

# Temporal and ontogenetic variation in the diet of squid (*Loligo forbesii* Streenstrup) in Scottish waters

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**Abstract** The squid *Loligo forbesii* is the only cephalopod species currently targeted by fisheries in the northern NE Atlantic. An active predator, it feeds primarily on fish, crustaceans and cephalopods. During 15 years since the only previous large-scale study of the diet of this species in Scottish waters, there have been substantial changes in marine fish abundances. The present study evaluates sources of variation (temporal, ontogenetic) in diet composition and prey size preferences of *L. forbesii*, including a comparison of contemporary (July 2006–June 2007) and historical (1990–1992) dietary datasets. Results revealed significant size-related and seasonal variation in diet composition and prey size. Teleost fish of the families Ammodytidae and Gobiidae were eaten by squid of all sampled sizes, although occurrence of gobies was generally more frequent in smaller squids, while Gadidae were eaten more frequently by larger squids. Cannibalism was also more frequent in larger squids. Compared to the 1990–1992 dataset, clupeid fish were less important in the diet of squid in 2006–2007, while the importance of gobies increased, and the size of

gobies eaten also increased. The trend in gadoids differed according to the index used: their frequency of occurrence was considerably higher in 2006–2007 than in 1990–1992, but their numerical importance was slightly lower. In general, results provided little evidence that changes in the diet of *L. forbesii* correspond with changes in fish abundance, at least at the scales at which these are measured.

**Keywords** Diet · *Loligo forbesii* · Trophic interactions · Long-term trends

## Introduction

Cephalopods play key roles as both predators and prey in marine ecosystems (e.g. Boyle, 1990; Hastie et al., 2009a). Cephalopods are usually short-lived and their populations typically display a high production to biomass ratio (Boyle & Boletzky, 1996; Caddy & Rodhouse, 1998). They provide important food resources for a range of predators, including toothed whales, seabirds and demersal fish (e.g. Furness, 1994; Daly et al., 2001; Piatkowski et al., 2001). Most cephalopod species are active predators, whose high metabolic rates result in high energy demands. Their prey includes fish, crustaceans, other molluscs, ophiuroids, polychaetes, chaetognaths and siphonophores (Martins, 1982; Nixon, 1987; Rodhouse, 1996; Boyle

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& Rodhouse, 2005). Since the cephalopod oesophagus passes through the brain, prey are usually cut into small pieces by the chitinous mandibles prior to ingestion and some prey had parts may be discarded rather than ingested (Bidder, 1950; Boycott, 1961; Porteiro et al., 1990). Consequently, stomach contents may provide a rather incomplete record of feeding. Nevertheless, this remains the main source of information and can still provide useful information.

The factors influencing prey selection in cephalopods are not well understood. In principle, several types of explanations are possible: (a) functional explanations related to evolutionary advantage (e.g. optimal foraging theory, Pyke, 1984); (b) mechanistic explanations dealing with the process by which prey selection occurs (e.g. morphological constraints, behavioural mechanisms); (c) explanation related to empirical relationships (e.g. dietary variation with season) for which the mechanism and/or function may or may not be apparent. Most dietary studies provide only empirical evidence of diet selection. Captive studies, however, have provided some insights into both selectivity and potential biases in stomach contents, e.g. squids may not ingest the heads of large fish (Porteiro et al., 1990).

*Loligo forbesii* is the only cephalopod currently targeted by fisheries in the northern NE Atlantic, although several other species are landed as by-catches (Pierce et al., 2010). Like most loliginid squids, it has a short life cycle of 1–2 years, the seasonal timing of which varies across its geographical range (Holme, 1974; Ngoile, 1987; Guerra et al., 1994; Pierce et al., 1994a; Collins et al., 1995). The main prey groups are fish, crustaceans and other cephalopods (e.g. Martins, 1982; Ngoile, 1987; Collins et al., 1994; Guerra & Rocha, 1994; Pierce et al., 1994b; Stowasser, 2004). Cannibalism is recorded most frequently in larger individuals (Collins & Pierce, 1996). The only previous large-scale study of the diet of this species in Scottish waters (1990–1992) demonstrated both size-related and seasonal variation in diet: Pierce et al. (1994b) reported that the main prey groups were fishes of the families Gadidae, Clupeidae and Ammodytidae, the first two of these families being more important in Winter, while the latter were more common prey in Summer.

It is a general feature of predator–prey relationships that prey size increases with predator size (e.g. Preciado et al., 2008, in relation to demersal fish). While there have been few studies on predator

size–prey size relationship in cephalopods, increases in prey size with predator size have been previously reported in the squids *Todarodes sagittatus* (Quetglas et al., 1999) and *L. forbesii* (Collins & Pierce, 1996).

Over long (e.g. decadal) time-scales and due to changes in marine community composition, shifts in dominant prey species may be expected to occur. Over the last two decades, stocks of some of the important prey of *L. forbesii*, especially sandeels and gadoids, have declined (ICES, 2009, 2010). The North Sea has experienced a rapid increase of sea temperature in comparison with other large marine ecosystems (Belkin, 2009), which is likely to have impacted on resident marine species. Dulvy et al. (2008) and Perry et al. (2005) showed that there were changes in fish distribution according to depth (moving towards deeper water) and latitude (moving towards the north for large gadoids and the south for small gadoids) in the North Sea.

Comparison of results on diet of *L. forbesii* from 1990–1992 in Scottish waters with two other smaller-scale studies suggests that there have been changes in diet composition, although it is difficult to completely rule out sampling biases. The main prey species found during 1984–1986 by Ngoile (1987) were Argentine (*Argentina sphyraena*), Norway pout (*Trisopterus esmarkii*), whiting (*Merlangius merlangus*) and sandeel (*Ammodytes* sp.). In a more recent study by Stowasser (2004), the most frequently identified fish were *Trisopterus* sp., silvery pout (*Gadiculus argenteus*) and transparent goby (*Aphia minuta*).

The objectives of this study are:

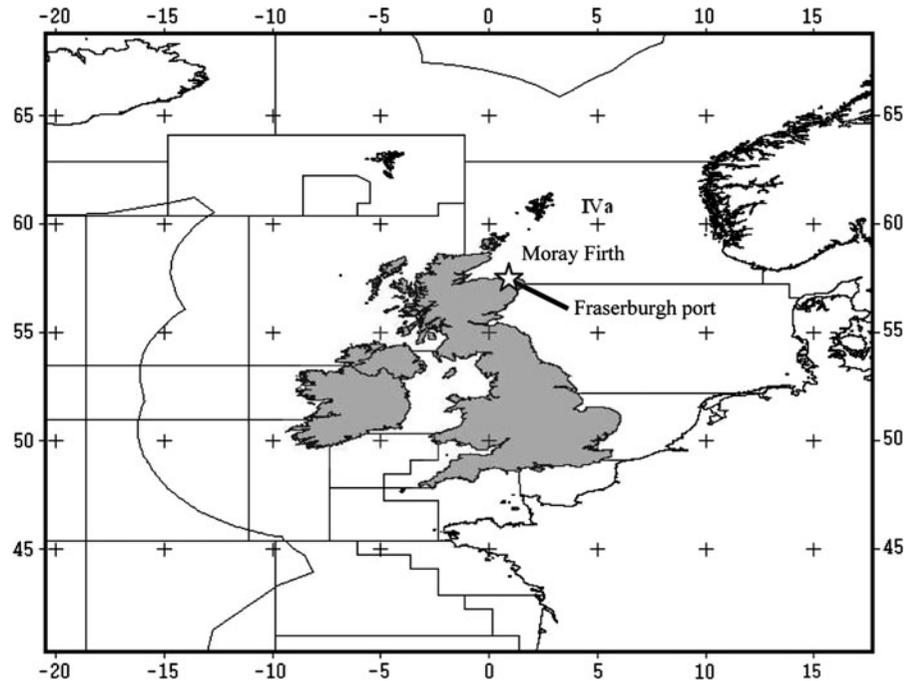
- (a) to describe the diet of *L. forbesii* in Scottish waters during 2006–2007, evaluating the importance of seasonal and ontogenetic variation in diet composition and prey size
- (b) to determine whether there has been a shift in feeding patterns of *L. forbesii* since the last major study in 1990–1992 and whether any such changes can be related to changes in prey availability

## Materials and methods

### Diet data for 2006–2007

Monthly samples of *L. forbesii* from the Moray Firth, northern North Sea, were collected from commercial

**Fig. 1** Location of the port of Fraserburgh in the Moray Firth, ICES fishery subdivision IVa



trawler landings in the Scottish port of Fraserburgh (Fig. 1) from July 2006 until June 2007. In total, 360 stomachs (typically 30 per month, selected at random) were sampled. Biological data were also recorded as follows: dorsal mantle length (ML), body weight (BW), sex, maturity stage (a scale from I to V, following Boyle & Ngoile, 1993; Pierce et al., 1994a), and mantle weight (MW). Samples were stored frozen ( $-20^{\circ}\text{C}$ ) prior to analysis.

Stomach contents were thawed at room temperature and sorted by using a low-power, stereo microscope. Contents were initially sorted into major groups: fish, cephalopods, crustaceans, and others, and then classified to family, genus, and species, as far as possible, based mainly on identification of hard parts. The presence of fish was determined from bones (including vertebrae), otoliths, lenses, scales, fin rays, and flesh. Reference material and published guides (Härkönen, 1986; Watt et al., 1997; Scharf et al., 1998) were used to support identifications. Cephalopods were recognised from beaks, sucker rings, statoliths, gladius, lenses, and flesh. Squid beaks were identified to the lowest possible taxonomic level using Clarke's (1986) guide. Crustaceans were recognised and identified from exoskeletons, eyes, and flesh, while zooplankton were identified using the guide of Conway et al. (2003).

Dietary information was quantified using standard indices. Percent frequency of occurrence ( $\%F$ ) refers to the percentage of stomachs containing a particular prey type (and when summed across all prey types, often exceeds 100% due to stomachs containing prey more than one type (e.g., Hyslop, 1980). For graphical presentations, we used modified percentage frequency of occurrence, in which  $\%F$  values were rescaled to sum to 100% across all prey types. We also calculated percentage numerical importance ( $\%N$ ) for each prey type, this being the total number of individuals of a particular prey type, summed across all stomachs, expressed as a percentage of the total number of individuals of all prey types (Breiby & Jobling, 1985). All such indices have limitations (see Hyslop, 1980; Tollit et al., 2010). Both  $\%F$  and  $\%N$  may underestimate the importance of rapidly digested prey and of large fish prey (since squids do not always consume the heads; Porteiro et al., 1990) while  $\%N$  will tend to overestimate the dietary importance of small prey.

Fish size was estimated from measurement of otolith size, using published relationships between otolith length (OL) and width (OW) and fish length (FL) (Härkönen, 1986). Because fish otoliths and cephalopod beaks (from which prey size can also be estimated) were encountered in stomachs relatively

rarely, we did not attempt to estimate overall diet composition in terms of % weight.

### Historical data

In order to assess possible changes in diet over the last 15 years, raw data on *L. forbesii* diet collected during 1990–1992 (see Pierce et al., 1994b; Collins & Pierce, 1996) were re-analyzed. These data were obtained from squid caught in Scottish waters using various gears, by both commercial and research vessels. Sources of variation were assumed to be similar to those for 2006–2007, with the addition of region, since the 1990s data came from three different regions: North Sea (including the Moray Firth), West coast (i.e. ICES subdivision VIa), and Rockall (ICES subdivision VIb). We also compared dietary results in the North Sea from the two time periods (1990–1992 and 2006–2007).

### Data exploration and preliminary analyses

Data exploration was undertaken to identify unusual data points, determine appropriate distributions for response variables, to indicate collinearity between explanatory variables and to display evidence of interactions between effects of explanatory variables. This involved use of Cleveland dotplots, pair plots and co-plots and calculation of the variance inflation factor (VIF). Subsequent analyses were carried out for data from 1990–1992 and 2006–2007 both separately and (for the sub-set of North Sea data) together. Results on diet composition are summarised in graphical and tabular form to identify the main size-related, seasonal, regional and between-study period patterns. Preliminary analysis of dietary preferences was carried out using simple non-parametric statistics: Spearman Rank correlations (for relationships between prey size and predator size, Kruskal–Wallis tests (for size difference among prey species) and Mann–Whitney *U* tests (for prey size differences between the two study periods). These tests were carried out using SPSS 16.

### Statistical modelling

Generalized additive modelling (GAM) was applied to investigate sources of variation in dietary preferences. Binomial GAMs with logit link functions were

fitted to presence-absence data for three important categories of fish prey, namely sandeels, gadoids, and gobies. There were insufficient records to do GAMs for any gadid species on their own. GAMs with Gaussian distribution were applied for analysis of prey size. The latter analyses used prey length data (for single prey species and combined across prey species), either fish length (FL) or otolith length (OL). OL could be used for analyses of size in individual prey species while for analyses in which data from several species were combined, FL was used. For most prey species, a better fit to a normal distribution was achieved by log transformation ( $\log_{10}(x)$ ) of length data.

For all these analyses the set of putative explanatory variables comprised month (or season), individual (predator) dorsal mantle length (ML), region, predator sex and (when datasets from both time periods were combined) time period. Interactions between explanatory variables were also considered. For those analyses of prey size in which data from several prey species were combined, species identity was also included as an explanatory variable.

Mantle length was log-transformed to reduce the influence of a small number of high values. ML was fitted as a smoother with the constraint  $k = 4$  (i.e. maximum of 3 degrees of freedom) to avoid “over-fitting” (i.e. in this context, to avoid fitting over-complex relationships that would be biologically unrealistic). Coplots indicated a strong interaction between effects of ML and season on response variables. Therefore smoothers for the effect of ML were fitted separately for data from each season and results compared with those from the equivalent model in which a single smoother for ML was fitted, using an *F* test. A significant *F* value confirmed the need to include the interaction. Such a procedure was also applied for other nominal variables (region, sex and year) to determine if their effects interacted with that of ML.

For all model fitting, a combined forwards and backwards selection procedure was used to find the optimal model. Comparisons of models were usually based on values of the Akaike Information Criterion (AIC) (the lower AIC is the better model) and significance of individual explanatory variables. If optimal models contained non-significant terms, an *F* test was used to confirm that the non-significant term significantly improved the overall fit Model

validation included checking for influential data points (high “hat” values) and patterns in the distribution of residuals (Zuur et al., 2007). All data exploration and GAM modelling were carried out using Brodgar software V.2.6.5 (Highland Statistics Ltd.), which is a menu-driven interface for *R*.

## Results

### General characteristics of squid diet in 2006–2007

The set of samples from 2006–2007 consisted of stomach contents of 192 females, 158 males, and 10 individuals that could not be sexed. Observed mantle lengths (ML) ranged from 56–500 mm, and body weight (BW) ranged from 10–1845 g.

The most commonly occurring general prey category was fish (95.6% occurrence), followed by crustaceans (29.2%) and cephalopods (10.6%). Small numbers of bivalve molluscs and gastropods were also recorded, in 0.6 and 4.5% of stomachs, respectively. Among the fish remains, 10 families and 21 species of fish prey were identified, of which Gadidae (43.9%), Ammodytidae (23.1%), and Gobiidae (19.7%) were the most frequently occurring prey families. The most frequently occurring fish prey species observed were Norway pout (*T. esmarkii*), silvery pout (*G. argenteus*), and lesser sandeel (*Ammodytes marinus*). Most crustacean remains were completely macerated and difficult to identify. However, decapods and copepods (mainly *Temora turbinata*) were identified. Copepods were present during April–September, with most frequent occurrence in June. Cephalopod remains were identified in 10.6% of samples, including 1.4% of stomachs which contained *Loligo* sp. Further details of diet composition appear in Table 1.

### Variation in importance of different prey categories

Generalized additive modelling results (Table 2) showed that, in general, squid (predator) size, season and region were the most important factors explaining variability in the occurrence of sandeels, gobies and gadoids in squid diet. There were also some differences in male and female diet. There were

**Table 1** Prey species of *Loligo forbesii*, 2006–2007 (%F = percent frequency of occurrence)

Prey type	%F (n = 360)
Fish (total)	95.6
Ammodytidae (Sandeels)	
<i>Ammodytes</i> spp.	13.6
<i>Ammodytes marinus</i>	6.7
<i>Hyperoplus lanceolatus</i>	2.8
Argentiniidae	
<i>Argentina silus</i> (Greater argentine)	0.3
<i>Argentina sphyraena</i> (Argentine)	1.1
Bothidae	
<i>Arnoglossus laterna</i> (Scaldfish)	0.8
Callionymidae	
<i>Callionymus</i> spp.	1.4
<i>Callionymus lyra</i> (Dragonet)	0.3
Carangidae	
<i>Trachurus trachurus</i> (Scad)	2.2
Clupeidae	
Unidentified Clupeidae	4.4
Gadidae (Cods and haddocks etc.)	
<i>Micromesistius poutassou</i> (Blue whiting)	0.8
<i>Merlangius merlangus</i> (Whiting)	3.6
<i>Trisopterus</i> spp.	9.2
<i>Trisopterus esmarkii</i> (Norway pout)	11.1
<i>Trisopterus minutus</i> (Poor cod)	0.6
<i>Melanogrammus aeglefinus</i> (Haddock)	2.2
<i>Gadus morhua</i> (Cod)	1.4
<i>Gadiculus argenteus</i> (Silver pout)	8.3
<i>Enchelyopus cimbrius</i> (Four-bearded rockling)	0.8
Unidentified Gadidae	5.8
Gobiidae	
<i>Gobiusculus flavescens</i> (Two-spot goby)	0.3
<i>Aphia minuta</i> (Transparent goby)	5.3
<i>Pomatoschistus</i> spp.	10.3
Unidentified Gobiidae	3.9
Pleuronectidae	
<i>Hippoglossoides platessoides</i> (Long rough dab)	0.8
Pholidae	
<i>Pholis gunnellus</i> (Butterfish)	0.8
Unidentified fish	11.9
Crustaceans (total)	29.2
Order Decapoda	
Unidentified Decapoda	4.7

**Table 1** continued

Prey type	%F (n = 360)
Order Calanoida	
Temoridae	
<i>Temora turbinata</i>	0.6
Unidentified Calanoida	2.8
Unidentified crustaceans	21.1
Cephalopods (total)	10.6
Loliginidae	
<i>Loligo</i> sp.	1.4
Unidentified cephalopods	9.2
Bivalves (total)	0.6
Gastropods (total)	4.5

significant interactions between effects of size and season in several of the final models, notably those for presence of sandeel in the diet, and there was a significant size–sex–study period interaction in the case of gobies.

#### Seasonal patterns

Fish, crustaceans and cephalopods were found in the diet of *L. forbesii* all the year round during 2006–2007. The percentage occurrence of fish prey decreased during August–October, whilst that of crustacean prey increased in that period (Fig. 2). Cephalopod remains were most frequently found in stomachs during February and October. Three main families of fish prey, Ammodytidae, Gadidae and Gobiidae were present in the diet of *L. forbesii* in every season. Gadidae were the most commonly occurring fish prey in the Winter, Spring and Autumn diet, occurring in 52.1, 32.9, and 28.6% of the stomachs, respectively, while Ammodytidae were the most frequently occurring in the Summer diet (present in 36.2% of stomachs).

Generalized additive modelling results confirmed significant seasonal differences in the occurrence of sandeels, gadoids and gobies in squid diet. From the combined data for the two study periods (North Sea only), sandeels were eaten most frequently in Summer, followed by Autumn, Spring and Winter, respectively. Gobies were found in the diet most frequently in Summer, followed by Autumn, Spring and Winter, respectively. For gadoids, the separate GAM analyses of occurrence data for 1990–1992 and 2006–2007 indicated that gadoids tended to be eaten

more frequently in Autumn, and less frequently in Spring (Table 2).

#### Size-related dietary variation

Fish were the most frequently occurring broad prey category in all size-classes of squid (with %F > 50% in all size classes) but their occurrence tended to increase in larger size classes of squid. Otoliths of *Callionymus lyra* and *Pholis gunnellus* were found only in smaller squids (<100 mm ML), while those of *Trachurus trachurus* were present only in larger squids (242–352 mm ML). Fish in family Ammodytidae and Gobiidae were found in a wide range of squid sizes (75–354 mm ML) but were most common in the diet of small *L. forbesii* (Fig. 3). On the other hand, gadoids tended to be found more frequently in large squids. A Kruskal–Wallis test indicated significant variation ( $P = 0.032$ ) in the median mantle length of *L. forbesii* that had eaten different fish prey groups (Ammodytidae, Gadidae, Gobiidae, Argentinidae, and other fish prey), confirming that at least some of the trends described above are statistically significant. The percentage occurrence of crustacean prey declined from 30–40% in squid 56–145 mm ML to 6–19% in squid >145 mm ML. Cephalopod remains were found in squid from 70 mm ML upwards but tended to be found mainly in larger squids (60% occurrence in squid > 150 mm ML).

GAM results confirmed significant effects of squid size on the incidence of sandeels, gadoids and gobies in squid diet (Fig. 4) but present a less clear picture than suggested by examination of the raw data. Size-related trends in diet are illustrated in Fig. 4. Results were not completely consistent but gobies tended to be eaten more frequently by smaller squids (except for female squid in 2006–2007) and gadoids tended to be eaten more frequently by larger squid. Trends for sandeel consumption varied between seasons, with occurrence of sandeels in the 1990–1992 study peaking in larger squid in Spring but the opposite trend being apparent in Autumn.

#### Differences between the two study periods

Diet data collected in North Sea during 1990–1992 by Pierce et al. (1994b) were compared with the present dataset. It should be noted that the squid in the 1990–1992 sample from the North Sea were on

**Table 2** Results of binomial GAM models for the presence of various fish prey in the diet of *Loligo forbesii*

Prey group	Final model	DE (%)
<i>2006–2007</i>		
Sandeel ( <i>n</i> = 345)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> < 0.001 (Q3 > Q2 > Q4 > Q1); s(ML):Winter, <i>P</i> = 0.605, df = 1; s(ML):Spring, <i>P</i> = 0.364, df = 2; s(ML):Summer, <i>P</i> = 0.095, df = 1; s(ML):Autumn, <i>P</i> = 0.033, df = 1	21.7
Gadoid ( <i>n</i> = 340)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4) s(ML), <i>P</i> < 0.001, df = 3; Season, <i>P</i> = 0.012 (Q4 > Q1 > Q3 > Q2)	16.0
Gobies ( <i>n</i> = 338)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> = 0.037 (Q2 > Q4 > Q1 > Q3); s(ML):Winter, <i>P</i> = 0.051, df = 1; s(ML):Spring, <i>P</i> = 0.109, df = 1; s(ML):Summer, <i>P</i> = 0.009, df = 2.4; s(ML):Autumn, <i>P</i> = 0.060, df = 1	29.7
<i>1990–1992</i>		
Sandeel ( <i>n</i> = 1311)	Y1 ~ 1 + as.factor(season) + as.factor(region) + s(ML, <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> < 0.001 (Q2 > Q3 > Q4 > Q1); Region, <i>P</i> < 0.001 (RA > NS > WC); s(ML):Winter, <i>P</i> = 0.412, df = 1.4; s(ML):Spring, <i>P</i> = 0.008, df = 1; s(ML):Summer, <i>P</i> = 0.132, df = 1; s(ML):Autumn, <i>P</i> = 0.009, df = 1	9.7
Gadoid ( <i>n</i> = 1282)	Y1 ~ 1 + as.factor(sex) + as.factor(season) + as.factor(region) + s(ML, <i>k</i> = 4) s(ML), <i>P</i> < 0.001, df = 2; Season, <i>P</i> < 0.001 (Q4 > Q3 > Q1 > Q2); Sex, <i>P</i> = 0.03 (F > M); Region, <i>P</i> < 0.001 (WC > NS > RA)	8.0
Gobies ( <i>n</i> = 1311)	Y1 ~ 1 + as.factor(region) + s(ML, <i>k</i> = 4) s(ML), <i>P</i> = 0.012, df = 1.6; Region, <i>P</i> = 1 (NS > WC > RA)	19.9
<i>1990–2007</i>		
Sandeel ( <i>n</i> = 716)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> < 0.001 (Q3 > Q4 > Q2 > Q1); s(ML):Winter, <i>P</i> = 0.002, df = 2.5; s(ML):Spring, <i>P</i> = 0.147, df = 1; s(ML):Summer, <i>P</i> = 0.003, df = 3; s(ML):Autumn, <i>P</i> = 0.058, df = 2	14.2
Gadoid ( <i>n</i> = 701)	Y1 ~ 1 + as.factor(year) + s(ML, <i>k</i> = 4, by = as.factor(season)) Year, <i>P</i> < 0.001 (Y2 > Y1); s(ML):Winter, <i>P</i> = 0.872, df = 1; s(ML):Spring, <i>P</i> = 0.037, df = 2.9; s(ML):Summer, <i>P</i> < 0.001, df = 2.4; s(ML):Autumn, <i>P</i> = 0.004, df = 1	10.9
Gobies ( <i>n</i> = 701)	Y1 ~ 1 + as.factor(sex) + as.factor(year) + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(year:sex)) Season, <i>P</i> = 0.188 (Q3 > Q4 > Q2 > Q1); Year, <i>P</i> = 0.038 (Y2 > Y1); Sex, <i>P</i> = 0.158 (F > M); s(ML):Y1 and female, <i>P</i> = 0.683, df = 1; s(ML):Y1 and male, <i>P</i> = 0.019, df = 1; s(ML):Y2 and female, <i>P</i> = 0.002, df = 1; s(ML):Y2 and male, <i>P</i> = 0.285, df = 1.5	13.3

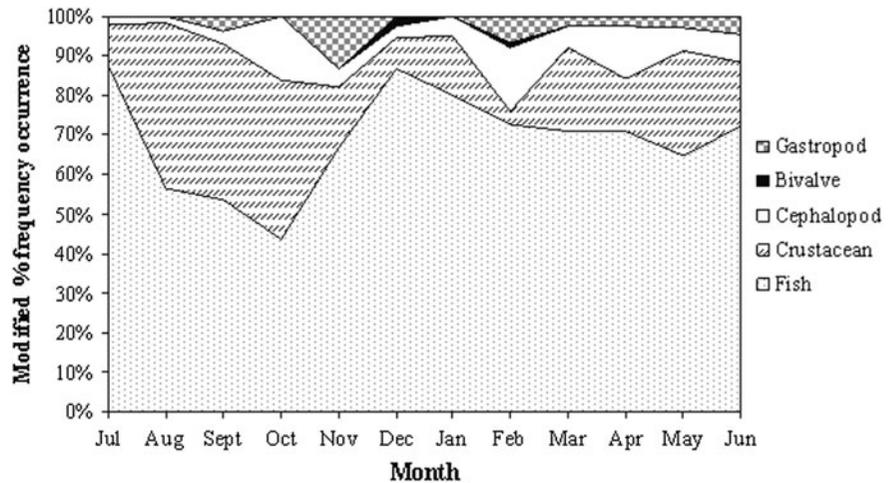
For explanatory variables remaining in the final models, the table gives associated *P* values and direction of differences is indicated in parentheses. For fitted smoothers, both *P* values and degrees of freedom (df, a value of 1 indicates a linear fit) are given. Significant smoothers are illustrated in Fig. 4

ML dorsal mantle length, DE deviance explained, Y1 dataset in 1990–1992, Y2 Dataset in 2006–2007, Q1 Winter, Q2 Spring, Q3 Summer, Q4 Autumn, F female, M Male, NS North Sea, WC West Coast, RC Rockall

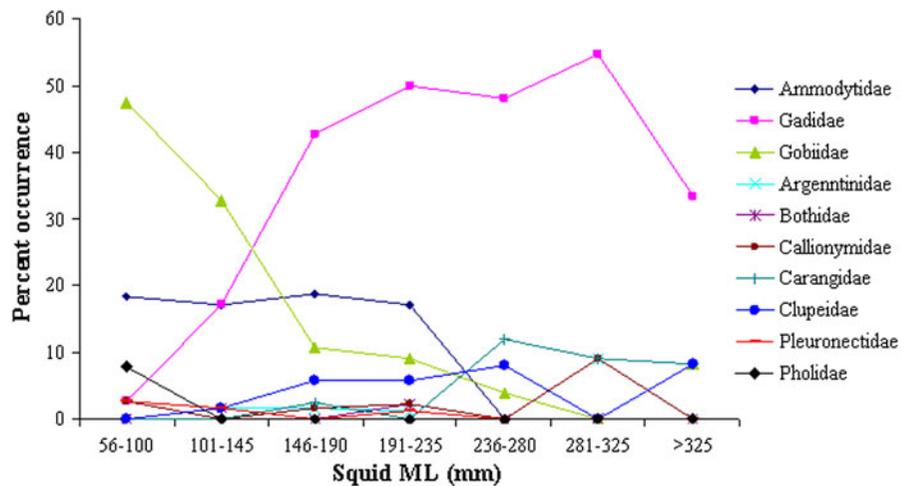
average larger (in terms of median mantle length) than those sampled in 2006–2007 (Mann–Whitney *U* test, *P* < 0.001). In both datasets, fish were the most important food source of *L. forbesii*, followed by crustaceans and cephalopods. Differences were apparent in the types of fish prey eaten (see Table 3). Clupeids, sandeels and gadoids were the most important prey groups in 1990–1992, while gobies, sandeels and gadoids were the most important prey groups in 2006–2007. Clupeids and, to a lesser

extent, gadoids declined in numerical importance in 2006–2007 compared to 1990–1992, although the frequency of occurrence of gadoids was higher in 2006–2007. Among the Gadidae, smaller species (*Trisopterus* spp.) increased in terms of both percent frequency and numerical importance in 2006–2007 compared to 1990–1992. Conversely, percent frequency and numerical importance for large gadoid species (e.g. whiting) tended to be lower in 2006–2007 compared to 1990–1992. Sandeels were

**Fig. 2** Monthly variation in the diet of *Loligo forbesii* (2006–2007). The graph displays the modified percent frequency of occurrence of the main prey groups in non-empty stomachs



**Fig. 3** Percent frequency of occurrence of identified fish prey in non-empty stomachs ( $n = 360$ , sampled from July 2006 to June 2007) of *Loligo forbesii* for different size classes of squid. Samples sizes of each size class were 38, 64, 122, 88, 25, 11, and 12



more important, in terms of both frequency of occurrence and numbers, in the 2006–2007 dataset. Three fish prey groups were recorded in 2006–2007 but not in 1990–1992: Argentinidae (*A. silus* and *A. sphyraena*), Bothidae (*Arnoglossus laterna*) and Pholidae (*P. gunnellus*).

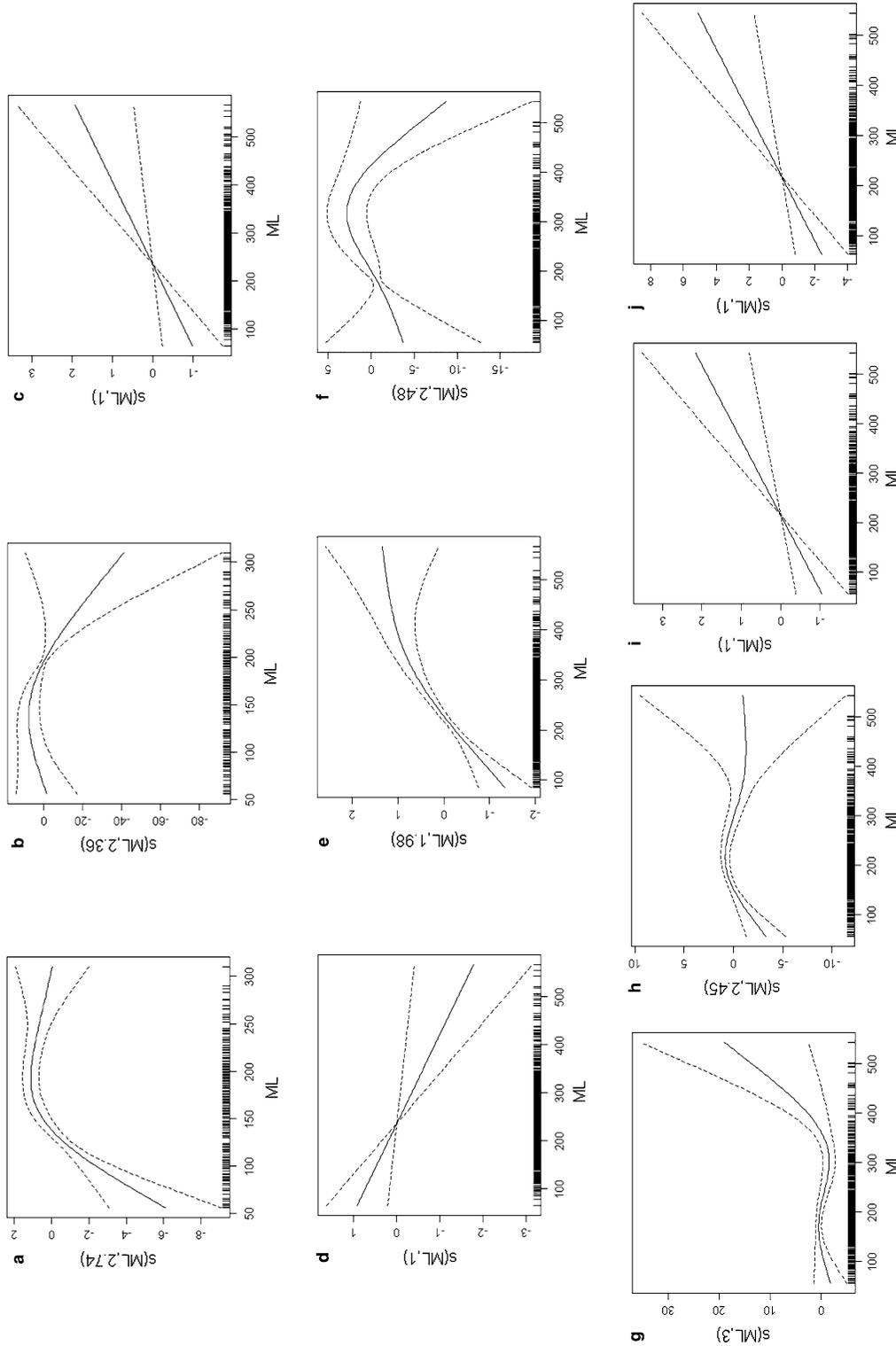
Comparing cephalopod remains in the stomachs between the two periods, it seems that cephalopod species identified in 1990–1992 were more diverse than in 2006–2007. Both *Alloteuthis subulata* and *Loligo* species were found in 1990–1992, while only *Loligo* species were recorded in 2006–2007. Crustacean remains identified in both periods consisted of decapods and copepods. Gastropod and bivalves were present only in 2006–2007.

Generalized additive modelling results from analysis the combined (North Sea) data set for 1990–1992

and 2006–2007 indicated that the frequency of occurrence of both gobies and gadoids was significantly higher in 2006–2007 than in 1990–1992. However, once seasonal and size-related dietary variation had been taken into account, the frequency of occurrence of sandeels did not differ between the two time periods.

#### Variation in prey size

In total, 329 otoliths were found in squid stomach contents in the 2006–2007 samples. However, only the 233 identifiable and intact otoliths were used to estimate the size of fish prey. The lengths of otoliths ranged from 0.33 to 6.29 mm, while the estimated fish prey sizes were 15.2–123.2 mm, in squid sizes of 74–354 mm ML (Table 4). Otoliths found in squid



**Fig. 4** GAM Smoothing curves for the effect of squid size on the presence of various fish prey in the diet of *Loligo forbesii*. The x axis represents the dorsal mantle length (ML) and dotted lines represent the 95% confidence intervals of smoothing curve. Where from both periods, i.e., 1990–2007, are used, results refer to the North Sea (NS) only. Only statistically significant relationships are illustrated: **a** Gadoids eaten in NS 2006–2007 ( $P < 0.001$ ), **b** Gobies in Summer diet in NS 2006–2007 ( $P = 0.009$ ), **c** Sandeels in Spring diet 1990–1992 ( $P = 0.008$ ), **d** Sandeels in Autumn diet 1990–1992 ( $P = 0.009$ ), **e** Gadoids eaten in 1990–1992 ( $P < 0.001$ ), **f** Sandeels in Winter diet in NS 1990–2007 ( $P = 0.002$ ), **g** Sandeels in Summer diet in NS 1990–2007 ( $P = 0.003$ ), **h** Gadoids in Summer diet in NS 2006–2007 ( $P = 0.002$ ) ( $P = 0.004$ ), **j** Gobies eaten in female squids in NS 2006–2007 ( $P = 0.002$ )

stomachs mostly belonged to Ammodytidae (mainly *A. marinus*), Gobiidae (mainly *A. minuta*), and Gadidae (mainly *T. esmarkii*). Otolith occurrence appeared to vary with season, with the highest occurrence of otoliths being found in Summer. Only transparent goby (*A. minuta*) otoliths could be found in the diet of *L. forbesii* in every season (Table 4).

Overall, there was a weak positive relationship between prey size and predator size (Spearman's  $r = 0.156$ ,  $P = 0.017$ ). Correlations between squid ML and the estimated size of three of the six commonest prey types were significant (transparent goby:  $r = 0.454$ ,  $P = 0.002$ ; other gobies:  $r = 0.762$ ,  $P = 0.002$ ; whiting:  $r = 0.810$ ,  $P = 0.004$ ). However, no significant correlation was observed for *A. marinus*, other sandeels or *T. esmarkii*.

#### GAM results on prey size

Generalized additive modelling results indicated that predator size, season, and prey type were the major factors influencing (fish) prey size, although some sex-related and regional differences were also apparent. For some prey groups there were also sex, region, and study period differences (Table 5). In the 1990–1992 sample, size of gadoids eaten varied with

region and sex, with larger sizes eaten in the North Sea and by female squids. GAM results from the combined data for the two periods (North Sea only) indicated that the smallest fish eaten were gobies, followed by gadoids, sandeels and other groups.

Regarding the effect of season on prey size, larger fish tended to be found in stomachs in Winter compared to other seasons. For all fish prey combined there was evidence of a positive relationship between squid size and prey size eaten in the North Sea in squid up to around 300 mm ML in 1990–1992 (Fig. 5d). Although there were differences between different prey types, study periods and seasons, the majority of statistically significant prey size-predator size relationships were positive over at least part of the squid size range (Fig. 5).

Generalized additive modelling results indicated that the size of gobies eaten (in the North Sea) differed significantly between the two study periods (with gobies eaten in 2006–2007 being larger). There was, however, a significant interaction between the effects of predator size and study period on the size of sandeels eaten.

Selecting data on prey size from the same area (ICES subdivision IV, North Sea) and period (Summer and Autumn), the median length of sandeels taken by *L. forbesii* in 1990–1992 appeared to be slightly

**Table 3** Numerical importance of different prey categories (as absolute numbers,  $N$ , and as a percentage of all prey individuals,  $\%N$ ), and frequency of occurrence ( $F$ , and as a

percentage of stomachs contained food,  $\%F$ ) in stomachs of *Loligo forbesii* in the North Sea, 1990–1992 and 2006–2007

Fish prey	1990–1992				2006–2007			
	$N$	$\%N$ ( $n = 130$ )	$F$	$\%F$ ( $n = 391$ )	$N$	$\%N$ ( $n = 391$ )	$F$	$\%F$ ( $n = 360$ )
Ammodytidae	29	22.4	32	8.2	122	31.2	83	23.1
Argentinidae	–	–	–	–	6	1.5	5	1.4
Bothidae	–	–	–	–	8	2.0	3	0.8
Callionymidae	1	0.8	1	0.3	1	0.3	6	1.7
Carangidae	1	0.8	1	0.3	2	0.5	8	2.2
Clupeidae	43	33.2	43	11.0	2	0.5	16	4.4
Gadidae	25	19.3	71	18.2	62	15.9	158	43.9
Whiting	9	6.9	12	3.1	11	2.8	13	3.6
<i>Trisopterus</i> spp.	9	6.9	10	2.6	23	5.9	75	20.8
Gobiidae	24	18.5	10	2.6	182	46.5	71	19.7
Pleuronectidae	2	1.5	2	0.5	2	0.5	3	0.8
Pholidae	–	–	–	–	4	1.0	3	0.8
Carangidae/Scombridae	5	3.9	5	1.3	–	–	–	–

Separate information is presented for the most common small (*Trisopterus* spp.) and large (whiting) gadids in the diet

**Table 4** Sizes of identified otoliths and estimated length of fish prey in the diet of *Loligo forbesii*, 2006–2007, along with biological characteristics of the squid

Prey	Size of identified otoliths		Estimated length of prey Mean $\pm$ SD (mm)	Biological data on squid which had eaten these prey types	
	N	Mean $\pm$ SD		ML (mm) Mean $\pm$ SD	Season
Family Ammodytidae					
Ammodytidae	7	0.96 $\pm$ 0.25 (0.45–1.18)	58.7 $\pm$ 13.2 (32.1–69.8)	212 $\pm$ 31 (145–233)	Sum
<i>Ammodytes</i> spp.	14	1.13 $\pm$ 0.36 (0.45–1.60)	67.6 $\pm$ 18.7 (32.1–91.8)	177 $\pm$ 25 (130–213)	Sum
<i>Ammodytes marinus</i>	58	1.28 $\pm$ 0.43 (0.48–2.15)	75.3 $\pm$ 22.3 (33.4–120.4)	175 $\pm$ 26 (75–219)	Sum and Spr
<i>Hyperoplus lanceolatus</i>	32	0.83 $\pm$ 0.41 (0.38–1.78)	43.3 $\pm$ 23.2 (17.3–96.9)	194 $\pm$ 35 (155–354)	Sum, Win and Spr
Family Argentinidae					
<i>Argentina silus</i>	1	1.48	69.6	160	Aut
<i>Argentina sphyraena</i>	5	2.08 $\pm$ 0.10 (1.90–2.13)	93.7 $\pm$ 4 (86.5–95.5)	162 $\pm$ 41 (123–204)	Aut and Win
Family Callionymidae					
<i>Callionymus lyra</i>	1	0.68	25.4	74	Aut
Family Carangidae					
<i>Trachurus trachurus</i>	2	4.25 $\pm$ 0.07 (4.20–4.30)	121.5 $\pm$ 2.5 (119.7–123.2)	279 $\pm$ 64 (242–352)	Win
Family Gadidae					
<i>Micromesistius poutassou</i>	5	5.34 $\pm$ 1.60 (2.50–6.26)	94.7 $\pm$ 40.7 (22.6–118)	179 $\pm$ 13 (162–197)	Sum
<i>Gadus morhua</i>	10	3.79 $\pm$ 1.09 (2.35–6.29)	60.9 $\pm$ 16.7 (33.8–91.6)	190 $\pm$ 12 (171–202)	Sum
<i>Trisopterus esmarkii</i>	23	2.89 $\pm$ 0.75 (2.15–5.40)	42.9 $\pm$ 22 (20.9–116.8)	181 $\pm$ 23 (147–227)	Sum and Win
<i>Merlangius merlangus</i>	10	4.05 $\pm$ 1.07 (2.27–5.00)	67.6 $\pm$ 21 (32.7–86.6)	161 $\pm$ 21 (122–202)	Sum
Family Gobiidae					
<i>Aphia minuta</i>	44	0.65 $\pm$ 0.27 (0.30–1.13)	36.8 $\pm$ 14.6 (18.1–62.3)	160 $\pm$ 32 (74–214)	All the year
<i>Gobiusculus flavescens</i>	4	0.56 $\pm$ 0.09 (0.45–0.65)	18.3 $\pm$ 3.1 (15.2–21.9)	91	Aut
<i>Pomatoschistus minutus</i>	9	0.83 $\pm$ 0.11 (0.63–0.98)	23.8 $\pm$ 4.4 (16.5–30.7)	211 $\pm$ 88 (116–354)	Sum and Win
Family Pholidae					
<i>Pholis gunnellus</i>	6	0.55 $\pm$ 0.07 (0.48–0.63)	59.9 $\pm$ 5.3 (53.4–66.5)	91 $\pm$ 1 (89–92)	Aut
Family Pleuronectidae					
<i>Hippoglossoides platessoides</i>	2	1.33 $\pm$ 0.64 (0.88–1.78)	39.5 $\pm$ 30.8 (17.8–61.3)	157 $\pm$ 72 (74–198)	Aut and Win
Total	233	1.55 $\pm$ 1.28 (0.30–6.29)	55.9 $\pm$ 27.5 (15.2–123.2)	175 $\pm$ 40 (74–354)	

Minimum and maximum are provided in parentheses

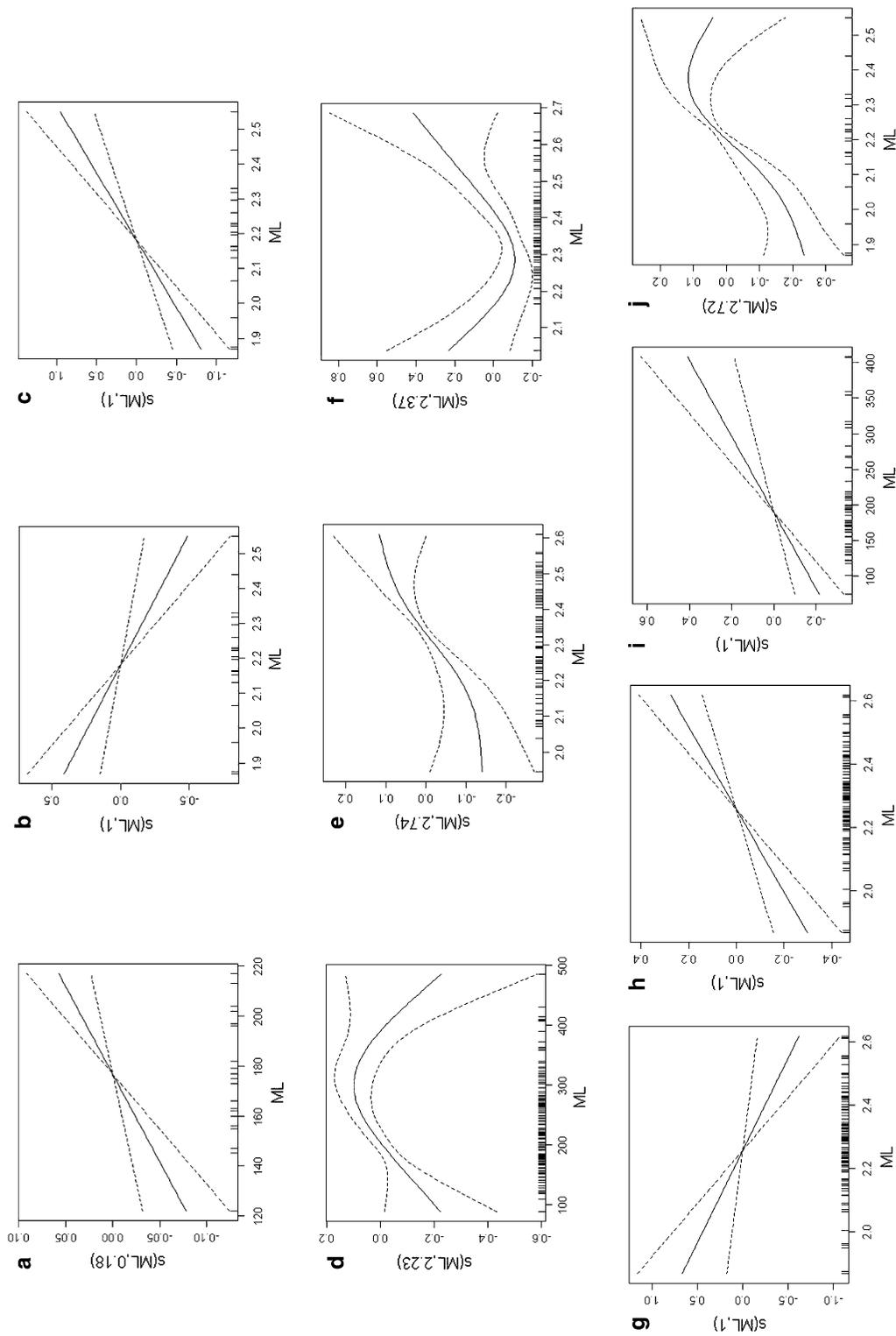
SD Standard deviation, Sum Summer, Aut Autumn, Win Winter, Spr Spring

**Table 5** Results of Gaussian GAM models for estimating fish length in the diet of *Loligo forbesii*

Prey group	Final model	DE (%)
<i>2006–2007</i>		
All prey size (FL <sup>a</sup> , <i>n</i> = 207)	Y1 ~ 1 + as.factor(Prey type) + as.factor(season) + s(ML, <i>k</i> = 4) s(ML), <i>P</i> = 0.040, df = 2; Prey type, <i>P</i> < 0.001 (OT > SA > GA > GO); Season, <i>P</i> < 0.001 (Q1 > Q3 > Q4 > Q2)	46.6
Sandseel (OL <sup>a</sup> , <i>n</i> = 109)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4) + ML:as.factor(season) s(ML), <i>P</i> = 0.025, df = 1; Season, <i>P</i> = 0.006 (Q3 > Q4 > Q1 and Q2); ML:season, <i>P</i> < 0.001, df = 3	52.1
Gadoid (FL <sup>a</sup> , <i>n</i> = 47)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> = 0.121 (Q1 > Q4 > Q3); s(ML):Winter, <i>P</i> = 0.002, df = 0.2; s(ML):Summer, <i>P</i> = 0.693, df = 0.9; s(ML):Autumn, <i>P</i> = 0.656, df = 0.8	13.5
Gobies (OL <sup>a</sup> , <i>n</i> = 57)	Y1 ~ 1 + as.factor(season) + s(ML <sup>a</sup> , <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> = 0.015 (Q1 > Q4 > Q3 > Q2); s(ML):Winter, <i>P</i> = 0.003, df = 1; s(ML):Spring, <i>P</i> = 0.972, df = 1; s(ML):Summer, <i>P</i> < 0.001, df = 1; s(ML):Autumn, <i>P</i> = 0.250, df = 1	61.6
<i>1990–1992</i>		
All prey size (FL <sup>a</sup> , <i>n</i> = 315)	Y1 ~ 1 + as.factor(pre type) + as.factor(sex) + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(region)) Prey type, <i>P</i> < 0.001 (SA > GA > OT > GO); Season, <i>P</i> < 0.001 (Q1 > Q2 > Q4 > Q3); Sex, <i>P</i> = 0.002 (F > M); s(ML):North Sea, <i>P</i> = 0.005, df = 2.2; s(ML):West coast, <i>P</i> = 0.160, df = 2.7; s(ML):Rockall, <i>P</i> = 0.051, df = 3	55
Sandseel (OL <sup>a</sup> , <i>n</i> = 153)	Y1 ~ 1 + as.factor(season) + s(ML <sup>a</sup> , <i>k</i> = 4, by = as.factor(season)) + ML <sup>a</sup> :as.factor(sex) Season, <i>P</i> < 0.001 (Q2 > Q3 > Q1 > Q4); s(ML):Winter, <i>P</i> = 0.961, df = 1; s(ML):Spring, <i>P</i> = 0.169, df = 1; s(ML):Summer, <i>P</i> = 0.003, df = 2.7; s(ML):Autumn, <i>P</i> = 0.746, df = 1; ML:sex, <i>P</i> = 0.002, df = 2	49.7
Gadoid (FL <sup>a</sup> , <i>n</i> = 116)	Y1 ~ 1 + as.factor(region) + as.factor(sex) + as.factor(season) + s(ML <sup>a</sup> , <i>k</i> = 4, by = as.factor(season)) Season, <i>P</i> < 0.001 (Q1 and Q2 > Q4 > Q3); Sex, <i>P</i> = 0.037 (F > M); Region, <i>P</i> = 0.007 (NS > RA > WC); s(ML):Winter, <i>P</i> = 0.591, df = 0.9; s(ML):Spring, <i>P</i> = 0.631, df = 0.2; s(ML):Summer, <i>P</i> = 0.002, df = 2.4; s(ML):Autumn, <i>P</i> = 0.079, df = 2.6	48.5
<i>1990–2007</i>		
All prey size (FL <sup>a</sup> , <i>n</i> = 361)	Y1 ~ 1 + as.factor(pre type) + as.factor(season) + s(ML <sup>a</sup> , <i>k</i> = 4, by = as.factor(season)) Prey type, <i>P</i> < 0.001 (OT > SA > GA > GO); Season, <i>P</i> < 0.001 (Q1 > Q3 > Q4 > Q2); s(ML):Winter, <i>P</i> = 0.568, df = 1; s(ML):Spring, <i>P</i> = 0.007, df = 1; s(ML):Summer, <i>P</i> = 0.012, df = 1.9; s(ML):Autumn, <i>P</i> < 0.001, df = 1	61
Sandseel (OL <sup>a</sup> , <i>n</i> = 171)	Y1 ~ 1 + as.factor(season) + s(ML, <i>k</i> = 4, by = as.factor(year)) Season, <i>P</i> < 0.001 (Q1 > Q4 > Q3 > Q2); s(ML):Y1, <i>P</i> < 0.001, df = 1; s(ML):Y2, <i>P</i> = 0.020, df = 2	48.5
Gadoid (FL <sup>a</sup> , <i>n</i> = 84)	Y1 ~ 1 + as.factor(season) + s(ML <sup>a</sup> , <i>k</i> = 4) s(ML), <i>P</i> = 0.016, df = 2; Season, <i>P</i> = 0.019 (Q1 and Q2 > Q4 > Q3)	22.1
Gobies (OL <sup>a</sup> , <i>n</i> = 86)	Y1 ~ 1 + as.factor(year) + as.factor(season) + s(ML <sup>a</sup> , <i>k</i> = 4) s(ML), <i>P</i> < 0.001, df = 3; Season, <i>P</i> < 0.001 (Q1 > Q4 > Q3 > Q2); Year, <i>P</i> < 0.001 (Y2 > Y1)	66.3

For explanatory variables remaining in the final models, the table gives associated *P* values, and the direction of differences is indicated in parentheses. For fitted smoothers, both *P* values and degrees of freedom (df, value of 1 indicates a linear fit) are given. Significant smoothers are illustrated in Fig. 5 (<sup>a</sup>Log-transformations: fish length (FL), otolith length (OL), and dorsal mantle length (ML))

DE deviance explained, Y1 dataset in 1990–1992, Y2 dataset in 2006–2007, Q1 Winter, Q2 Spring, Q Summer, Q4 Autumn, F female, M male, NS North Sea, WC West Coast, RC Rockall, SA Sandeels, GA Gadoids, OT other fish prey



**Fig. 5** GAM Smoothing curves for the effect of squid (predator) size on fish prey length in the diet of *Lolligo forbesii*. The x axis represents the dorsal mantle length (ML) and dotted lines represent the 95% confidence intervals of smoothing curve. Where from both periods, i.e. 1990–2007, are used, results refer to the North Sea (NS) only. Only statistically significant relationships are illustrated: **a** Gadoids in Winter diet in NS 2006–2007 ( $P = 0.002$ ), **b** Gobies in Winter diet in NS 2006–2007 ( $P = 0.003$ ), **c** Gobies in Summer diet in NS 2006–2007 ( $P < 0.001$ ), **d** Fish prey in NS 1990–1992 ( $P = 0.005$ ), **e** Sandeels in Summer diet in NS 1990–1992 ( $P = 0.003$ ), **f** Gadoids in Summer diet 1990–1992 ( $P = 0.002$ ), **g** Fish prey in Spring diet in NS 1990–2007 ( $P = 0.007$ ), **h** Fish prey in Autumn diet in NS 1990–2007 ( $P < 0.001$ ), **i** Sandeels eaten in 1990–1992 ( $P < 0.001$ ), **j** Gobies eaten in NS 1990–2007 ( $P < 0.001$ )

greater than in 2006–2007. However, Mann–Whitney  $U$  test showed no significant difference ( $P = 0.089$ ). There was no difference in median squid size between the two periods ( $P = 0.692$ ).

## Discussion

It is apparent from this study that fish were the most important prey for *L. forbesii* in Scottish waters in 2006–2007, followed by crustaceans and cephalopods, as previously reported for this area (Ngoile, 1987; Pierce et al., 1994b; Collins & Pierce, 1996; Stowasser, 2004), as well as in Irish waters (Collins et al., 1994).

### Regional variation in diet

The dominant prey species in the diet of *L. forbesii* differ between regions, presumably influenced by local abundances (i.e. availability) of potential prey species. The dominant fish species in the Azores was horse mackerel (*T. picturatus*) (Martins, 1982), while sprat (*S. sprattus*), poor cod (*T. minutus*) and transparent goby (*A. minuta*) dominated the diet in Irish waters (Collins et al., 1994). In Scottish waters, gadoids and sandeels were the most frequently occurring groups as also found in the previous study by Pierce et al. (1994b). It should be noted that Gadidae (mainly, *Trisopterus* spp., and *M. merlangus*), Ammodytidae (mainly *Ammodytes* spp.), Argentinidae (mainly *Argentina* spp.) and flatfish, which were identified by both Ngoile (1987) and Pierce et al. (1994b) in the diet of this species, were also found in the present study.

### Seasonal variation in diet

Seasonal variation was one of the important sources of variation in diet composition and size selectivity of *L. forbesii* in Scottish waters, which it is in agreement with previous studies by Pierce et al. (1994b) and Collins & Pierce (1996), and suggests that seasonal changes in prey availability may be important in determining squid diet. Moreover, in the present study copepods occurred more often in June. This is consistent with the peak period of copepod abundance on the eastern coast of Scotland (Broekhuizen & McKenzie, 1995).

### Size-related variation

The development of the prey capture, ingestion and digestion systems (e.g. tentacles, beaks, digestive tract) during the cephalopod lifespan seems likely to be a crucial process influencing the prey selection (Boucher-Rodoni et al., 1987), defining the morphological constraints on foraging, feeding and digestion. In *L. forbesii*, it is apparent that most juveniles fed on small crustaceans or smaller fish, and then switched to eating mainly fish and cephalopods as they grew. Again, this corroborates the findings of previous studies by Collins et al. (1994) and Pierce et al. (1994b).

As seen in this study, Collins et al. (1994) and Collins & Pierce (1996) also noted that cannibalism in *L. forbesii* occurs more frequently in larger squids rather than in smaller squids. This is consistent with studies on other squid species including *L. pealei* (Macy, 1982), *T. sagittatus* (Lordan et al., 2001), *Illex argentinus* (Mouat et al., 2001) and *Dosidicus gigas* (Markaida & Sosa-Nishizaki, 2003). Cannibalism in squid may occur because of food shortage (Macy, 1982; Lordan et al., 2001). However, cannibalism in larger *L. forbesii* may be a function of abundance, for example occurring often when abundance is high (Pierce et al., 1998; Hastie et al., 2009b), as suggested for *Loligo vulgaris* in the Saharan Bank (Coelho et al., 1997).

### Long-term trends in diet: species eaten

The increases in percent occurrence and numerical importance of gobies in the 2006–2007 diet of *L. forbesii* in the North Sea, compared to 1990–1992, may indicate that gobies have effectively replaced clupeids as a prey source. Among the clupeid prey, sprat was the most frequently found species (see also Collins et al., 1994). Although ICES advice indicates that the state of the North Sea Survey data showed that sprat abundance was lower (although increasing) in 1990–1992 than in 2006–2007 (although its abundance was then decreasing, see ICES, 2009). Abundance (spawning stock biomass, SSB) of herring in the North Sea seems to have been rather similar in both periods. Thus, we have no clear evidence that consumption of sprat by squid is related to sprat abundance.

Change in diet composition of *L. forbesii* in Scottish waters over time may have occurred due to changes in prey and predator abundances in the

marine ecosystem. Rogers & Ellis (2000) found that there was a decrease in abundance of large species of demersal fish in British waters, while smaller and non-target fish species increased, due to the long-term impact of commercial fisheries. Jennings et al. (1999) noted that Norway pout has markedly increased in abundance in recent years. Additional evidence is apparent in stock status reports prepared by ICES (2009). During 2005–2007, SSB of sandeel and Norway pout tended to increase at the same time as SSB of herring, whiting and haddock tended to decrease (Fig. 6). Declining abundance of large fish, whiting and haddock, could be beneficial for large squids because their food in the North Sea is similar in prey species composition (Hislop et al., 1996; Greenstreet et al., 1998).

However, as for clupeids, a detailed examination of dietary importance and abundance of gadids again provides little evidence that squid predation tracks stock abundance. In the case of gadoids in the diet, although there was a slight decline in numerical importance, this was not consistent with the trend in percentage occurrence in the diet, which was upwards (Table 3). Among the gadids, whiting decreased in importance in the diet while *Trisopterus* spp. increased. Whiting abundance (SSB) in the North Sea declined substantially between 1990–1992 and 2006–2007 (consistent with dietary results) but Norway pout abundance was fairly similar in both

time-periods (although it had reached a historic low point in 2005).

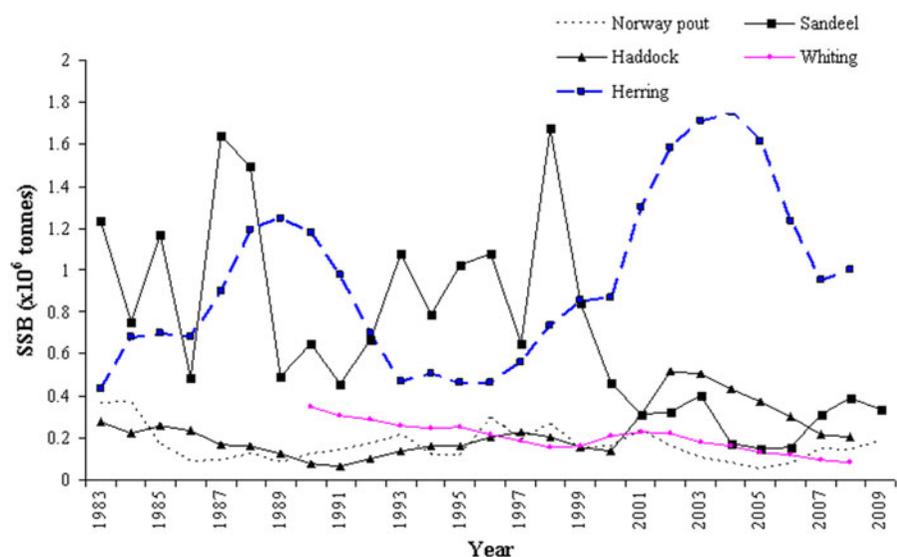
#### Long-terms trends in diet: prey size

In addition to changes in species composition, the size composition of the fish community in the North Sea ecosystem has been affected by fishing pressure and climate change (Jennings et al., 2002; Ottersen et al., 2006). Aside from the decline of larger species and truncation of the age structure in many species, there are numerous reports of decreases in size-at-age and age at maturity in fished stocks, e.g. cod in the Barents sea (Ottersen et al., 2006) and in the North sea (Yoneda & Wright, 2004), and sandeels in the northwestern North Sea (Wanless et al., 2004).

Given the above-mentioned changes in the relative abundance of large and small fish, it might have been predicted that a shift towards smaller prey would be seen in squid diet. However, the only statistically significant difference in the size of prey eaten in 1990–1992 and 2006–2007 was that squid took bigger gobies in 2006–2007 compared to 1990–1992. In the case of gobies, since they are not commercially important, there is little available information on trends in stock abundance or size structure.

The findings from the present study suggest that there have been significant changes in the diet of *L. forbesii* over the last 15 years. While seasonal

**Fig. 6** Spawning stock biomass (SSB, millions of tonnes) of herring, sandeel, Norway pout, whiting and haddock in the North Sea (data from ICES, 2009)



shifts in diet were previously attributed to changes in prey abundance (or availability, see Pierce et al., 1994b), we have been able to find little or no evidence that long-term interannual trends in squid diet are related to fish abundance. This may be a sampling issue (e.g. the relatively small numbers of stomachs examined) and it is also possible that the available abundance measures for commercially exploited fish stocks are simply at the wrong spatial scale to be relevant to predation by *L. forbesii*. In addition, it may be necessary to derive abundance indices specifically related to the size classes of fish taken by *L. forbesii*.

Any long-term shift in the diet of apparently opportunistic predators such as cephalopods is a very important consideration in the construction of large-scale, trophic network models. Therefore, it would be worthwhile to monitor future changes in squid diet in the North Sea. To ensure comparable results, sampling protocol should consider the possible influence of fishing gear, study area, and seasonal pattern on the results. In principle, predators such as *Loligo forbesii* may represent a useful biological indicator of changes in the size- and species-composition of fish communities. However, results of this study caution against uncritical use of such indicators.

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## References

Belkin, I. M., 2009. Rapid warming of large marine ecosystems. *Progress in Oceanography* 81: 207–213.

Bidder, A. M., 1950. The digestive mechanism of the European squids *Loligo vulgaris*, *Loligo forbesii*, *Alloteuthis media* and *Alloteuthis subulata*. *Quarterly Journal of Microscopical Science* S3-91(13): 1–43.

Boucher-Rodoni, R., E. Boucaud-Camou & K. Mangold, 1987. Comparative reviews. In Boyle, P. R. (ed.), *Cephalopod Life Cycles*. Academic Press, London: 85–108.

Boycott, B. B., 1961. The functional organization of the brain of the cuttlefish *Sepia officinalis*. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 153(953): 503–534.

Boyle, P. R., 1990. Cephalopod biology in the fisheries context. *Fisheries Research* 8: 313–321.

Boyle, P. R. & S. V. Boletzky, 1996. Cephalopod Populations: Definition and Dynamics. *Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences* 351(1343): 985–1002.

Boyle, P. R. & M. A. K. Ngoile, 1993. Assessment of maturity state and seasonality of reproduction in *Loligo forbesii* (Cephalopoda: Loliginidae) from Scottish waters. In Okutani, T., R. K. O'Dor & T. Kubodera (eds), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo: 37–48.

Boyle, P. R. & P. Rodhouse, 2005. *Cephalopods: Ecology and Fisheries*. Blackwell Science, Oxford.

Breiby, A. & M. Jobling, 1985. Predatory role of the flying squid (*Todarodes sagittatus*) in north Norwegian waters. *NAFO Scientific Council Studies* 9: 125–132.

Broekhuizen, N. & E. McKenzie, 1995. Patterns of abundance for *Calanus* and smaller copepods in the North Sea: time series decomposition of two CPR data sets. *Marine Ecology Progress Series* 118: 103–120.

Caddy, J. F. & P. G. Rodhouse, 1998. Cephalopod and groundfish landings: Evidence for ecological change in global fisheries? *Review in Fish Biology and Fisheries* 8(4): 431–444.

Clarke, M. R. (ed.), 1986. *A Handbook for the Identification of Cephalopod Beaks*. Clarendon Press, Oxford.

Coelho, M., P. Domingues, E. Balguerias, M. Fernandez & J. P. Andrade, 1997. A comparative study of the diet of *Loligo vulgaris* (Lamarck, 1799) (Mollusca: Cephalopoda) from the south coast of Portugal and the Saharan Bank (Central-East Atlantic). *Fisheries Research* 29: 245–255.

Collins, M. A. & G. J. Pierce, 1996. Size selectivity in the diet of *Loligo forbesii* (Cephalopoda: Loliginidae). *Journal of the Marine Biological Association of the United Kingdom* 76: 1081–1090.

Collins, M. A., S. De Grave, C. Lordan, G. M. Burnell & P. G. Rodhouse, 1994. Diet of the squid *Loligo forbesii* Steenstrup (Cephalopoda: Loliginidae) in Irish waters. *ICES Journal of Marine Science* 51: 337–344.

Collins, M. A., G. M. Burnell & P. G. Rodhouse, 1995. Distribution and demography of *Loligo forbesii* in the Irish Sea. *Biology and Environment* 95B: 49–57.

Conway, D. V. P., R. G. White, J. Hugues-Dit-Ciles, C. P. Gallienne & D. B. Robins, 2003. *Guide to the Coastal and Surface Zooplankton of the South-Western Indian Ocean*. Marine Biological Association of the United Kingdom, Occasional Publication No 15.

Daly, H. I., G. J. Pierce, M. B. Santos, J. Royer, S. K. Cho, G. Stowasser, J.-P. Robin & S. M. Henderson, 2001. Cephalopod consumption by trawl caught fish in Scottish and English Channel waters. *Fisheries Research* 52(1–2): 51–64.

Dulvy, N. K., S. I. Rogers, S. Jennings, V. Stelzenmuller, S. R. Dye & H. R. Skjoldal, 2008. Climate change and deepening of the North Sea fish assemblage: a biotic indicator of warming seas. *Journal of Applied Ecology* 45: 1029–1039.

Furness, R. W., 1994. An estimate of the quantity of squid consumed by seabirds in the eastern North Atlantic and adjoining seas. *Fisheries Research* 21: 165–177.

- Greenstreet, S. P. R., J. A. McMillan & E. Armstrong, 1998. Seasonal variation in the importance of pelagic fish in the diet of piscivorous fish in the Moray Firth, NE Scotland: a response to variation in prey abundance? *ICES Journal of Marine Science* 55: 121–133.
- Guerra, A. & F. Rocha, 1994. The life history of *Loligo vulgaris* and *Loligo forbesi* (Cephalopoda: Loliginidae) in Galician waters (NW Spain). *Fisheries Research* 21: 43–69.
- Guerra, A., P. Sánchez & F. Rocha, 1994. The Spanish fishery for *Loligo*: recent trends. *Fisheries Research* 21: 217–230.
- Härkönen, T., 1986. Guide to the Otoliths of the Bony Fishes of the Northeast Atlantic. Danbiu Aps, Biological Consultants, Sweden.
- Hastie, L. C., G. J. Pierce, J. Wang, I. Bruno, A. Moreno, U. Piatkowski & J.-P. Robin, 2009a. Cephalopods in the North-Eastern Atlantic: species, biogeography, ecology, exploitation and conservation. *Oceanography and Marine Biology* 47: 111–190.
- Hastie, L., G. Pierce, C. Pita, M. Viana, J. Smith & S. Wangvoralak, 2009b. Squid Fishing in UK Waters: A Report to SEAFISH Industry Authority, SFIA, Grimsby: 84 pp [available on internet at [http://www.seafish.org/pdf.pl?file=seafish/Documents/AberdeenUni\\_SquidFishinginUKWaters.pdf](http://www.seafish.org/pdf.pl?file=seafish/Documents/AberdeenUni_SquidFishinginUKWaters.pdf)].
- Hislop, J. R. G., 1996. Changes in North Sea gadoid stocks. *ICES Journal of Marine Science* 53: 1146–1156.
- Holme, N. A., 1974. The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. *Journal of the Marine Biological Association of the United Kingdom* 54: 481–503.
- Hyslop, E. J., 1980. Stomach contents analysis: a review of methods and their application. *Journal of Fish Biology* 17: 411–429.
- ICES, 2009. Report of the ICES Advisory Committee 2009. ICES Advice, 2009. Book 6. ICES, Copenhagen.
- ICES, 2010. Report of the ICES Advisory Committee 2010. ICES Advice, 2010. Book 6. ICES, Copenhagen.
- Jennings, S., S. P. R. Greenstreet & J. D. Reynolds, 1999. Structural change in an exploited fish community: A consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* 68: 617–627.
- Jennings, S., S. P. R. Greenstreet, L. Hill, G. J. Piet, J. K. Pinnegar & K. J. Warr, 2002. Long-term trends in the trophic structure of the North Sea fish community: evidence from stable-isotope analysis, size-spectra and community metrics. *Marine Biology* 141: 1085–1097.
- Lordan, C., M. A. Collins, L. N. Key & E. D. Browne, 2001. The biology of the ommastrephid squid, *Todarodes sagittatus*, in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* 81: 299–306.
- Macy, W. K., 1982. Feeding Patterns of the Long-Finned Squid, *Loligo pealei*, in New England Waters. *Biological Bulletin* 162: 28–38.
- Markaida, U. & O. Sosa-Nishizaki, 2003. Food and feeding habits of jumbo squid *Dosidicus gigas* (Cephalopoda: Ommastrephidae) from the Gulf of California, Mexico. *Journal of the Marine Biological Association of the United Kingdom* 83: 507–522.
- Martins, H. R., 1982. Biological studies of the exploited stock of *Loligo forbesi* (Mollusca: Cephalopoda) in the Azores. *Journal of the Marine Biological Association* 62: 799–808.
- Mouat, B., M. A. Collins & J. Pompert, 2001. Patterns in the diet of *Illex argentinus* (Cephalopoda: Ommastrephidae) from the Falkland Islands jigging fishery. *Fisheries Research* 52: 41–49.
- Ngoile, M. A. K., 1987. Fishery biology of the squid *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. PhD Thesis, University of Aberdeen, UK.
- Nixon, M., 1987. Comparative reviews. In Boyle, P. R. (ed.), *Cephalopod Life Cycles*. Academic Press, London: 201–219.
- Ottersen, G., D. O. Hjermann & N. C. Stenseth, 2006. Changes in spawning stock structure strengthen the link between climate and recruitment in a heavily fished cod (*Gadus morhua*) stock. *Fisheries Oceanography* 15: 230–243.
- Perry, A. L., P. J. Low, J. R. Ellis & J. D. Reynolds, 2005. Ecology: climate change and distribution shifts in marine fishes. *Science* 308: 1912–1915.
- Piatkowski, U., G. J. Pierce & M. Morais da Cunha, 2001. Impact of cephalopods in the food chain and their interaction with the environment and fisheries: an overview. *Fisheries Research* 52: 5–10.
- Pierce, G., P. Belcari, P. Bustamante, L. Challier, Y. Cherel, Á. González, Á. Guerra, P. Jereb, N. Koueta, E. Lefkaditou, A. Moreno, J. Pereira, U. Piatkowski, C. Pita, J.-P. Robin, B. Roel, M. B. Santos, M. Santurtun, S. Seixas, P. Shaw, J. Smith, G. Stowasser, V. Valavanis, R. Villanueva, J. Wang, S. Wangvoralak, M. Weis, & K. Zumholz, 2010. The future of cephalopod populations, fisheries, culture, and research in Europe. In Pierce, G. et al. (eds), *Cephalopod Biology and Fisheries in Europe*. ICES Cooperative Research Report 303: 86–118.
- Pierce, G. J., P. R. Boyle, L. C. Hastie & L. Key, 1994a. The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fisheries Research* 21: 17–41.
- Pierce, G. J., P. R. Boyle, L. C. Hastie & M. B. Santos, 1994b. Diets of squid *Loligo forbesi* and *Loligo vulgaris* in the northeast Atlantic. *Fisheries Research* 21: 149–163.
- Pierce, G. J., N. Bailey, Y. Stratoudakis & A. Newton, 1998. Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. *ICES Journal of Marine Science* 55: 14–33.
- Porteiro, F. M., H. R. Martins & R. T. Hanlon, 1990. Some observations on the behaviour of adult squids, *Loligo forbesi*, in captivity. *Journal of the Marine Biological Association of the United Kingdom* 70: 459–472.
- Preciado, I., F. Velasco & I. Olaso, 2008. The role of pelagic fish as forage for the demersal fish community in the southern Bay of Biscay. *Journal of Marine Systems* 72: 407–417.
- Pyke, G. H., 1984. Optimal foraging theory: a critical review. *Annual review of ecology and systematics* 15: 523–575.
- Quetglas, A., F. Alemany, A. Carbonell, P. Merella & P. Sánchez, 1999. Diet of the European flying squid *Todarodes sagittatus* (Cephalopoda: Ommastrephidae) in the Balearic Sea (western Mediterranean). *Journal of the Marine Biological Association of the United Kingdom* 79: 479–486.

- Rodhouse, P. O., 1996. Role as consumers. Philosophical Transactions of the Royal Society B: Biological Sciences 351: 1003–1022.
- Rogers, S. I. & J. R. Ellis, 2000. Changes in the demersal fish assemblages of British coastal waters during the 20th century. ICES Journal of Marine Science 57: 866–881.
- Scharf, F. S., R. M. Yetter, A. P. Summers & F. Juanes, 1998. Enhancing diet analyses of piscivorous fishes in the Northwest Atlantic through identification and reconstruction of original prey sizes from ingested remains. Fishery Bulletin 96: 575–588.
- Stowasser, G., 2004. Squid and Their Prey: Insights from Fatty Acid and Stable Isotope Analysis. Ph.D. Thesis, University of Aberdeen, UK.
- Tollit, D. L., G. J. Pierce, K. A. Hobson, W. Don Bowen & S. J. Iverson, 2010. Diet. In Boyd, I. L., W. Don Bowen & S. J. Iverson (eds), Marine Mammal Ecology and Conservation: A Handbook of Techniques. Oxford University Press, New York: 191–221.
- Wanless, S., P. J. Wright, M. P. Harris & D. A. Elston, 2004. Evidence for decrease in size of lesser sandeels *Ammodytes marinus* in a North Sea aggregation over a 30-yr period. Marine Ecology Progress Series 279: 237–246.
- Watt, J., G. J. Pierce & P. R. Boyle, 1997. Guide to the Identification of North Sea Fish Using Premaxillae and Vertebrae. ICES Cooperation Research Report No. 220. International Council for the Exploration of the Sea, Denmark: 231.
- Yoneda, M. & P. J. Wright, 2004. Temporal and spatial variation in reproductive investment of Atlantic cod *Gadus morhua* in the northern North Sea and Scottish west coast. Marine Ecology Progress Series 276: 237–248.
- Zuur, A. F., E. N. Ieno & G. M. Smith, 2007. Analysing Ecological Data. Springer, New York.