prop\_rock) presence–absence. The final

set of explanatory variables used in the analysis was: depth (log-transformed), SST, SAL, cosine aspect, sine aspect, STD slope, prop\_mud, prop\_sand, prop\_gravel and prop\_rock.

Generalised additive models (GAMs) (Hastie and Tibshirani, 1990; Zuur et al., 2007, 2009) using a binomial distribution and logit link function were fitted to presence–absence data. For catch rate (given presence), log-transformation resulted in satisfactory fits using Gaussian GAMs. Degrees of freedom for the smoothers fitted to individual explanatory variables used in the models were restricted to a maximum value of 3 (by setting the knot value ( $k$ ) of 4) in order to avoid over-fitting during cross validation. Optimal models were determined using combined 'forwards' and 'backwards' stepwise selection,<sup>1</sup> being those with the lowest Akaike information criterion (AIC) value (Akaike, 1973) and (normally) in which all explanatory variables retained had significant effects ( $p < 0.05$ ). The selection process also took into account explanatory variable significance (i.e., normally adding the variable with lowest  $p$ -value or removing the variable with the highest  $p$ -value, which generally agreed with changes in AIC), deviance explained (favouring high values) and parsimony (i.e., favouring the simplest model). Model validation included visual examination of residual plots for patterns and (for Gaussian GAMs) normality, and examining 'hat value' plots for presence of influential data points or outliers (points with hat values > 1). All data exploration and model-fitting was carried out using Brodgar v.2.5.6 software ([www.brodgar.com](http://www.brodgar.com), Highland Statistics Ltd.).

In the GAM output, interpretation of the direction of the effect of a continuous explanatory variable on the response variable requires consideration of the confidence bands on the plot showing the 'smoother' for the partial effect of the explanatory variable: where a horizontal line (i.e., zero trend) could be drawn within the confidence limits, there is no significant trend—as often occurs at the extremes of the  $x$ -axis, where wide confidence limits reflect low data density.

Most of the GAM fits were relatively simple curves which could in principle be described by a GLM. So to provide an example of how this would work, a GLM was run for catch rate of mature squid in autumn, using the explanatory variables found to be significant in the corresponding GAM. Where relationships were not linear, quadratic terms (i.e., explanatory variable squared) were included among the predictors.

### 3. Results

For clarity of presentation we focus on the results of the abundance (given presence) models, while also summarizing results from the presence–absence models and highlighting where the two sets of models support or contradict each other. It should be noted that maturity is inferred from size and, therefore, 'immature' squid are essentially the smallest animals and 'mature' squid are the largest ones.

The explanatory variables included in the final GAMs for squid catch-rate-given-presence for each maturity and season combination, along with information on the direction of the effects on squid catch rate and the statistical significance of these effects,

<sup>1</sup> Stepwise regression procedures have been widely criticised in the literature and in some disciplines they are no longer used. In particular, the stepwise procedure can be seen as constantly modifying the hypothesis tested to better fit the data. In addition, any empirical model-fitting process may generate models based on coincidental relationships or which are sub-optimal due to missing variables, although this can be minimised by using those explanatory variables that are expected to affect the responses variable. The use of stepwise models in the present study should be viewed as a hypothesis generating exercise rather than formal hypothesis testing: all resulting models should ideally be tested against independent data sets.

**Table 1**  
Summary of optimum generalised additive models for catch-rate-given-presence of *L. forbesii*. For each model, the table shows sample size (*N*), percentage of deviance explained (DE), Akaike Information Criterion (AIC) value and the effects of explanatory variables. For each explanatory variable, the table indicates the predominant direction of the effect (positive +, negative –,  $\cap$ -shaped or  $\cup$ -shaped), if apparent (with degrees of freedom in parentheses for smoothers), and the associated statistic (*F* for smoothers, *t* for categorical variables, with the associated probability in parentheses). Where there was no significant effect, the relevant cell in the table is left blank. The explanatory variables were log-transformed depth, average SST, average salinity, cosine aspect, sine aspect, percentages of mud and gravel, presence-absence of rock, standard deviation of slope.

Sub-set ( <i>N</i> )	Effects of predictor variables: direction and significance								DE	AIC
	Depth	SST	Salinity	Cos aspect	Sin aspect	Mud	Gravel	Rock Std slope		
<b>Stages 0–2, Winter (577)</b>	+(3.0) 21.2 (< 0.0001)		–(1.7) 10.2 (0.0001)		+(2.5) 4.9 (0.0044)	–(1.0) 33.3 (< 0.0001)	+(2.8) 9.2 (< 0.0001)		26.9	1585.85
<b>Stages 0–2, Spring (149)</b>	$\cap$ (2.5) 3.9 (0.0435)	+(2.8) 3.9 (0.0119)							15.2	352.19
<b>Stages 0–2, Summer (145)</b>	–(2.4) 15.7 (< 0.0001)	–(2.0) 3.4 (0.0365)				+			25.1	313.76
<b>Stages 0–2, Autumn (399)</b>	–(2.1) 16.2 (< 0.0001)			$\cup$ (2.8) 3.8 (0.0129)		–(1.9) 4.5 (0.0129)			13.6	945.95
<b>Stage 3, Winter (587)</b>	(2.9) 22.5 (< 0.0001)		–(1.9) 34.8 (< 0.0001)		+(2.8) 3.4 (0.1943)	–(1.0) 9.6 (0.0020)	+(1.9) 15.4 (< 0.0001)		26.2	1014.44
<b>Stage 3, Spring (124)</b>	–(1.0) 10.5 (0.00157)		+(2.2) 23.0 (< 0.0001)				+(1.0) 17.5 (< 0.0001)		47.1	176.36
<b>Stage 3, Autumn (368)</b>			+(1.0); 5.9 (0.0156)	–(2.8) 3.9 (0.0116)			+(1.0) 45.1 (< 0.0001)		16.6	674.2
<b>Stages 4–5, Winter(608)</b>	+(2.9) 10.4 (< 0.0001)	$\cap$ (2.9) 3.9 (0.0092)	–(2.5) 16.1 (< 0.0001)			$\cap$ (2.8) 3.4 (0.0197)	+(1.0) 43.9 (< 0.0001)		16.2	862.7
<b>Stages 4–5, Spring (127)</b>	–(2.9) 11.7 (< 0.0001)		+(2.3) 20.2 (< 0.0001)				+(1.0) 4.7 (0.00268)		46	282.84
<b>Stages 4–5, Autumn (370)</b>	–(1.0) 9.7 (0.0020)		+(1.0) 11.2 (0.0009)		+(1.0) 8.3 (0.0043)		+(2.0) 25.3 (< 0.0001)		16.9	684.5

plus goodness of fit metrics, are summarised in Table 1. The models explained between 13.6% and 47.1% of deviance, higher values being associated with smaller sample sizes (as might be expected). The presence-absence models (see Table 2 for a summary and Appendix B for details) tended to have lower values of % deviance explained, ranging from 4.5% to 37.1%, with the lowest values consistently seen in autumn. Model residuals deviated slightly from normal for immature squid in winter, spring and summer, and for maturing squid in autumn, but otherwise all fits were reasonably good.

Based on examination of plots of smoothers (see Figs. 1–3, and Appendix B) and taking into account confidence limits, almost all trends can be described as increasing or decreasing and the remainder show either a peak (i.e., an optimal value of the predictor variable) or, more rarely, a trough (i.e., a point at which catch rate is lowest). In many cases trends are evident only in the mid-range of values of the explanatory variable, with wide confidence limits at the extremes reflecting lower data density.

### 3.1. Immature squid

GAM smoothers for the partial effect of explanatory variables on the abundance of immature squid across seasons are shown in Fig. 1. The most striking feature of the habitat preferences of these smaller squid is a shift from deeper waters in winter to shallower waters in summer and autumn. Note that the individuals involved probably belong to at least two different cohorts since older squid usually disappear by summer and a new generation is then recruited. The presence-absence models show a similar seasonal shift in depth preferences, while also suggesting a preference for gravel substrate and avoidance of mud.

Generally, winter abundance of immature squid increased with increasing depth, although the trend becomes non-significant in the shallowest and deepest waters. Squid abundance decreased nearly linearly with increasing salinity. There was no effect of sine of seabed aspect up to a value of approximately 0.15, but abundance increased at higher values, indicating an association of high abundance with eastward-facing seabed topography. The abundance of immature squid during winter decreased linearly as the proportion of mud increased, and increased with increasing proportion of gravel. Presence-absence model results for immature squid in winter were consistent with the abundance models in relation to effects of depth, salinity, mud and gravel. Immature squid presence in winter increased between temperatures of 6–8 °C but was unaffected by seabed aspect.

The spring abundance of immature squid increased with increasing depth up to a logged depth value of about 2.15 (approximately 140 m), thereafter decreasing with increasing depth. The partial effect of increasing average SST on squid abundance was positive for temperature values between approximately 7.25 °C and 9.75 °C. The same two variables, along with the proportion of gravel, also appeared in the final model of immature squid presence in spring, all showing a generally positive relationship with squid presence, although presence reached an asymptote at around 8 °C.

In summer, abundance of immature squid decreased with increasing depth, although no trend was evident at shallower depths. The most favourable SST for high squid abundance was approximately 11.5 °C, with abundance declining at higher temperatures. Presence of mud had a positive effect on squid abundance. Presence of immature squid in summer also decreased with increasing depth but the presence model otherwise differed from



**Table 2**

Summary of optimum binomial generalised additive models for presence–absence of *L. forbesii*. For each model, the table shows sample size (*N*), percentage of deviance explained (DE), Akaike Information Criterion (AIC) value and the effects of explanatory variables. For each explanatory variable, the table indicates the predominant direction of the effect (positive +, negative –, *n*-shaped or *u*-shaped), if apparent (with degrees of freedom for smoothers), the associated statistic (Chi-squared value for smoothers, *z*-value for categorical variables, with the associated probability values for significance of smoothers and factors in parentheses). Where there was no significant effect, the relevant cell in the table is left blank. The explanatory variables were log-transformed depth, average SST, average salinity, cosine aspect, sine aspect, percentages of mud and gravel, presence–absence of rock, and standard deviation of slope.

Sub-set (N)	Effects of predictor variables: direction and significance									DE	AIC
	Depth	SST	Salinity	Cos aspect	Sin aspect	Mud	Gravel	Rock	Std slope		
<b>Stages 0–2, Winter (1763)</b>	+(1.2) 110.2 ( < 0.0001)	<i>u</i> (2.9) 52.3 ( < 0.0001)	<i>n</i> (2.8) 20.8 ( < 0.0001)			–(2.8) 83.9 ( < 0.0001)				16.3	1887.14
<b>Stages 0–2, Spring (586)</b>	+(1.8) 58.9 ( < 0.0001)	+(2.7) 10.3 (0.0121)					+(1.8) 28.0 ( < 0.0001)			22.8	527.36
<b>Stages 0–2, Summer (1413)</b>	–(2.0) 95.5 ( < 0.0001)		<i>n</i> (2.4) 9.1 (0.0171)		–(1.8) 12.7 (0.0014)		+(2.8) 93.2 ( < 0.0001)	+	7.3 ( < 0.0001)	25.2	721.64
<b>Stages 0–2, Autumn (1020)</b>	–(1.8) 9.1 (0.0086)	+(1.1) 6.5 (0.0130)	<i>n</i> (2.9) 27.8 ( < 0.0001)							4.53	1317.1
<b>Stage 3, Winter (1759)</b>	+(1.1) 115.4 ( < 0.0001)	<i>u</i> 3.0 76.0 ( < 0.0001)	–(2.9) 43.9 ( < 0.0001)			–(1.0) 23.8 ( < 0.0001)	+(2.4) 24.9 ( < 0.0001)			18.1	1857.97
<b>Stage 3, Spring (586)</b>	+(2.0) 48.4 ( < 0.0001)	+(1.9) 6.6 (0.0327)	+(1.7) 8.0 (0.0130)			–(1.0) 19.4 ( < 0.0001)		+	3.9 ( < 0.0001)	28.3	450.91
<b>Stage 3, Summer (1316)</b>	–(1.0) 104.7 ( < 0.0001)		<i>n</i> (2.8) 44.7 ( < 0.0001)				+(2.8) 245.5 ( < 0.0001)		+(1.0) 16.9 ( < 0.0001)	31.7	303.96
<b>Stage 3, Autumn (1020)</b>	–(2.2) 8.7 (0.0152)	+(2.7) 8.0 (0.0362)	<i>n</i> (2.9) 21.9 ( < 0.0001)							4.84	1286.89
<b>Stages 4–5, Winter (1759)</b>	+(2.7) 76.3 ( < 0.0001)	<i>u</i> <i>n</i> (3.0) 72.2 ( < 0.0001)	<i>n</i> (2.9) 30.9 ( < 0.0001)			–(1.0) 18.3 ( < 0.0001)	+(2.4) 27.4 ( < 0.0001)			17.5	1897.98
<b>Stages 4–5, Spring (586)</b>	+(1.7) 22.6 ( < 0.0001)	+(1.0) 4.4 (0.0363)	+(1.0) 4.0 (0.0465)				+(1.9) 50.9 ( < 0.0001)	+	4.4 ( < 0.0001)	29.8	445.59
<b>Stages 4–5, Summer (1413)</b>	–(1.0) 44.5 ( < 0.0001)		<i>n</i> (2.8) 28.8 ( < 0.0001)			–	+(2.2) 92.8 ( < 0.0001)	+	9.8 ( < 0.0001)	28.7	331
<b>Stages 4–5, Autumn (1020)</b>	–(2.1) 8.5 (0.0158)	+(2.7) 7.8 (0.0398)	<i>n</i> (2.9) 32.4 ( < 0.0001)							4.9	1288.06

the abundance model, and included effects of salinity (peak presence around 34.7), sine of seabed aspect (negative relationship), gravel (positive relationship) and the presence of rock (positive relationship, Table 2).

In autumn, abundance of immature squid decreased with increasing depth. Squid abundance decreased with increasing values of cosine of seabed aspect up to a value of approximately 0.2, while further increases had a positive effect, indicating that lowest abundance of squid was associated with eastward-facing slopes. Abundance of immature squid during autumn decreased as the proportion of mud increased from zero up to around 0.2; beyond this point confidence limits are too wide to detect any trend. The final model for presence of immature squid in winter also shows a negative relationship with depth but otherwise reveals relationships not seen in the abundance model: presence increased with increasing SST and peaked at a salinity of around 35.2‰.

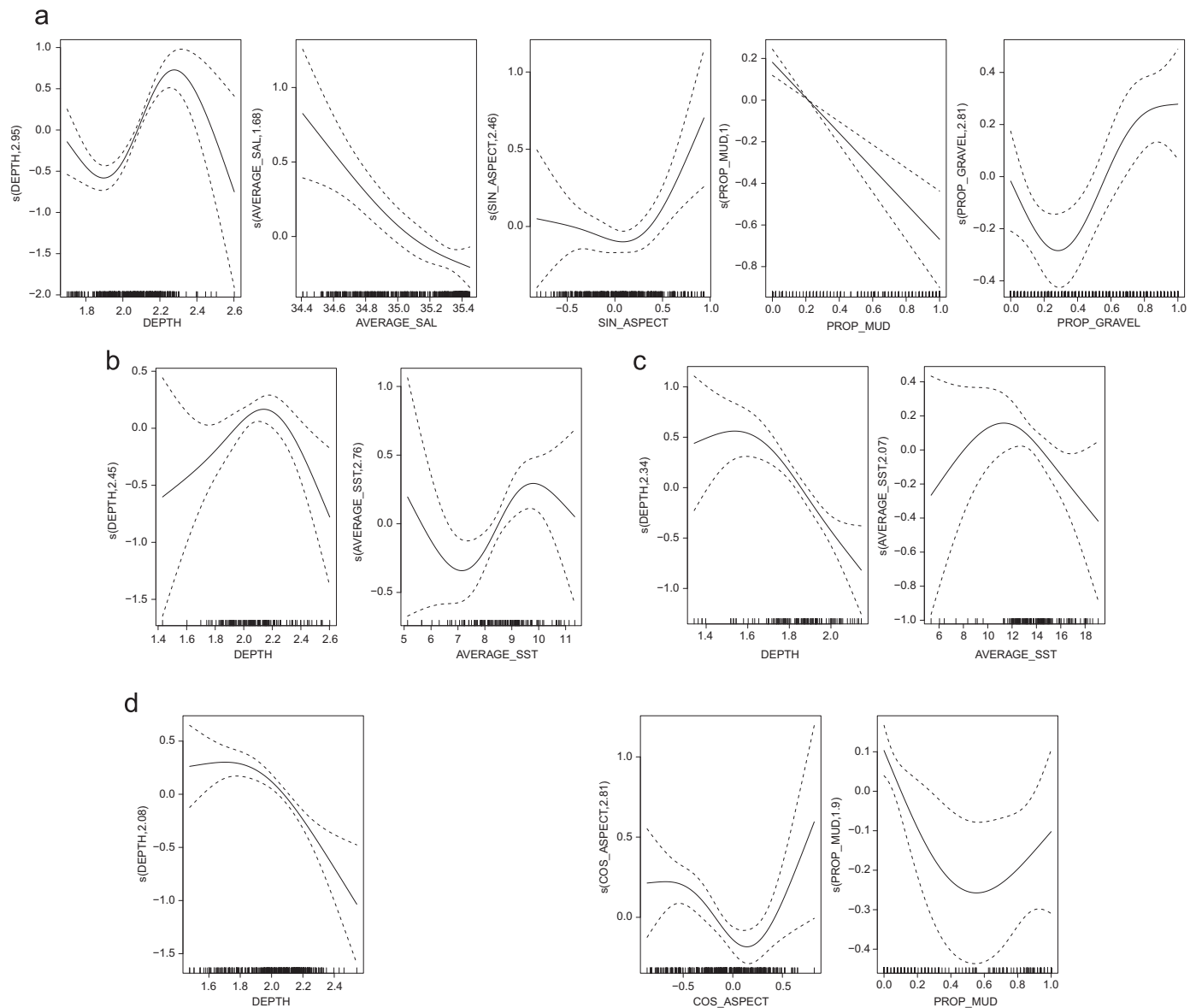
### 3.2. Maturing squid

GAM smoothers for the partial effect of explanatory variables on the abundance of maturing squid across seasons are shown in Fig. 2. There were insufficient data to construct habitat models for maturing squid in summer. Maturing squid showed similar

seasonal trends in depth preferences to those seen in immature squid: e.g., presence models indicate a preference for deeper waters in winter and spring, and for shallower waters in summer and autumn. A preference for gravel substrate, weakly apparent in immature squid in winter, is seen for maturing squid in all three seasons for which abundance models could be fitted, as well as for winter and summer in the presence models.

Winter abundance of maturing squid increased with increasing depth up to a logged depth value of just less than 2.3 (approximately 140 m), after which confidence limits become too wide to confirm a significant trend. Squid abundance decreased with increasing salinity and increased with increasing values of sine of seabed aspect, indicating an association of high squid abundance with eastward-facing seabed topography. The abundance of maturing squid during winter decreased linearly as the proportion of mud increased, and increased almost linearly as the proportion of gravel increased. Squid presence also showed positive relationships with depth and proportion of gravel, and negative relationships with salinity and proportion of mud. Squid presence was lowest at around 6 °C.

The spring abundance of maturing squid decreased linearly with increasing depth but increased with increasing salinity, the opposite of what was seen in winter. Interestingly, the relationship with salinity is not what would be expected if both depth and



**Fig. 1.** GAM smoothing curves fitted to partial effects of explanatory variables on winter, spring, summer and autumn catch-rates-given-presence in *L. forbesii* of maturity stages 0–2 (immature squid). Smoothers are shown only for continuous variables with significant effects. Dashed lines represent 95% confidence intervals around the main effects.

salinity relationships were simply a consequence of movements inshore (hence closer to freshwater inputs) and vice versa. The abundance of maturing squid during spring increased linearly as the proportion of gravel increased. The presence model is somewhat different: presence increased with increasing depth but also with increasing values of salinity and SST (at least up to approximately 8 °C). Squid presence decreased as the proportion of mud increased and increased in the presence of rock (Table 2).

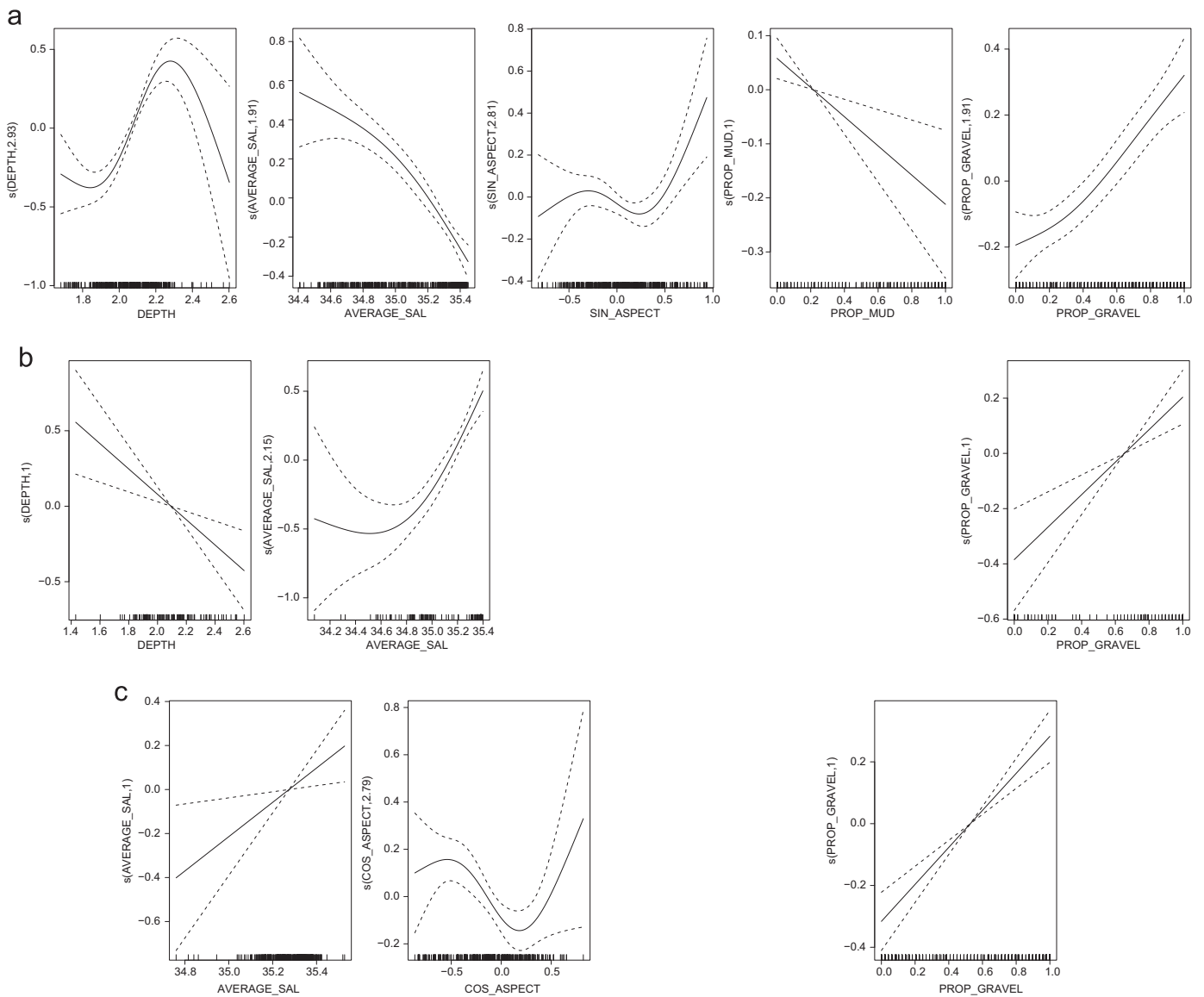
GAM analysis of maturing squid in summer was possible only with the presence-absence data. Presence of maturing squid decreased with increasing depth. Squid presence has highest at a salinity of 34.75‰. The presence of maturing squid during summer increased as the proportion of gravel increased, as well as with increasing values for standard deviation of slope.

In autumn, as in spring, abundance of maturing squid increased with increasing salinity and as the proportion of gravel increased. Squid abundance decreased with increasing cosine of seabed aspect in the range  $-0.5$  to  $+0.25$  (i.e., decreasing as aspect shifts from SE to ENE). Although the abundance model showed no

significant relationship with depth, the presence of mature squid in autumn decreased (weakly) with increasing depth. Presence peaked at a salinity of approximately 35.25‰. The partial effect of increasing SST on squid presence was positive in the range 6.5 °C to approximately 12 °C.

### 3.3. Mature squid

GAM smoothers for the partial effect of explanatory variables on the abundance of mature squid are shown in Fig. 3. As for maturing squid, no models of abundance could be fitted for summer. The seasonal trends in depth and salinity preferences are similar to those in immature and maturing squid, with a clear shift from preferring deeper water and lower salinity in winter to preferring shallower water and higher salinity later in the year. As in maturing squid, a preference for substrates high in gravel is apparent in all three seasons for which models could be fitted. Presence models show similar seasonal trends in depth preference



**Fig. 2.** GAM smoothing curves fitted to partial effects of explanatory variables on winter, spring and autumn catch-rates-given-presence in *L. forbesii* of maturity stage 3 (maturing squid). Smoothers are shown only for continuous variables with significant effects. Dashed lines represent 95% confidence intervals around the main effects. There were too few maturing squid present in summer to construct a model.

(although not for salinity preferences) and a similar preference for more gravelly substrates.

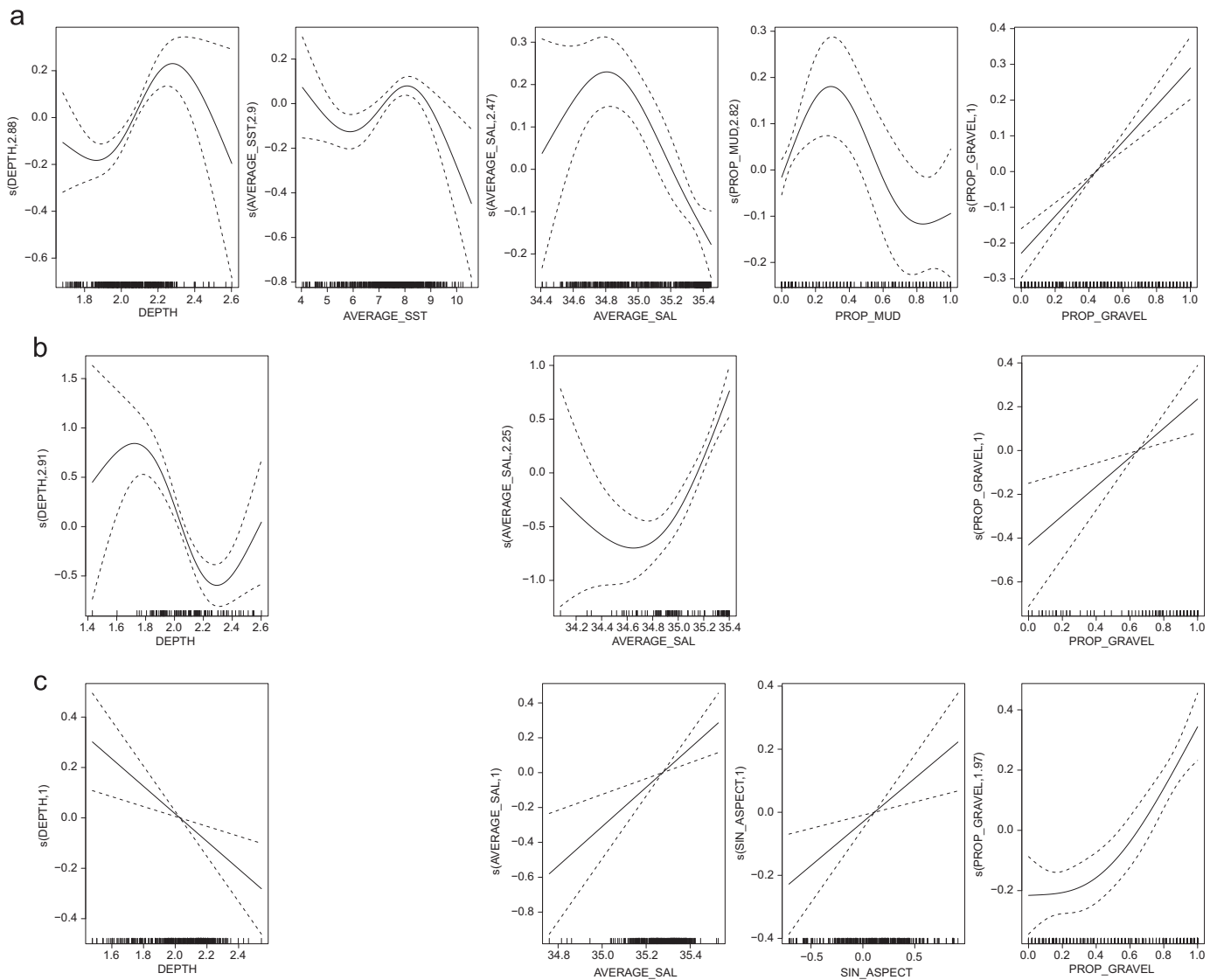
Winter abundance of mature squid increased with depth, up to a logged depth value of 2.3 (approximately 140 m). Abundance declined with increasing salinity above a value of 34.8‰. The most favourable SST for high squid abundance was approximately 8 °C. Abundance was highest when proportion of mud reached around 30% and also increased linearly as the proportion of gravel increased. The presence model also showed positive relationships with depth and proportion of gravel. In other respects the model differed: there was a salinity optimum around 34.7‰, presence was negatively related to the proportion of mud, and the relationship between presence and temperature was complex.

In contrast to winter, spring abundance of mature squid decreased with increasing depth, up to a logged depth of 2.3 (approximately 140 m). Mature squid abundance increased with increasing salinity and as the proportion of gravel increased. Presence of mature squid in spring increased with increasing

salinity and increasing proportion of gravel in the substrate but other trends differed from the abundance model: presence increased with increasing SST, increasing depth, and the presence of rock (Table 2).

The summer presence of mature squid decreased linearly with increasing depth. Squid presence was highest at a salinity of approximately 34.75‰. The presence of mature squid during summer increased as the proportion of gravel and mud increased. Squid presence was also higher when rock was present.

The autumn abundance of mature squid decreased linearly with increasing depth, and increased linearly with increasing salinity and sine of seabed aspect, with the latter trend indicating a preference for eastward-facing seabed topography. Abundance of mature squid in autumn also increased as the proportion of gravel increased. As for the abundance model, squid presence decreased as depth increased, but other trends differed: squid presence peaked at a salinity of approximately 35.25‰ and the partial effect of increasing average SST on squid presence was positive in the range 6.5 °C to approximately 12 °C.



**Fig. 3.** GAM smoothing curves fitted to partial effects of explanatory variables on winter, spring, summer and autumn catch-rates-given-presence in *L. forbesii* of maturity stages 4 and 5 (mature squid). Smoothers are shown only for continuous variables with significant effects. Dashed lines represent 95% confidence intervals around the main effects. There were too few mature squid present in summer to construct a model.

### 3.4. Generalised linear modelling

The final GLM model for abundance of mature (stages 4–5) squid in autumn was as follows:

Catch rate =  $-390 - 0.016 \text{ DEPTH} + 11.1 \text{ AVERAGE\_SAL} + 2.43 \text{ SIN\_ASPECT} + 4.9 \text{ PROP\_GRAVEL}$  (% deviance explained = 11%).

Note that the effect of gravel was not originally linear ( $df=2$ ; see Table 1) but inclusion of  $\text{PROP\_GRAVEL}^2$  as well as  $\text{PROP\_GRAVEL}$  did not improve the fit, so the quadratic term was dropped from the final GLM.

## 4. Discussion

The commercially important loliginid squids, octopuses and cuttlefish occur mainly in continental shelf waters, associated with particular depth ranges and requiring suitable substrates to attach their eggs. Habitat preferences change over the life cycle: both loliginid squid and common octopus have planktonic paralarvae, while both loliginid squid and cuttlefish undertake ontogenetic migrations between spawning and feeding grounds.

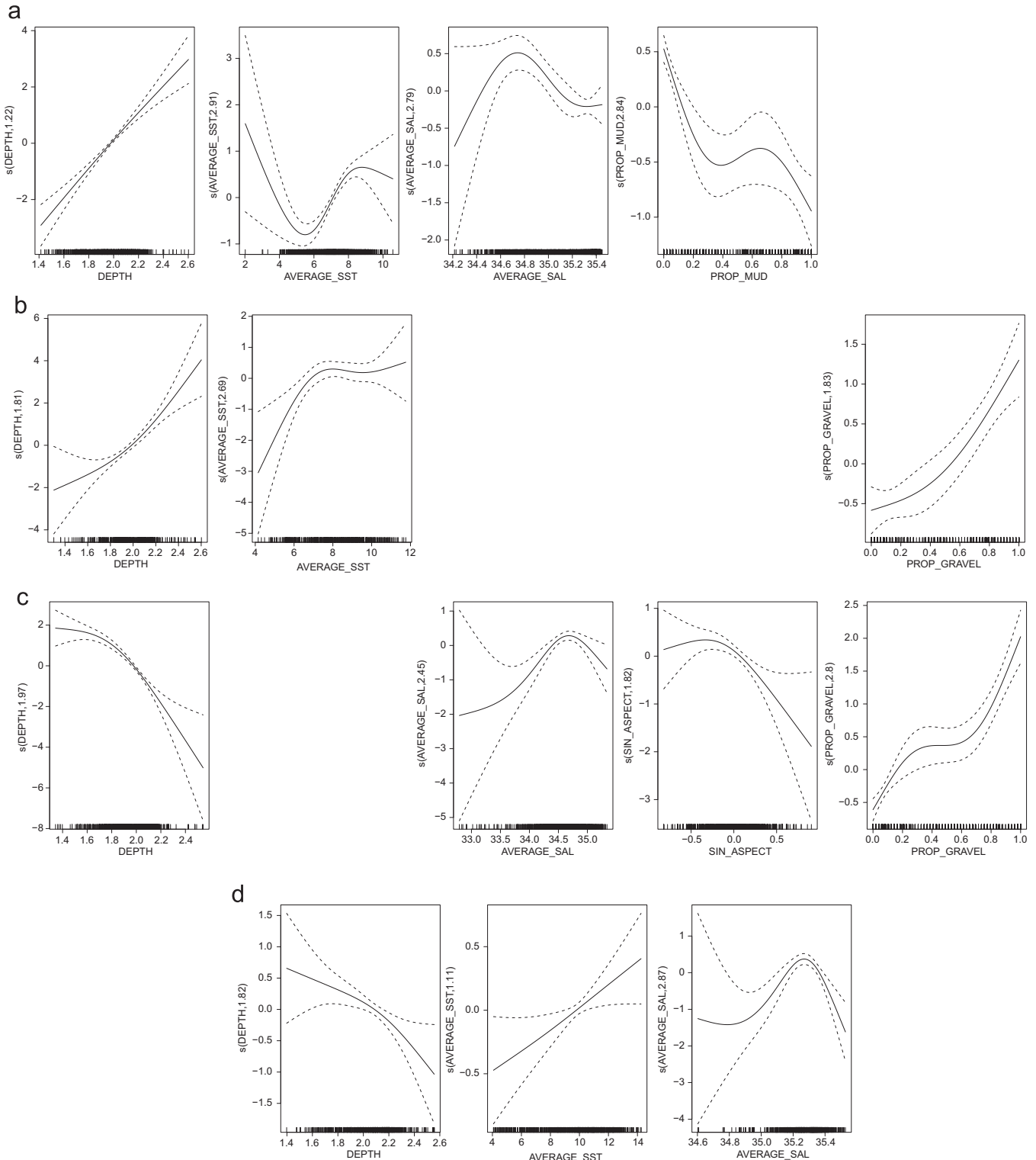
The seasonality of the life cycle thus implies that habitat preferences will change seasonally. Oceanic squids often undertake extensive ontogenetic migrations (e.g., *Todarodes pacificus*, Mokrín et al., 2002; Kawabata et al., 2006) and have no requirement for substrates for egg attachment (as their eggs are free-floating). They may show preferences in relation to depth and for oceanographic conditions associated with high productivity or are suitable for egg-laying and paralarval growth. Modelling habitat preferences is therefore potentially valuable for all cephalopods.

Model results indicate that *L. forbesii* has preferred seasonal habitats that can be satisfactorily characterised based on depth, substrate and oceanographic variables. It should be borne in mind that the environmental effects described are 'partial' effects (i.e., residual effects, once effects of other variables retained in the model have been taken into account) and apparent optima may thus be modified in practice by the combined effect of several variables. Deviance explained by individual ranged from 4.5% to 47%. While such values can be considered satisfactory, it should be borne in mind that verification using independent data sets (e.g., future years' data) is desirable before such models are to applied in management.



The GAM framework used here is just one option for modelling habitat use of marine organisms (e.g., Redfern et al., 2006; Pierce et al., 2008; Valavanis et al. 2008) but has several advantages, e.g., readily accommodating non-linear relationships with environmental variables. On the other hand, the fact that habitat preferences cannot be expressed as simple equations discourages some users. Where fitted relationships approximate to a known functional form it is relatively straightforward to substitute an

(approximately) equivalent GLM although, as seen, this can result in an appreciable drop in deviance explained even when departure from linearity is not very marked. The present analysis attempted to generate habitat preference models for two measures of the occurrence of squid for three size/maturity classes in four seasons, giving a possible total of 24 final models (reduced to 22 models due to lack of data on abundance of maturing and mature squid in summer). Thus, an indication of the generality of an



**Fig. A1.** GAM smoothing curves fitted to partial effects of explanatory variables on winter, spring, summer and autumn presence of *L. forbesii* of maturity stages 0–2 (immature squid). Smoothers are shown only for continuous variables with significant effects. Dashed lines represent 95% confidence intervals around the main effects.

environmental relationship may be obtained from the number of models in which it appears.

4.1. Depth preferences

The depth with highest squid abundance showed a predictable seasonal pattern, with a general preference for deeper waters in the

first quarter of the year (winter), and a clear preference for shallow waters in the last quarter (autumn). At first sight, this is broadly consistent with previously described ontogenetic migrations and the dominance of a cohort which recruits in summer and autumn and breeds in later autumn and winter (e.g., Pierce et al., 1994; Viana et al., 2009). In Scotland, the main fishing season for squid is in the autumn and the directed fishery starts

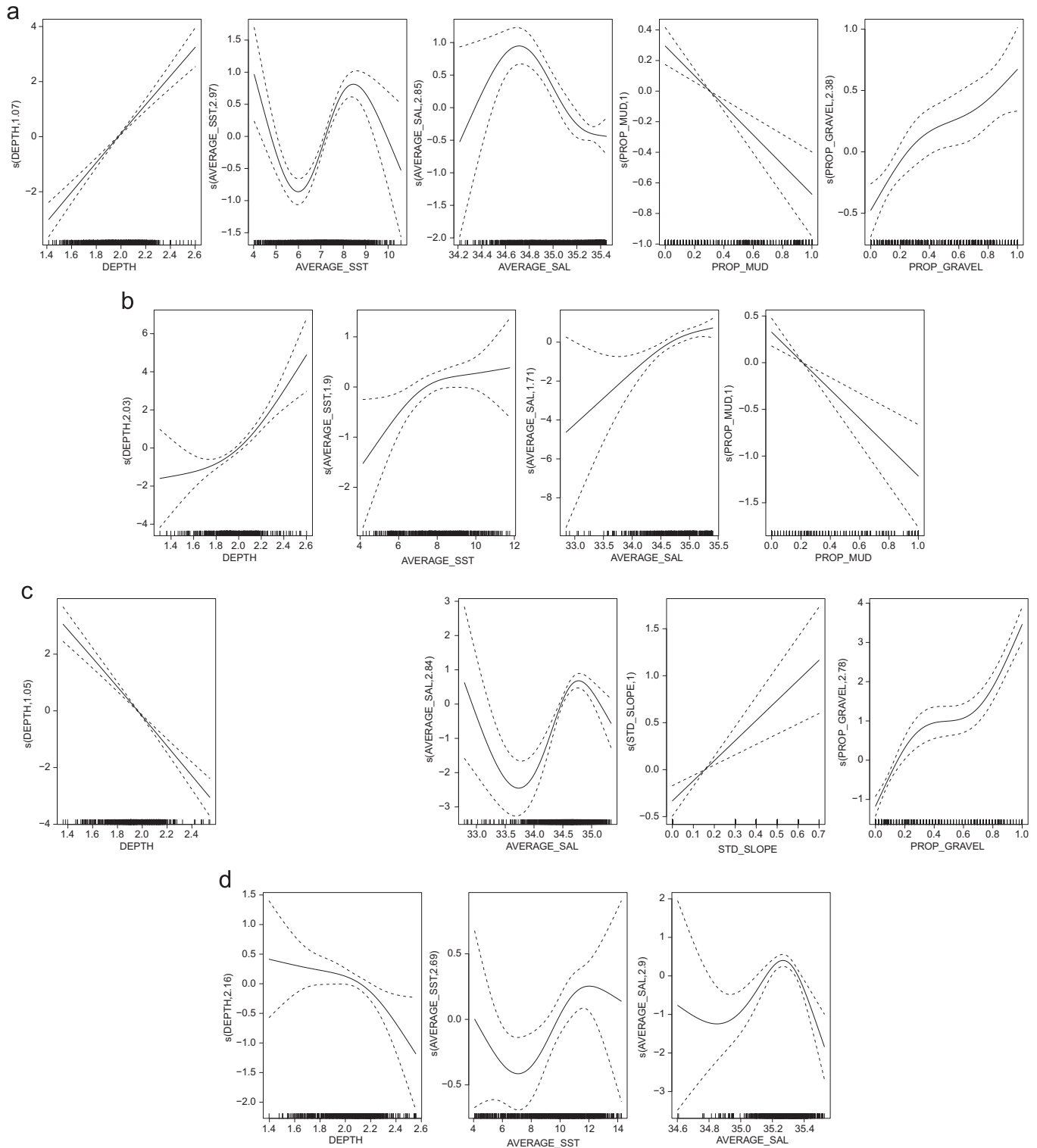
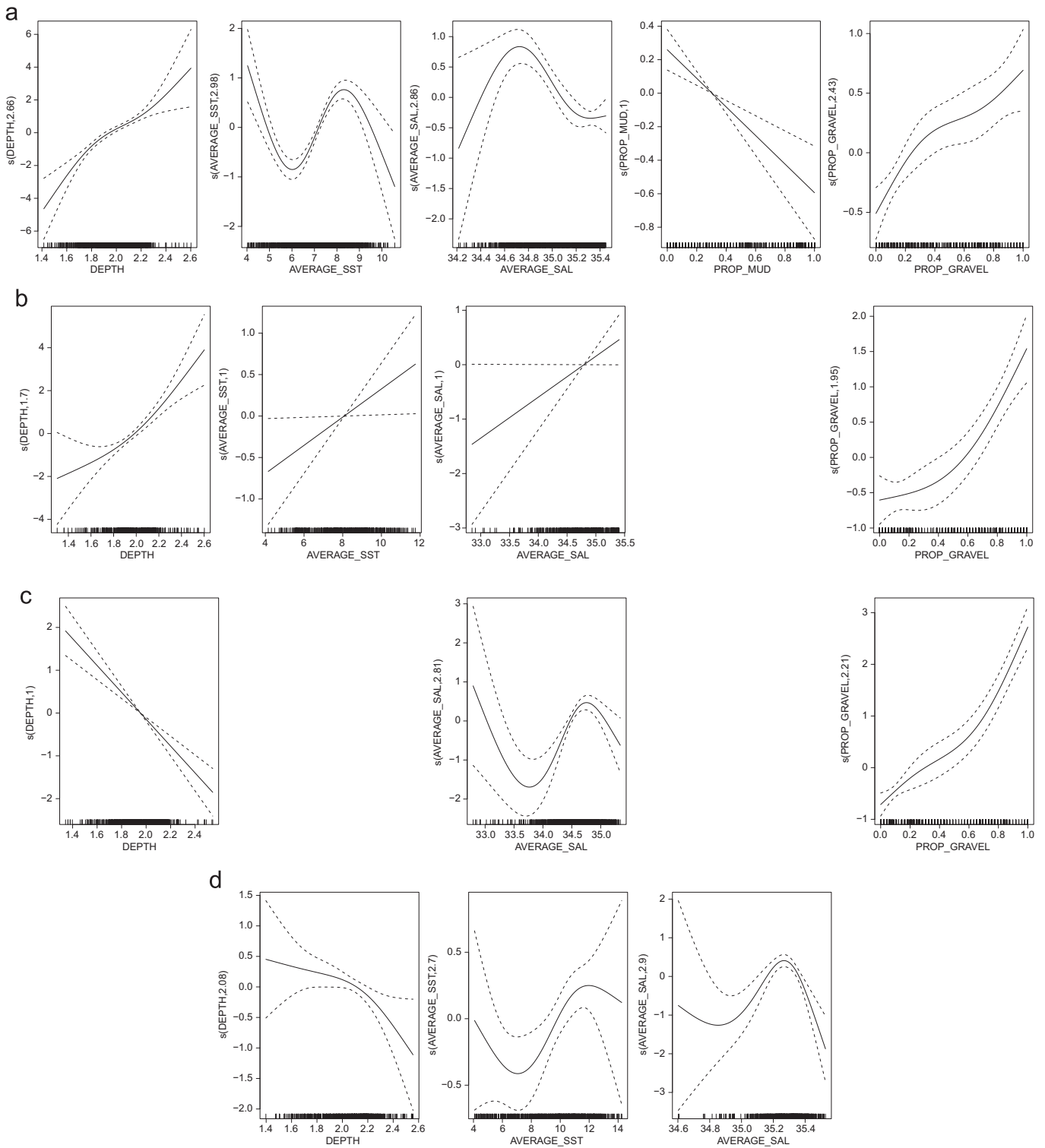


Fig. A2. GAM smoothing curves fitted to partial effects of explanatory variables on winter, spring and autumn presence of *L. forbesii* of maturity stage 3 (maturing squid). Smoothers are shown only for continuous variables with significant effects. Dashed lines represent 95% confidence intervals around the main effects. There were too few maturing squid present in summer to construct a model.



**Fig. A3.** GAM smoothing curves fitted to partial effects of explanatory variables on winter, spring, summer and autumn presence of *L. forbesii* of maturity stages 4 and 5 (mature squid). Smoothers are shown only for continuous variables with significant effects. Dashed lines represent 95% confidence intervals around the main effects. There were too few mature squid present in summer to construct a model.

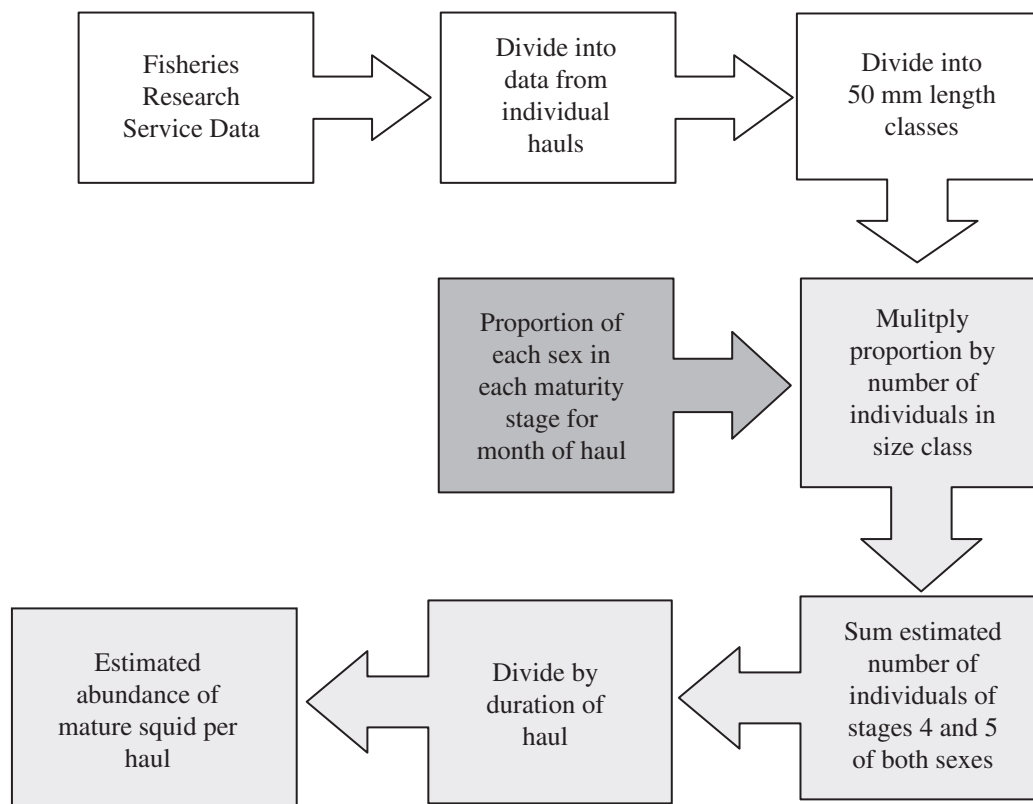
in late summer in near-shore waters, where recruitment apparently occurs. Fishing tends to move into deeper waters towards the end of autumn (Young et al., 2006; Smith, 2011), presumably following migration of the young squid away from the coast, as has been described in various loliginids (e.g., *L. gahi*, Arkhipkin et al., 2004).

Inshore spawning has previously been inferred both from the appearance of new recruits close inshore (e.g., Young et al. 2006) and from the occurrence of egg masses on creels in coastal waters (e.g., Lum-Kong et al., 1992). However, a shift in depth preference towards deeper waters, from autumn to winter, was seen in the largest squid as well as in smaller animals in the present study,

**Table B1**

An example of the calculated proportions of mature squid of each sex produced for each month from the commercial fisheries and dedicated survey data. Data are for the month of January.

Size class (mm)	Males					Females				
	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
0–50	0.400	0.000	0.000	0.000	0.000	0.600	0.000	0.000	0.000	0.000
50–100	0.400	0.000	0.000	0.000	0.000	0.600	0.000	0.000	0.000	0.000
100–150	0.265	0.121	0.107	0.056	0.112	0.093	0.228	0.019	0.000	0.000
150–200	0.006	0.081	0.036	0.059	0.209	0.003	0.174	0.196	0.120	0.117
200–250	0.000	0.038	0.040	0.026	0.142	0.000	0.004	0.051	0.214	0.484
250–300	0.000	0.007	0.058	0.014	0.314	0.000	0.000	0.007	0.159	0.440
300–350	0.000	0.000	0.018	0.024	0.642	0.000	0.000	0.000	0.085	0.230
350–400	0.000	0.000	0.000	0.000	0.966	0.000	0.000	0.000	0.017	0.017
400–450	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
450–500	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000
> 550	0.000	0.000	0.000	0.000	1.000	0.000	0.000	0.000	0.000	0.000



**Fig. B1.** Flow chart of procedure to estimate abundance of mature squid per haul from Fisheries Research Services (FRS) data.

suggesting that spawning animals also move further offshore over this period. Thus, most spawning may take place in deeper waters rather than close inshore, indicating a need for further research to identify spawning areas in this species.

Although the present data set did not allow it, due to the fact that trawl surveys normally take only a single haul per ICES rectangle, it would also be interesting to explore evidence of diurnal cycles in catch rate, e.g., due to vertical migration.

High variance in bottom topography has been identified as a preferred habitat feature in some top predators in shallow sea environmental hotspots, possibly due its positive effect on vertical mixing (Scott et al., 2010), presumably linked to high prey abundance. However, in the present study, standard deviation of seabed slope appeared in only one of the final models.

Cosine or sine of seabed aspect appeared in five of the abundance models. Where a preference was seen in winter, it was for eastward-facing slopes. This may simply indicate that squid are more common on the east coast during winter. In autumn, mature squid were most abundant, and immature and maturing squid least abundant, on east-facing slopes, suggesting some spatial separation of the size/maturity classes despite similar depth preferences. While this could reflect the general orientation of the coast in areas inhabited by each maturity stage, aspect can also indicate whether sites face prevailing currents and are thus, for example, better oxygenated, which may be particularly important for embryonic development (Roberts, 2005). In the study area, the most important large-scale inflow of water is from the North Atlantic current, from which east-facing slopes are least likely to

benefit. The relationship between squid abundance and local topography clearly requires further investigation, probably at a smaller spatial scale.

#### 4.2. Seabed substrate

In general, squid avoided mud (evident in four out of five abundance models in which % mud appeared) showed preferences for gravel (apparent in seven abundance models) and rocky (four presence models) substrates. One of the main preys of *L. forbesii* in UK waters is sandeel (Wangvoralak et al., 2011). Sandeels are burrowing species, predominantly found on sandy substrates with a low silt/clay fraction that would otherwise impede respiration (see Holland et al., 2005 and references therein). Gravel and rock might be expected to provide opportunities for attachment of egg strings. Previous reports have described eggs of this species on hard substrates such as static fishing gear and large rocks, albeit in areas of sandy or muddy bottoms (Roper et al., 1984; Smith, 2011).

Fishers who target squid in the Moray Firth (NE Scotland) have reported high squid catches over sandy bottoms and have made no mention of gravel or rock being suitable substrates (Smith, 2011). The difficulty of trawling over rocks (e.g., risk of damage to nets) may account for the fact that fishers did not mention rocky substrates, but the discrepancy between models and interview data may also be an issue of scale. In future, better spatial coverage and improved habitat use models might be obtained using information from commercial vessels.

#### 4.3. Effects of SST and salinity

There was a significant effect of SST in three of the abundance GAMs and in nine of the presence models. The temperatures most favoured by mature squid during winter were in the range 8–8.75 °C. The possibility of improving fishing efficiency by targeting of areas with favourable water temperature is worth further investigation. Robin and Denis (1999) found that returns from fishing on *Loligo* spp. in the English Channel could be predicted using SST data from the previous winter.

Salinity figured in seven of the final abundance models and eleven of the presence models. The most favourable values for salinity covered the range 34.4–35.5‰. In winter and summer, regardless of maturity stage, 'preferred' salinity was always less than 35‰, while in spring and autumn (with one exception), preferred salinity values were above 35‰. This difference was not simply an indirect consequence of shifting depth preferences (coastal waters tend to have a greater freshwater influence); in fact, preferences for shallow depths generally coincided with preferences for higher salinities, suggesting that squid avoid areas of high freshwater influence when close inshore. Laboratory studies on *L. vulgaris* have shown that rearing in salinities below 34‰ can produce embryonic mortality at very early developmental stages (Sen, 2004). The catch rate of *Loligo* spp. by commercial fishing vessels has been shown to be positively correlated with salinity in UK waters (Waluda and Pierce, 1998; Pierce and Boyle, 2003) but, for both salinity and SST, it is necessary to disentangle effects on annual abundance and effects on distribution within years.

#### 4.4. Future research and wider applicability

There is clearly scope to build on this analysis by evaluating other potential predictors of squid presence and abundance, e.g., local productivity, which can be inferred from Chl-*a* concentration. Although sometimes obscured by time-lags and spatial displacement, relationships between local abundance of many fishery resource species and

local primary productivity are well-established (Downing et al., 1990; King, 2007). In the present study, Chl-*a* data were available for too few haul locations (in time and space) to permit their inclusion in the models. In addition, meso-scale oceanographic features which represent productivity 'hotspots', such as fronts and eddies, can be both mobile and transient. A possible way forward is the coupling of real-time data on squid catches, e.g., from commercial vessels, with real-time satellite data. This approach may be particularly useful for pelagic squids, for which physical environmental characteristics such as sea depth and seabed substrate data are likely to be less important.

It will also be important to understand regional current systems and how these interact with squid life cycles. In the southwest Atlantic, the effects of oceanography on the distribution and abundance of *I. argentinus* are intimately linked with the life cycle and the role of currents in determining migration routes between spawning and feeding grounds (Waluda et al., 1999, 2001).

A major limitation of most habitat models for marine species is the unavailability of data on the sub-surface ocean environment. For example, the temperature in the water column will affect oxygen availability, an important issue given the high metabolic rates of squid species (e.g., *Dosidicus gigas*, Gilly et al., 2006; Rosa and Seibel, 2010).

In the future, fisheries in Europe will most likely be managed within the broader context of integrated marine management or marine spatial planning and, in this context, the ability to identify preferred habitats of resource species assumes even greater importance, potentially allowing more efficient targeting of the stock by fishers while enabling protection of critical habitats. Statistical model outputs can be linked to GIS-based tools to predict resource distribution ahead of and during a fishing season (e.g., Valavanis et al., 2004). Trialling such approaches with relatively minor resource species such as *L. forbesii* might be an attractive option to allow practical and implementation issues to be addressed.

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## Appendix A

### A.1. Smoothers for presence-absence models

See Figs. A1–A3.

## Appendix B

### B.1. Modelling the fine-scale distribution of *L. forbesii* per maturity class for fishery trawl data

This analysis was based on the data collected during fisheries research cruises from 1982 to 1999. The original aim was to model the distribution of maturity stages 4 and 5 squid (see Ngoile (1987) for a description of the 5-point maturity scale) during the autumn



and winter spawning seasons and compare it to the distribution of both other maturity stages (1–3) during the same spawning seasons and to the occurrence of squid in general, and was restricted to positive hauls (those where *L. forbesii* were recorded). However, the available data only had information on the length of each specimen caught in a haul and no information on the sex or maturity status of individual specimens. Therefore, data from commercial fish landings and dedicated research cruises in 2004 and 2005 were used to estimate the proportion of mature individuals within each fisheries research cruise haul. The data from commercial fish landings and dedicated research cruises were divided into individual months and into 50 mm length classes. The proportion of squid of each sex in each maturity class (1–5) for each month was calculated from these data (e.g., Table B1). When no data were available, it was assumed that all individuals over 500 mm were stage 5 males. These assumptions were based on the known biology of the species.

In order to estimate the proportion of mature squid in each haul of the Fisheries Research Services (FRS, Aberdeen, Scotland, UK) data, the data from each haul were first divided into 50 mm length classes and months. The frequency of individuals within each of these month and length classes was then multiplied by the appropriate the month-, length class- and sex-specific proportion to provide an estimate of the number of squid of each sex and stage. To estimate the total number of mature squid per haul, the estimated number of male and female squid of stages 4 and 5 were combined (Fig B1). The estimated proportion of mature squid in each haul was multiplied by the duration of the haul to give an estimated abundance of mature squid per hour of trawling. This process was repeated to produce an estimated abundance of immature and maturing squid (stages 1–3) per hour of trawling.

## References

- Agnew, D.J., Beddington, J.R., Hill, S.L., 2002. The potential use of environmental information to manage squid stocks. *Can. J. Fish. Aquat. Sci.* 59, 1851–1857.
- Akaike, H., 1973. Information theory as an extension of the maximum likelihood principle. In: Petrov, B.N., Csaksi, F. (Eds.), 2nd International Symposium on Information Theory. Akademiai Kiado, Budapest, pp. 267–281.
- Arkhkipkin, A.I., Grzebielec, R., Sirota, A.M., Remeslo, A.V., Polishchuk, I.A., Middleton, D.J.A., 2004. The influence of seasonal environmental changes on ontogenic migrations of the squid *Loligo gahi* on the Falkland shelf. *Fish. Oceanogr.* 13, 1–9.
- Bellido, J.M., Pierce, G.J., Wang, J., 2001. Modelling intra-annual variation in abundance of squid *Loligo forbesii* in Scottish waters using generalised additive models. *Fish. Res.* 52, 23–39.
- Blanc, A., Pinczon du Sel, G., Daguzan, J., 1998. Habitat and diet of early stages of *Sepia officinalis* L. (Cephalopoda) in Morbihan Bay, France. *J. Mollus. Stud.* 64, 263–274.
- Cañadas, A., Sagarminaga, R., De Stephens, R., Urquiola, E., Hammond, P.S., 2005. Habitat preference modelling as a conservation tool: proposals for marine protected areas for cetaceans in southern Spanish waters. *Aquat. Conserv.: Mar. Freshwater Ecosyst.* 15, 495–521.
- Downing, J.A., Plante, C., Lalonde, S., 1990. Fish production correlated with primary productivity, not the morphoedaphic index. *Can. J. Fish. Aquat. Sci.* 47, 1929–1936.
- Georgakarakos, S., Haralambous, J., Valavanis, V., Arvanitidis, C., Koutsoubas, D., Kapantagakis, A., 2002. Loliginid and ommastrephid stock prediction in Greek waters using time series analysis techniques. *Bull. Mar. Sci.* 71, 269–287.
- Gilly, W.F., Markaida, U., Baxter, C.H., Block, B.A., Boustany, A., Zeidberg, L., Reisenbichler, K., Robinson, B., Bazzino, G., Salinas, C., 2006. Vertical and horizontal migrations by the squid *Dosidicus gigas* revealed by electronic tagging. *Mar. Ecol. Prog. Ser.* 324, 1–17.
- Hastie, L.C., 1996. Estimation of trawl cod-end selectivity for squid (*Loligo forbesii*), based on Scottish research vessel survey data. *ICES J. Mar. Sci.* 53, 741–744.
- Hastie, T., Tibshirani, R.J., 1990. Generalized Additive Models. Chapman and Hall/CRC, London.
- Holland, G.J., Greenstreet, S.P.R., Gibb, I.M., Fraser, H.M., Robertson, M.R., 2005. Identifying sandeel *Ammodytes marinus* sediment habitat preferences in the marine environment. *Mar. Ecol. Prog. Ser.* 303, 269–282.
- Ichii, T., Mahapatra, K., Sakai, M., Okada, Y., 2009. Life history of the neon flying squid: effect of the oceanographic regime in the North Pacific Ocean. *Mar. Ecol. Prog. Ser.* 378, 1–11.
- Kawabata, A., Yatsu, A., Ueno, Y., Suyama, S., Kurita, Y., 2006. Spatial distribution of the Japanese common squid, *Todarodes pacificus*, during its northward migration in the western North Pacific Ocean. *Fish. Oceanogr.* 15, 113–124.
- King, M., 2007. Fisheries Biology, Assessment and Management, 2nd ed. Wiley-Blackwell, Oxford.
- Lum-Kong, A., Pierce, G.J., Yau, C., 1992. Timing of spawning and recruitment in *Loligo forbesii* Steenstrup (Cephalopoda: Loliginidae) in Scottish Waters. *J. Mar. Biol. Assoc. UK* 72, 301–311.
- Mokrin, N.M., Novikov, Y.u.V., Zuenko, Y.u.I., 2002. Seasonal migrations and oceanographic conditions for concentration of the Japanese flying squid (*Todarodes pacificus* Steenstrup, 1880) in the northwestern Japan Sea. *Bull. Mar. Sci.* 71, 487–499.
- Ngoile M.A.K., 1987. Fishery biology of the squid *Loligo forbesii* (Cephalopoda: Loliginidae) in Scottish waters. Ph.D. Thesis, University of Aberdeen.
- Pierce, G.J., Bailey, N., Stratoudakis, Y., Newton, A., 1998. Distribution and abundance of the fished population of *Loligo forbesii* in Scottish waters: analysis of research cruise data. *ICES J. Mar. Sci.* 55, 14–33.
- Pierce, G.J., Boyle, P.R., 2003. Empirical modelling of interannual trends in abundance of squid (*Loligo forbesii*) in Scottish waters. *Fish. Res.* 59, 305–326.
- Pierce, G.J., Boyle, P.R., Hastie, L.C., Key, L., 1994. The life history of *Loligo forbesii* (Cephalopoda: Loliginidae) in Scottish waters. *Fish. Res.* 21, 17–41.
- Pierce, G.J., Valavanis, V.D., Guerra, A., Jereb, P., Orsi-Relini, L., Bellido, J.M., Katara, I., Piatkowski, U., Pereria, J., Balguerias, E., Sobrino, I., Lefkaditou, E., Wang, J., Santurtun, S., Boyle, P.R., Hastie, L.C., MacLeod, C.D., Smith, J.M., Viana, M., González, A.F., Zuur, A.F., 2008. A review of cephalopod–environment interactions in European Seas. *Hydrobiologia* 612, 49–70.
- Pierce, G.J., Zuur, A.F., Smith, J.M., Santos, M.B., Bailey, N., Chen, C.-S., Boyle, P.R., 2005. Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesii*) in Scottish (UK) waters. *Aquat. Living Res.* 18, 327–340.
- Redfern, J.V., Ferguson, M.C., Becker, E.A., Hyrenback, K.D., Good, C., Kaschner, K., Baumgartner, M.F., Forney, K.A., Ballance, L.T., Fauchald, P., Halpin, P., Hamazaki, T., Pershing, A.J., Qian, S.S., Read, A., Reilly, S.B., Torres, L., Werner, F., 2006. Techniques for cetacean-habitat modelling. *Mar. Ecol. Prog. Ser.* 310, 271–295.
- Roberts, M.J., 2005. Chokka squid (*Loligo vulgaris reynaudii*) abundance linked to changes in South Africa's Agulhas Bank ecosystem during spawning and the early life cycle. *ICES J. Mar. Sci.* 62, 33–55.
- Robin, J.-P., Denis, V., 1999. Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *J. Appl. Ecol.* 36, 101–110.
- Roper, C.F.E., Sweeney, M.J., Nauen, C.E., 1984. Cephalopods of the world. An annotated and illustrated catalogue of species of interest to fisheries. FAO Fisheries Synopsis No. 125, vol. 3.
- Rosa, R., Seibel, B.A., 2010. Metabolic physiology of the Humboldt squid, *Dosidicus gigas*: implications for vertical migration in a pronounced oxygen minimum zone. *Prog. Oceanogr.* 86, 72–80.
- Sanchez, P., Demestre, M., Recasens, L., Maynou, F., Martin, P., 2008. Combining GIS and GAMS to identify potential habitats of squid *Loligo vulgaris* in the North-western Mediterranean. *Hydrobiologia* 612, 91–98.
- Sauer, W.H.H., Smale, M.J., Lipinski, M.R., 1992. The location of spawning grounds, spawning and schooling behaviour of the squid *Loligo vulgaris reynaudii* (Cephalopoda: Myopsida) off the Eastern Cape Coast, South Africa. *Mar. Biol.* 114, 97–107.
- Scott, B.E., Sharples, J., Ross, O.N., Wang, J., Pierce, G.J., Camphuysen, C.J., 2010. Sub-surface hotspots in shallow seas: fine-scale limited locations of top predator foraging habitat indicated by tidal mixing and sub-surface chlorophyll. *Mar. Ecol. Prog. Ser.* 408, 207–226.
- Sen, H., 2004. A preliminary study on the effects of salinity on egg development of European squid (*Loligo vulgaris* Lamarck, 1798). *Isr. J. Aquacult. – Bamid* 56, 93–99.
- Sims, D.W., Genner, M.J., Southward, A.J., Hawkins, S.J., 2001. Timing of squid migration reflects North Atlantic climate variability. *Proc. R. Soc. London* 268, 2607–2611.
- Smith, J.M., 2011. Growth investment and distribution of the squid *Loligo forbesii* (Cephalopoda: Loliginidae) in Northeast Atlantic waters. Ph.D. Thesis, University of Aberdeen.
- Valavanis, V.D., Georgakarakos, S., Koutsoubas, D., Arvanitidis, C., Haralambous, J., 2002. Development of a marine information system for cephalopod fisheries in eastern Mediterranean. *Bull. Mar. Sci.* 71, 867–882.
- Valavanis, V.D., Georgakarakos, S., Kapantagakis, A., Palialexis, A., Katara, I., 2004. A GIS environmental modelling approach to essential fish habitat designation. *Ecol. Model.* 178, 417–427.
- Valavanis, V.D., Pierce, G.P., Zuur, A.F., Palialexis, A., Saveliev, A., Katara, I., Wang, J., 2008. Modelling of essential fish habitat based on remote sensing, spatial analysis and GIS. *Hydrobiologia* 612, 5–20.
- Viana, M., Pierce, G.J., Illian, J., MacLeod, C.D., Bailey, N., Wang, J., Hastie, L.C., 2009. Seasonal movements of veined squid *Loligo forbesii* in Scottish (UK) waters. *Aquat. Living Resour.* 22, 1–15.
- Waluda, C.M., Pierce, G.J., 1998. Temporal and spatial patterns in the distribution of squid *Loligo* spp. in the United Kingdom waters. *S. Afr. J. Mar. Sci.* 20, 323–336.
- Waluda, C.M., Rodhouse, P.G., Trathan, P.N., Pierce, G.J., 2001. Remotely sensed mesoscale oceanography and the distribution of *Illex argentinus* in the South Atlantic. *Fish. Oceanogr.* 10, 207–216.
- Waluda, C.M., Trathan, P.N., Rodhouse, P.G., 1999. Influence of oceanographic variability on recruitment in the *Illex argentinus* (Cephalopoda: Ommastrephidae) fishery in the south Atlantic. *Mar. Ecol. Prog. Ser.* 183, 159–167.

- Wang, J., Pierce, G.J., Boyle, P.R., Denis, V., Robin, J.-P., Bellido, J.M., 2003. Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences – a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters. *ICES J. Mar. Sci.* 60, 1149–1158.
- Wangvoralak, S., Hastie, L.C., Pierce, G.J., 2011. Temporal and ontogenic variation in the diet of squid (*Loligo forbesii* Steenstrup) in Scottish waters. *Hydrobiologia* 670, 223–240.
- Young, I.A.G., Pierce, G.J., Stowasser, G., Santos, M.B., Wang, J., Boyle, P.R., Shaw, P.W., Bailey, N., Tuck, I., Collins, M.A., 2006. The Moray Firth directed squid fishery. *Fish. Res.* 78, 39–43.
- Zuur, A.F., Ieno, E.N., Smith, G.M., 2007. *Analysing Ecological Data*. Springer, New York.
- Zuur, A.F., Ieno, E.N., Walker, N.J., Saveliev, A.A., Smith, G.M., 2009. *Mixed Effects Models and Extensions in Ecology with R*. Springer, New York.
- Zuur, A.F., Pierce, G.J., 2004. Common trends in Northeast Atlantic squid time series. *Neth. J. Sea Res.* 52, 57–72.