

Interannual variation in life-cycle characteristics of the veined squid (*Loligo forbesi*) in Scottish (UK) waters

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Abstract – The loliginid squid *Loligo forbesi* has a flexible life-cycle, involving variable size and age at maturity, presence of summer and winter breeding populations, and extended periods of breeding and recruitment. This paper reviews life history data collected since 1983 from the commercial fishery in Scottish (UK) waters, alongside fishery data collected since 1970, and examines (a) the relationship between body size and timing of maturation, (b) evidence for shifts in the relative abundance of the summer and winter breeding populations, and (c) the possible role of environmental signals in determining the timing of breeding. Evidence from fishery data suggests that, since the 1970s, the summer breeding population has declined while the winter breeding population now dominates and breeds later than was previously the case. Length-weight relationships and size at maturity showed significant inter-annual and seasonal variation during the period 1983-2001. Males are shown to decline in relative weight as they mature while females increase in relative weight; possible interpretations are discussed. High autumn/winter temperatures (high winter NAO values) were associated with high squid abundance and precocious maturation and tended to favour high abundance in the following year, along with increased body weight at length and a decrease in the proportion of animals breeding in December. High abundance in summer, conversely, leads to a fall of body weight at length in the following year. Thus there may be alternation of precocious and slow maturation, and/or summer and winter breeding, driven by a combination of environmental conditions and intraspecific competition.

Key words: Life history / Maturation / Population dynamics / Time series / Environmental factors

Résumé – Variation interannuelles des caractéristiques du cycle de vie du calmar (*Loligo forbesi*) en Ecosse (UK). Le calmar LoliGINIDÉ *Loligo forbesi* possède un cycle de vie variable, ce qui se traduit par des différences de taille ou d'âge à la maturité sexuelle, par la présence de populations de reproducteurs d'été et d'hiver, et par des périodes prolongées de reproduction et de recrutement. Cet article analyse des données sur le cycle biologique rassemblées depuis 1983 à partir de la pêche commerciale dans les eaux écossaises (UK), ainsi que les données de pêche rassemblées depuis 1970, et examine (a) le rapport entre la taille et la chronologie de la maturation sexuelle, (b) la réalité des variations dans l'abondance relative des groupes de reproducteurs d'été et d'hiver et (c) le rôle possible des signaux environnementaux qui déterminent le déroulement de la reproduction. D'après les données de pêche, il semble que, depuis les années 70, la population des reproducteurs d'été a diminué alors que celle des reproducteurs d'hiver est maintenant dominante. La reproduction de ce groupe hivernal étant aussi plus tardive qu'avant. Les relations longueur-poids et la taille à l'acquisition de la maturité ont montré des variations significatives interannuelles et saisonnières pendant la période 1983-2001. Le rapport poids/taille diminue chez les mâles arrivant à maturité tandis que chez les femelles le poids relatif augmente, les interprétations possibles de ces tendances sont discutées. Les températures élevées en automne et en hiver (valeurs de l'Oscillation Nord-Atlantique élevées d'hiver) ont été associées à l'abondance élevée des calmars et à leur maturation précoce. Ces températures semblent favoriser une abondance élevée l'année suivante, ainsi que l'augmentation du rapport entre le poids et la taille et la diminution de la proportion des reproducteurs en décembre. Réciproquement, l'abondance élevée des calmars en été, mène à une chute du rapport poids/taille l'année suivante. Ainsi, il peut y avoir une alternance dans la maturation précoce et lente, et/ou reproduction d'été et d'hiver, sous la dépendance combinée des conditions environnementales et de la compétition intra-spécifique.

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1 Introduction

The veined squid *Loligo forbesi* has been exploited as a fishery resource around the British Isles for at least 100 years (see Thomas 1969; Pierce et al. 1994a). Interest in its biology dates back at least to the 1970s, when Holme (1974) published a description of the life history of the species in the English Channel. This work already provided some clues as to the complexity of the life-cycle for, although the species was apparently annual, two breeding populations were present, one breeding in winter and one in summer.

In Scottish waters (Fig. 1), studies in the 1980s indicated an annual life-cycle with breeding in the winter (Ngoile 1987; Lum-Kong 1989). However, two peaks of recruitment were seen, in April and in autumn. Further indications of complexity in the life cycle included evidence of two sizes at maturity in males (Boyle and Ngoile 1993a), recruitment throughout the year and morphological differences between coastal animals and samples taken at Rockall (Boyle and Ngoile 1993b). The current picture is of a relatively small population (a few millions of post-recruit animals; Young et al. 2004), genetically homogeneous in Scottish coastal waters (excluding Rockall, Shaw et al. 1994).

Later studies (e.g. Collins et al. 1997) essentially confirmed the picture established by Ngoile (1987) of an annual life-cycle with a winter breeding peak and the most important period of recruitment being autumn. It is apparent that the coastal population comprises at least two or three micro-cohorts, each of which follows a different growth trajectory (Collins et al. 1999). It has been argued that some of the apparent variability in seasonality of the life cycle reflects variation in the relative strength of summer and winter breeding populations (Zuur and Pierce 2004). For example, the April peak of recruitment could derive from summer breeding animals of the previous year.

Thus, superimposed on the basic annual life-cycle, in addition to individual variation, there may be variation due to presence of winter and summer breeders, inshore and off-shore populations, and large and small sizes at maturity. Unlike relatively long-lived fish species, squid populations are not buffered against environmental change by the presence of several (yearly) age classes: any factor which affects recruitment success has an immediate impact on population size and, potentially, subsequent reproductive success. There is considerable evidence that distribution and local abundance of squids, including *Loligo forbesi*, are affected by environmental variation (e.g. Pierce et al. 1998; Bellido et al. 2001; Pierce and Boyle 2003; Waluda et al. 2004) and studies on various squid species indicate that recruitment success, growth patterns, fecundity and breeding success may also vary in relation to environmental conditions (e.g. Robin and Denis 1999; Waluda et al. 1999; Dawe et al. 2000; Pecl et al. 2004).

Given that the life-cycle of *Loligo forbesi* displays substantial plasticity (Boyle et al. 1995; Collins et al. 1995a,b), we hypothesize that (a) changes in typical life-cycle characteristics of the species might be evident over the medium- to long-term and that (b) such changes occur in response to changing environmental conditions.

In this paper we examine interannual variation in the relative importance of summer and winter breeding, length-weight relationships, size at maturity and the timing of maturity in *Loligo forbesi* in Scottish waters, and ask whether such variation can be related to environmental signals, notably the North Atlantic Oscillation Index – which provides a general indication of the strength of Atlantic inflow into coastal waters of Scotland.

Catch-per-unit effort (CPUE) data from commercial bottom trawling may be used as an approximate relative abundance index (see Pierce et al. 1994a; Pierce and Boyle 2003). It can also be argued that the peak of the fishery is driven by recruitment (see Fig. 2, data from Pierce et al. 1994a,b) and is normally 3–4 months ahead of the peak in the proportion of mature animals. Thus by examining interannual trends in the month-to-month pattern of CPUE we may obtain an indication of interannual variation in the importance of winter and summer breeding. A formal analysis of interannual trends in monthly CPUE series (1970–2000) was presented in Zuur and Pierce (2004). Here we briefly re-examine the same data to see whether information on the timing of breeding can be extracted.

We then examine variation in two basic biological variables, weight at length and maturity at length. Weight at length is expected to follow a standard power curve. However, we also expect variation in relation to the process of maturation. Thus, gonads and somatic tissue(s) may have different growth rates, gonad growth may incur a different energetic cost to growing somatic tissue, mature animals could feed less actively, and gonad growth may involve utilisation of some somatic tissues as an energy source. In females, body weight is expected to decline once maturity is reached, as a consequence of the release of eggs. Female *Loligo forbesi* probably lay several batches of eggs once mature (Rocha and Guerra 1996). In males, the situation is more complex, involving the cumulative production of spermatophores and their loss during mating over a lengthy period of maturity. While the male is still growing this may not be noticeable but as growth slows smaller increase in weight will be increasingly offset by loss of spermatophores. Thus there is a fundamental biological difference between males and females in the weight/maturity relationships and this represents a confounding factor in interpreting body weight in mature males.

Collins et al. (1995c) noted that there was no decline in average stomach fullness with increasing maturity in *L. forbesi* and reported a relative decline in head and mantle mass with maturation in both male and female specimens collected from Irish waters. Several other studies also suggest that energy for maturation is derived from food rather than reserves in loliginid squid (Guerra and Castro 1994; Moltschaniwskyj and Semmens 2000; Ho et al. 2004). Similarly, in the ommastrephid squid *Illex argentinus*, Hatfield et al. (1992) argued that, even though mantle mass of female squid declined relative to mantle length in more mature squid, nutrient reserves for maturation were derived from food rather than from reserves. However, analysis of population samples by Smith et al. (2005), in addition to providing evidence of energy from food being diverted from somatic growth to maturation in *Loligo forbesi*, also found some circumstantial evidence of mobilisation of mantle tissue to grow gonads.

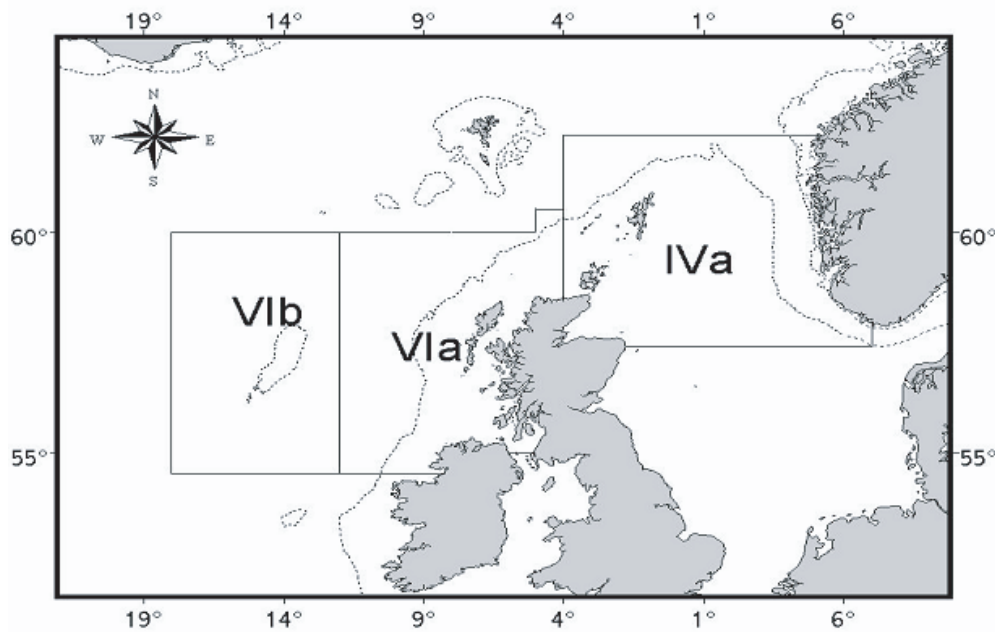


Fig. 1. Map showing the main fishery areas from which squid were sampled. Latitude is shown in degrees North, longitude in degrees West or East. The division into “West coast” (ICES area VIa) and East coast” (ICES area IVa) is at 4° West. The map also shows the 200 m depth contour. Squid catches occur throughout the continental shelf area up to around 200 m depth.

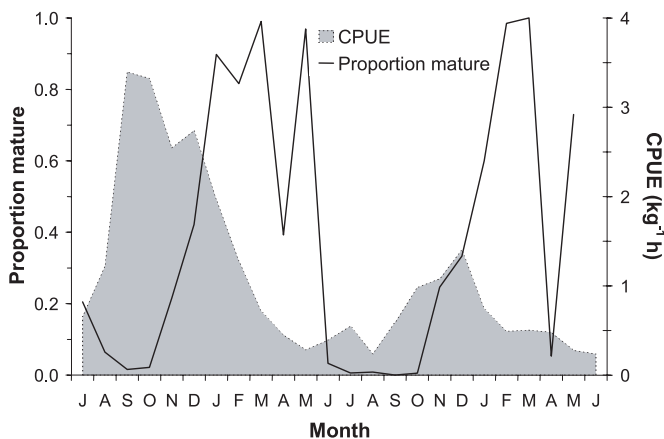


Fig. 2. Relationship between maturity patterns (monthly proportion mature for females, solid line) and fishery CPUE in Scottish coastal waters, July 1990 – June 1992 (monthly catch per unit effort kg h^{-1} by trawlers in Scottish coastal waters, shaded area). Data from Pierce et al. (1994a,b).

Seasonal variation in body weight is also expected, relating to changes in food availability, although it may be difficult to disentangle this from the effect of maturation. Lastly, we expect year-to-year differences in growth patterns, related to differences in water temperature (see, e.g., Forsythe 1993, 2004; Jackson et al. 1997) and/or food supply.

Maturation in many types of animal is commonly assumed to be size-dependent, with the proportion of animals that are mature typically increasing with body length following a logistic curve (i.e., a maturity ogive). Jackson et al. (1997) found that maturation in the loliginid squid *Lolliguncula brevis* is

more closely related to size than to age. However, maturation probably also requires a seasonal trigger and/or depends on accumulation of sufficient energy reserves (Mangold 1987). The rather consistent seasonal peaks of maturation in many loliginid species arguably support the existence of a seasonal trigger, while the occurrence of some mature animals throughout the year points to the role of additional factors (see, for example, Boyle et al. 1995; Perez et al. 2002). In the case of both weight and maturity at length, differences are expected between males and females. For example previous studies on *Loligo forbesi* show that males can mature at smaller (or larger) sizes than females, and mature slightly earlier in the year (Pierce et al. 1994b; Boyle et al. 1995).

If it is possible, by factoring out these various other effects, to tease out interannual differences in weight and maturity at length, these may be linked to environmental variation (e.g. larger weight and earlier maturation in warmer years). Another possibility is that there will be a relationship between body size and abundance: positive if both parameters represent a response to environmental conditions, negative (at least at high abundance levels) if there is density-dependent competition. The present study aims to test this series of related hypotheses using a set of biological data collected over 18 years (December 1983 – December 2001) and by reference to fishery data for 1970–2000.

2 Methods

2.1 Winter and summer breeding

Commercial landings of squid (kg) and fishing effort (hours) data for UK-registered fishing vessels landing in

Scotland during the period 1970–2000 were extracted from the Marine Laboratory database. Due to their high commercial value, discarding of even small *Loligo* catches is thought to be minimal (Young et al. 2004), so that landings can be assumed to accurately reflect catches. To obtain a reasonably consistent CPUE index we restricted the extraction to “light” and “heavy” single demersal trawls (henceforth referred to as “trawling”) from ICES areas IVa and VIa (henceforth referred to as “coastal waters”) and calculated an overall monthly CPUE index using total landings divided by total effort. Since 1998, due to a change in the recording system, Scottish fishing effort data are considered to substantially underestimate real effort (A. Shanks, FRS Marine Laboratory, pers. comm.). However, as we will demonstrate, although there is evidence that CPUE in 1999 and 2000 was underestimated, the month-to-month pattern of squid CPUE is driven by variation in the landings data. Examination of the latter confirmed that the underlying seasonal trend remains well-represented in post-1998 CPUE data.

The overall month-to-month variation in a year was summarised by treating CPUE in each month as a variable, separately for areas IVa and VIa, detrending the data by dividing each value by the relevant annual average (across both areas) and applying principal components analysis (PCA). Interpretation of the PCA output is supported by reference to graphical presentation of the raw CPUE data.

2.2 Length-weight relationships

Length-weight data were derived from monthly market samples collected between 1983 and 2001. Normally a single box of mixed squid was obtained from the market at Kinlochbervie on the west coast of Scotland every month, usually of squid caught in area VIa but occasionally of squid caught at Rockall (area VIb). Boxes typically contain 40–50 kg of squid, equivalent to around 200 individuals on average, with a range of approximately 55 to 675 individuals (the former at the peak of the breeding season, the latter during peak recruitment). This material was supplemented by irregular market sampling at east coast ports and by squid caught during research trawling surveys by FRV Scotia. This vessel typically deploys a trawl with a smaller cod-end mesh size than used commercially, thus providing a better sample of the lower end of the size range. This should not however bias estimates of parameters such as size-at-maturity. For almost all squid sampled, dorsal mantle length (DML), body weight, sex and maturity stage (on a 5-point scale, on which stages IV and V are mature, see Boyle and Ngoile 1993a; Pierce et al. 1994b) were recorded. Samples were classified by month, year and area (east coast or west coast, divided at 4° W, and Rockall). Monthly data were available for December 1983 to April 1986, July 1989 to September 1995 and March 1996 to December 2001. No weight data were available for squid collected during 1987–88.

The variables used in the analysis were: body weight, mantle length (both log-transformed), sex, maturity, region, month and year. Many different workers applied the 5-point maturity scale over the course of the date collection period so that, although it is relatively simple, consistency of use cannot be 100% assured. Nevertheless, the distinction between immature

(stages I–III) and mature (stages IV–V) is quite unambiguous, depending on presence of eggs in the oviducts or spermatophores in the Needham’s sac. On occasion animals were classified as falling between two stages.

Data were available for three regions: the East Coast of Scotland (coded as region 1), the West Coast of Scotland (region 2) and Rockall. Relatively few data were available for Rockall and these were therefore excluded from the analysis. For pre-1989 samples, the region of origin could not be identified and the entire analysis was therefore carried out in two stages, firstly for 1989–2001 and secondly for 1983–2001.

Scatter plots of log-transformed weight and length indicated a linear relationship and linear regression was therefore applied, with weight as the dependent variables, length and stage as linear explanatory variables, and year and month as factors. Interaction terms were also included. The interaction term for month can be thought of as the effect of month on the slope of the relationship with length. Since slope and intercept for the “month” effect tended to be collinear, length data were centred at zero and the analysis repeated. All analysis was carried out using Brodgar software (Highland Statistics Ltd).

2.3 Size at maturity

Data on maturity (0 – immature or 1 – mature; based on simplification of the original 5-point scale; see above), year, month and length were extracted for both sexes. As above, for 1989–2001, Rockall data were not used. The response variable (maturity) is binary. Preliminary application of a binomial generalised additive model (GAM) indicated that the relationship between maturity and length was non-linear. Hence, GAM is preferred to a generalised linear model (GLM). Because GAM can cope with non-linear relationships, we decided to use untransformed length in the models. The Akaike Information Criterion (AIC) was used in conjunction with a forward and backward selection procedure to identify the optimal model, i.e. whether factors or smoothers should be used for year and month, the appropriate number of degrees of freedom, and whether any of the components can be dropped from the model.

One possible interannual difference would be in the timing of maturity. This was investigated by repeating the analysis for animals from June (summer breeders) and December (winter breeders) only.

2.4 Relationships with abundance and environmental conditions

Annual trawl survey abundance indices (squid catch, kg per hour) were derived from survey data collected in the 1st and 4th quarter of each year for West coast of Scotland, and for the 1st quarter on the East coast (Marine Laboratory, unpublished data). For these season-area combinations, there were data from an average of over 50 hauls per year but there were too few data for other seasons to produce indices (e.g. less than 10 hauls per year for many years on the east coast in autumn). Having previously derived monthly commercial CPUE indices, we used the 1st axis PCA scores as an overall abundance index, as well as the monthly commercial CPUEs for East and West coasts.

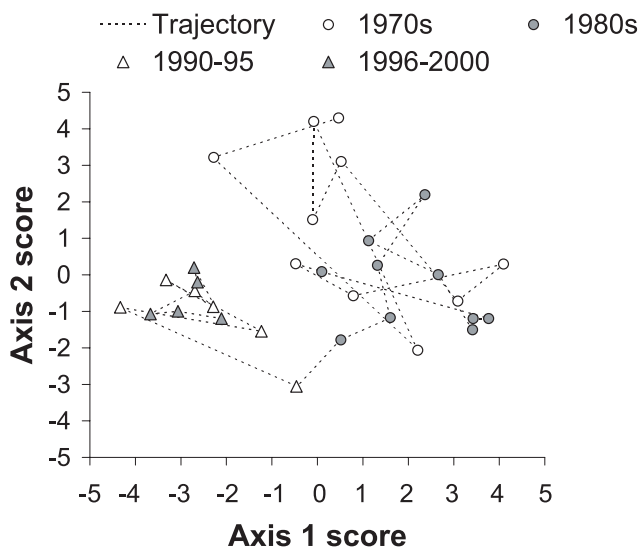


Fig. 3. PCA plot (axis 2 scores versus axis 1 scores). The original variables were de-trended CPUE data for each month in areas IVa and VIa ($N = 24$ variables). The first two axes explained 24.9% and 13.4% of variation in the data respectively.

Values of the winter North Atlantic Oscillation (NAO) index were downloaded from the University of East Anglia Climate Research Centre website. Note that winter NAO for a given year is the average of the monthly NAO values for January, February and the preceding December. Correlations were calculated between these indices and the fitted annual coefficients for effects of year on body weight and maturity at length. We also extracted data on the proportion of mature squid in December and June (an indication of timing of maturity) to determine whether these figures were correlated with abundance or NAO, including consideration of time-lags of 1 year.

3 Results

3.1 Timing of the fishery and inferences about the lifecycle

PCA results (Fig. 3) suggest a marked shift in monthly abundance patterns since 1990. These patterns are illustrated in chronological sequence in Figure 4. In the early 1970s, the fishery generally peaked around October and March–April (i.e. autumn and spring respectively), with an additional February (winter) peak in 1973. In the late 1970s, the spring peak shifted back to February–March and the October peak became dominant. The dominance of the October peak extended through the 1980s but with a further strong peak evident in June–July (summer) in several years. In the early 1990s the October peak became broader, extending through to January. By the late 1990s the timing of the peak had shifted to December or January and a secondary peak in June and July was again evident.

With reference to Figure 2, the above-described pattern may be tentatively interpreted as indicating the presence of winter and summer breeders in the 1970s, disappearance of the summer breeders for much of the 1980s. During the 1990s, the

spawning period apparently spread out over a longer period, subsequently narrowing towards a late winter peak, and with an apparent reappearance of summer breeders towards the end of the 1990s.

3.2 Length-weight relationships

3.2.1 Females

Regression analysis for (log-transformed) weight of females in 1989–2001 demonstrated significant effects of (log-transformed) length ($t = 231.46$, $p < 0.0001$), maturity stage ($t = 11.08$, $p < 0.0001$), region ($t = -3.37$, $p = 0.0008$), year, month, and the interactions of length with maturity stage ($t = 6.06$, $p < 0.0001$), month and year. Weights at length were generally higher in more mature females, and higher on the East Coast (region 1) than the West Coast (region 2). There was no significant region-length interaction. Note that main effects and interactions for month and year were entered into the analysis as factors and each therefore has multiple associated t values (not individually reported above). Thus, for the main effect of month, there is a t value for each comparison between month 12 and another month. In this instance, nine out of 11 values were statistically significant (all $p < 0.001$).

Coefficients for effects of year, month and the year-length and month-length interactions are illustrated in Figure 5. Females are generally heavier at length in January and in May to August than in other months. The interaction between effects of month and length on weight was generally more negative earlier in the year, i.e. the weight-length relationship has a shallower slope in the earlier months of the year. A year effect is also evident, with highest weights being recorded in 1997 and the lowest in 1989. There was also a year-length interaction, with the most pronounced effect relating to 1989 – although this may simply reflect the fact that data collection began mid-1989 so there were no observations for the earlier months of the year.

Using the full 1983–2001 data set (no data for 1987–88), very similar results were obtained. The seasonal pattern is virtually unchanged. Both main and interaction effects for year during 1983–86 are stronger than seen for 1989–2001 (Fig. 6), possibly because there were more months with missing data (e.g. only December data were available for 1983).

3.2.2 Males

Regression analysis for weight of males in 1989–2001 demonstrated significant effects of length ($t = 291.19$, $p < 0.0001$), maturity stage ($t = -24.59$, $p < 0.0001$), region ($t = -4.04$, $p = 0.0001$), year, month, and the interactions of length with maturity stage ($t = -11.51$, $p < 0.0001$), month and year. Weights at length were generally lower in more mature males, and higher on the East Coast (region 1) than the West Coast (region 2). There was no significant region-length interaction.

Coefficients for effects of year, month and the year-length and month-length interactions are illustrated in Figure 5. Males are generally heaviest at length in June and lightest in February. The interaction between effects of month and length

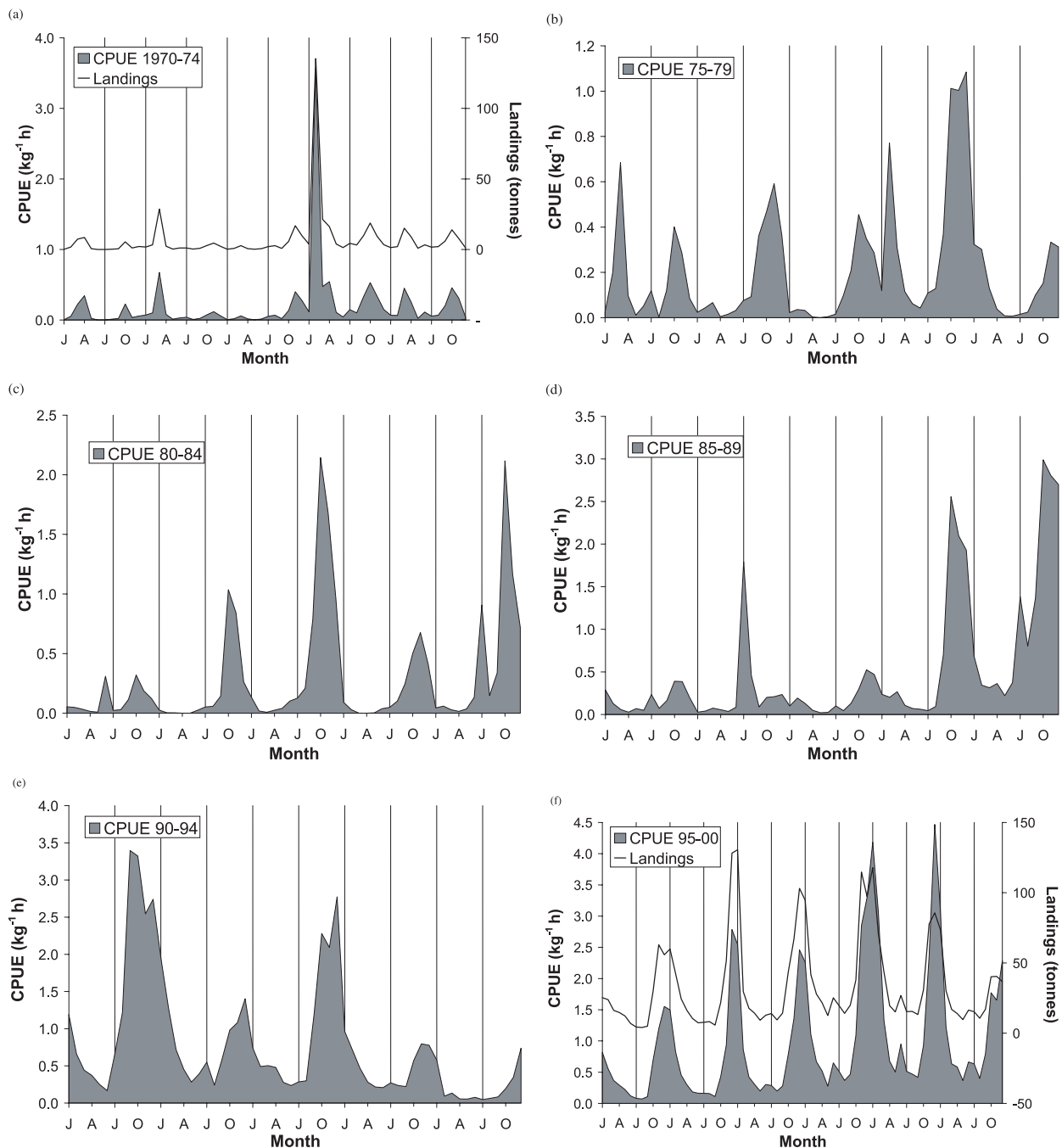


Fig. 4. Plots of monthly average trawling CPUE for squid in Scottish coastal waters: (a) 1970-1974; (b) 1975-1979; (c) 1980-1984; (d) 1985-1989; (e) 1990-1994; (f) 1995-2000. Plots (a) and (f) also show monthly landings (second *y* axis), demonstrating that landings and CPUE tend to follow similar trends. Vertical lines coincide with January (winter) and July (summer) in each year.

on weight was generally negative earlier in the year (i.e. the weight-length relationship has a shallower slope in the earliest months of the year) and the highest coefficient was recorded for May. These patterns are similar but not identical to those seen in females. The main year effect was also similar to that seen for females, with highest weights being recorded in 1997 and the lowest in 1989, and the year-length interaction was most pronounced for 1989. Again, analysis using the full 1983-2001 data set revealed similar patterns, with strong year effects evident for 1983-1986 (Fig. 6).

3.3 Size at maturity

3.3.1 Females

The optimal fitted model had the form:

$$\text{Logit (Maturity)} \sim \text{factor(Year)} + \text{factor(Month)} + s(\text{Length}, df = 11); \text{AIC} = 5071.0$$

where $s(X, df = \nu)$ indicates a smoothing spline for the effect of variable X with ν degrees of freedom.

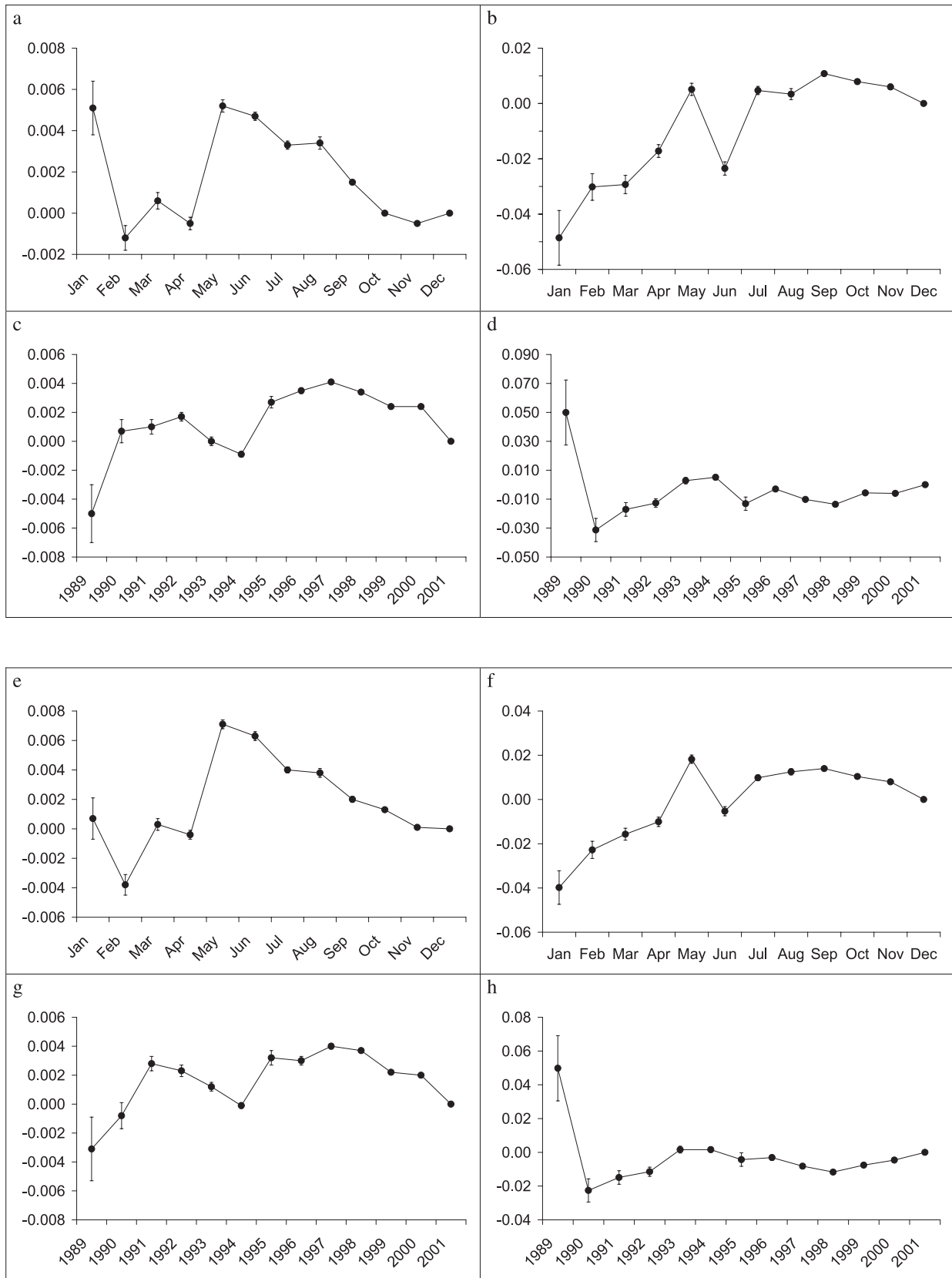


Fig. 5. Coefficients (± 1 standard error) for nominal variables affecting length-weight relationships in *Loligo forbesi*, 1989-2001: (a) Month (main effect) in females, (b) Month (interaction with length) in females, (c) Year (main effect) in females, (d) Year (interaction with length) in females, (e) Month (main effect) in males, (f) Month (interaction with length) in males, (g) Year (main effect) in males, (h) Year (interaction with length) in males.

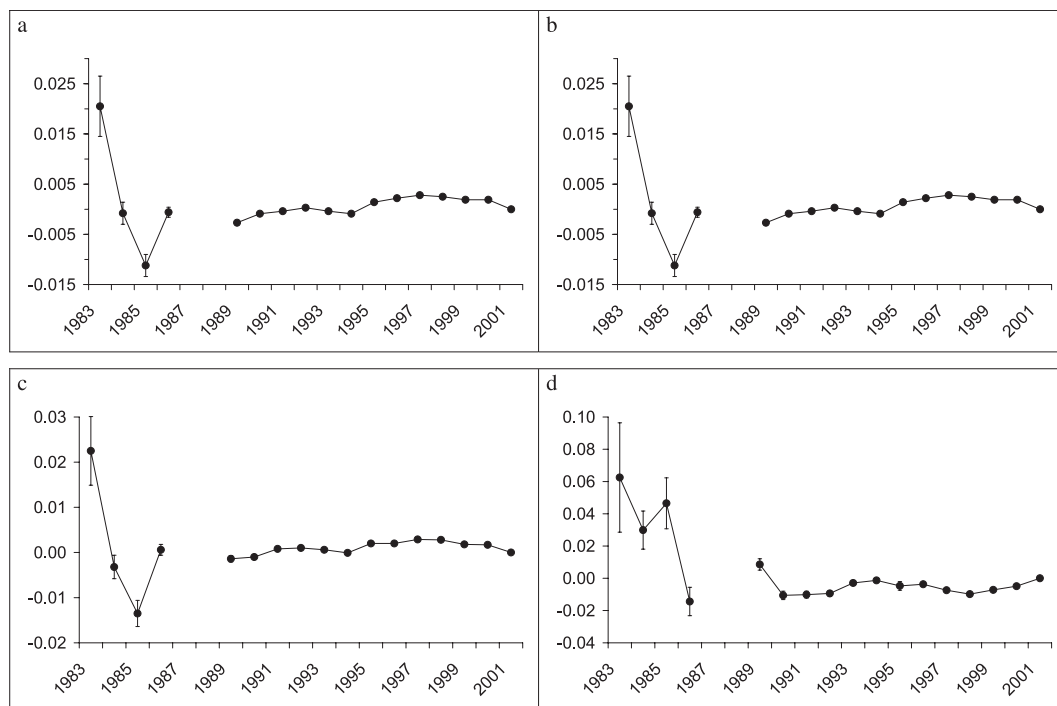


Fig. 6. Coefficients (± 1 standard error) for nominal variables affecting length-weight relationships in *Loligo forbesi*, 1983–2001: (a) Year (main effect) in females, (b) Year (interaction with length) in females, (c) Year (main effect) in males, (d) Year (interaction with length) in males.

Thus, year and month were fitted as factors, and 11 degrees of freedom were required for the relationship of maturity with length. It was necessary to remove data from the first year (1983) because the corresponding confidence interval was very large. The smoother for length (DML, cm) was highly significant ($\chi^2 = 397.3$, $p < 0.0001$). There was no overdispersion.

The effects of length, month and year on maturity are shown in Figure 7. It may be seen that peak maturity (at length) is in March and there are fewest mature animals (at length) in September.

3.3.2 Males

The optimal model for males was of rather similar structure to that obtained for females:

$$\text{Logit (Maturity)} \sim \text{factor(Year)} + \text{factor(Month)} + s(\text{Length}, df = 10); \text{AIC} = 8958.9.$$

Again, data for 1983 were removed. The smoother for length (DML, cm) was highly significant ($\chi^2 = 500.9$, $p < 0.0001$). There was no overdispersion.

The effects of length, month and year on maturity are shown in Figure 7. It can be seen that there is evidence of two peaks of maturity (as previously reported) in the partial plot for length, the first peak being at around 180 mm mantle length. It may be seen that peak maturity (at length) is in March and there are fewest mature animals (at length) in August, suggesting slightly earlier maturation in males, as previously reported. It may also be noted that the seasonal effect on male maturity is weaker than in females, as indicated by the lower numeric values on the y -axis of Figure 7e and compared to those in Figure 7b.

3.4 Size at maturity in the breeding season

The size-at maturity analysis was repeated using data for December and June only. An initial GAM analysis for all years with both June and December data, and including a term for the DML: month interaction, demonstrated that there were differences between the two months for both sexes. Separate analyses were therefore carried out.

For December, data for 1983 were removed since they gave a poor fit to the model. The best-fits GAMs (see Fig. 8), for females and males respectively, had the form:

Females:

$$\text{logit (Mature)} \sim s(\text{Year}, 4) + s(\text{Length}, df = 2); \text{AIC} = 788.0.$$

Males:

$$\text{logit (Mature)} \sim s(\text{Year}, 5) + s(\text{Length}, df = 3); \text{AIC} = 1582.6.$$

The effect of length in males was more complex than in females and the partial plots clearly indicate two sizes at maturity in the males.

The June data set contained relatively few 1 values (mature) compared to zeros. However, it was possible to fit year and body length effects as smoothers:

Females:

$$\text{logit (Mature)} \sim s(\text{Year}, 1) + s(\text{Length}, df = 2); \text{AIC} = 143.6.$$

$$\text{Males: logit (Mature)} \sim s(\text{Length}, df = 4); \text{AIC} = 349.8.$$

Note that, for females, the year effect was linear ($df = 1$), the relationship being negative (lower proportion of mature

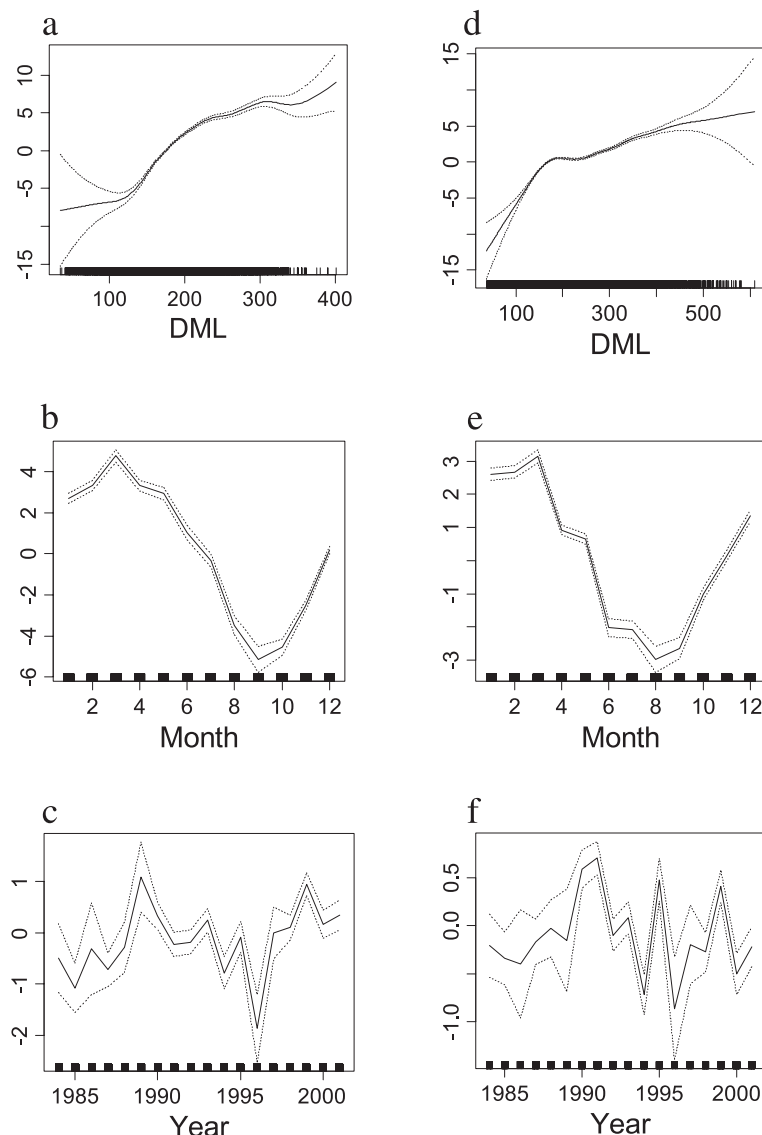


Fig. 7. Generalised additive model of maturity in squid: smoothers and factor coefficients for effects of (a) length (DML, mm) in females, (b) month in females, (c) year in females, (d) length (DML, mm) in males, (e) month in males and (f) year in males.

females in later years). The smoothers for length are rather similar to those for the December samples (Fig. 9). In females, the interannual trends in maturity in June and December are almost opposite. In males, the final model for June did not include a year effect.

3.5 Environmental correlates of interannual variation

3.5.1 Relationships between different biological indices

In general interannual trends in male parameters were repeated in females, e.g. weight at length in males was correlated with that in females (Table 1). In years when weight-at-length of both sexes was high, the proportion of mature males in the December samples was low. In years when maturity of both sexes at length was high (low size at maturity), the proportion of mature males in June was low (Table 1).

3.5.2 Weight at length

Interannual variation in weight at length was uncorrelated with either winter NAO or squid survey abundance: all correlations were non-significant. However, weight at length of males was negatively related to fishery abundance on the west coast during the preceding July ($R = -0.501$, $p = 0.040$) and a similar trend, not quite significant, was seen for females ($R = -0.482$, $p = 0.050$).

3.5.3 Proportion of mature animals

The simple proportion of males that were mature in the December sample, an index of the timing of maturation, was significantly negatively correlated with the winter NAO ($R = -0.557$, $p = 0.031$). There was a significant positive correlation between the winter NAO and the proportion mature for

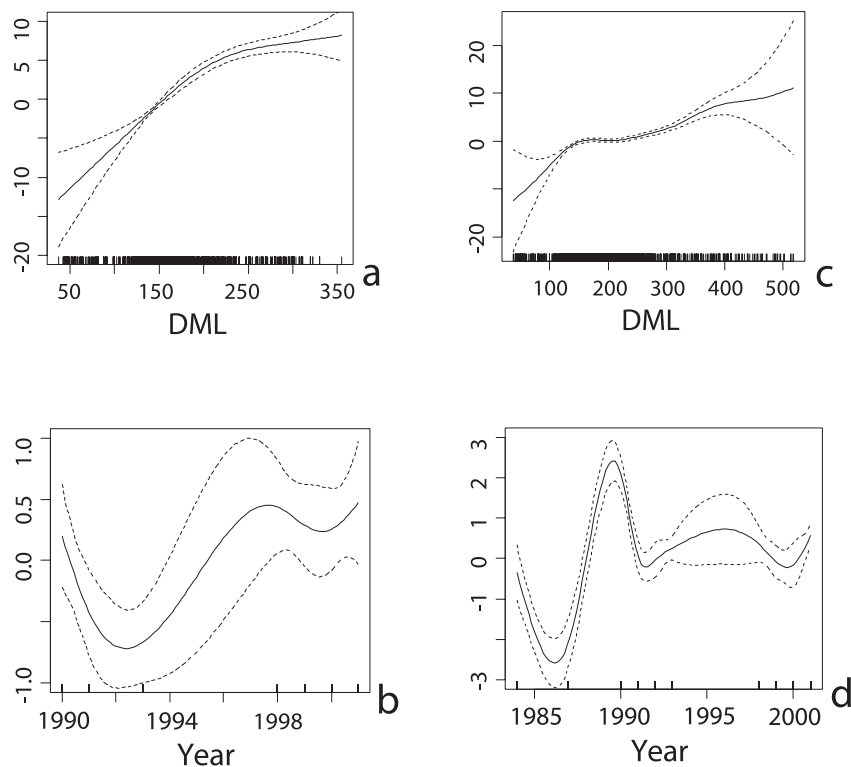


Fig. 8. Generalised additive model of maturity of squid in December: partial fits for effects of (a) length in females, (b) year in females, (c) length in males and (d) year in males.

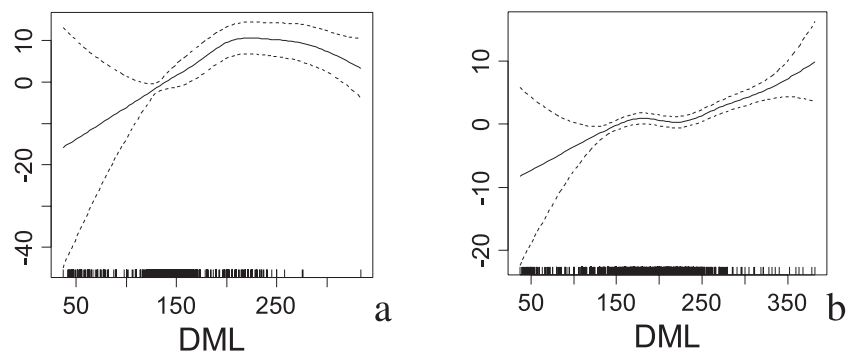


Fig. 9. Generalised additive model of maturity of squid in June: partial fits for effect length in (a) females and (b) males.

females in the samples in June ($R = 0.704$, $p = 0.023$). Note that the winter NAO for a given year refers to the *preceding* winter, i.e. an effect with a time-lag of six months (for maturity in June) to almost one year (for maturity in December).

The proportion of males that were mature in December was negatively correlated with autumn survey abundance on the West coast in the *previous* year ($R = -0.761$, $p = 0.004$). Similarly, the proportions of both sexes that were mature in December samples were negatively correlated with the previous year's fishery abundance on the West coast (area VIa) in October ($R = -0.601$, $p = 0.018$ for males, $R = -0.579$, $p = 0.024$ for females). It may be noted that winter NAO was significantly correlated with autumn survey abundance for the previous calendar year ($R = 0.531$, $p = 0.034$), i.e. squid abundance on the West coast towards the end of a calendar year is

correlated with the NAO values for the end of the same year and early part of the following year.

3.5.4 Maturity at length

The interannual component of variation in maturity at length (having removed seasonal variation) was positively related to the value of the winter NAO for the following calendar year, i.e. the relationship is with conditions at the end of the current calendar year ($R = 0.640$, $p = 0.003$ for females; $R = 0.485$, $p = 0.035$ for males).

Maturity at length in females was also positively related to fishery abundance of squid on the west coast during September to December in the same calendar year (September: $R = 0.616$, $p = 0.007$; October: $R = 0.530$, $p = 0.024$; November: $R = 0.578$, $P = 0.012$; December: $R = 0.547$, $p = 0.019$),

Table 1. Correlations between biological indices for the years 1983–2001. The top right part of the table contains the correlation coefficients while *p*-values appear (in parentheses) in the bottom left.

		Females				Males			
		%Mature June	%Mature December	Weight @ length	Maturity @ length	%Mature June	%Mature December	Weight @ length	Maturity @ length
Females	%Mature, June		−0.332	−0.166	−0.621	0.533	−0.327	0.022	−0.443
	%Mature, December	(0.422)		−0.357	0.221	−0.547	0.839	−0.416	−0.224
	Weight-at-length	(0.694)	(0.210)		−0.020	−0.177	−0.640	0.989	−0.069
	Maturity-at-length	(0.056)	(0.428)	(0.939)		−0.667	0.111	−0.004	0.547
Males	%Mature, June	(0.113)	(0.128)	(0.649)	(0.025)		−0.595	0.190	−0.710
	%Mature, December	(0.429)	(0.000)	(0.014)	(0.693)	(0.091)		−0.680	−0.053
	Weight-at-length	(0.959)	(0.139)	(0.000)	(0.988)	(0.624)	(0.007)		−0.030
	Maturity-at-length	(0.200)	(0.422)	(0.793)	(0.015)	(0.014)	(0.851)	(0.910)	

Significant correlations are indicated in bold.

and to squid abundance on the East coast in November and December (November: $R = 0.480$, $p = 0.044$; December: $R = 0.493$, $P = 0.038$). Maturity at length in males showed positive relationships with survey abundance on the East coast in August and September (August: $R = 0.561$, $p = 0.015$; September: $R = 0.588$, $p = 0.010$).

Furthermore, there were significant positive relationships between maturity at length in females and (a) fishery abundance on the West coast in the following year (during March to June and August to November; $R > 0.551$ in all these months; maximum correlation $R = 0.697$, $p = 0.002$ in September), (b) fishery abundance on the East coast in the following year (during February, June, July, November, December; $R > 0.485$ in all months; maximum correlation $R = 0.640$, $p = 0.007$ in July) and (c) winter survey abundance on the East coast in the following year ($R = 0.610$, $p = 0.006$). Male maturity at length was also positively related to fishery abundance on the east coast in February and March of the following year (February, $R = 0.489$, $p = 0.046$; March: $R = 0.486$, $p = 0.048$).

4 Discussion

4.1 Winter and summer breeding

Although interpretation of historical fishery data in terms of the life cycle is necessarily speculative, the shifting seasonal peaks of the fishery observed during the last 30 years are difficult to reconcile with a fixed annual life-cycle. Since there has been little targeting of squid but also relatively little discarding (Young et al. 2004), CPUE trends probably do reflect trends in abundance. The peaks in fishery landings are consistent with the presence of two seasonal population components that vary in absolute and relative importance. However, even allowing for this, the data suggest that the timing of the life-cycle shows

subtle shifts from year to year. Nevertheless, long-term monitoring of both life-cycle characteristics and the fishery is required to allow these hypotheses to be rigorously tested. Unfortunately this is presently unlikely to take place, since squid are non-quota species of relatively minor importance in UK waters; there is currently no routine biological sampling.

4.2 Weight at length

The analysis of weight at length data confirms that there are significant interannual changes in weight-at-length. Also of interest are the effects of month and maturity stage. In both sexes there appears to be a peak of weight at length in summer, as might be expected if this is the period of highest food availability. In females, there was also a peak in weight at length in January. It is tempting to associate the latter peak with maturity but, in fact, the maturity effect has already been removed. Extending the analysis back to 1983, by incorporating data from Ngoile (1987), there is evidence of wider fluctuations in weight-at-length.

With increasing maturity stage, males become lighter and females get heavier (at length). The latter trend presumably represents the consequence of ovary growth. While males probably invest less energy in gonad growth than females, the negative trend in body weight at length requires further explanation. Available evidence suggests food intake does not decline in mature males (Collins et al. 1995c). Previous work has suggested that energy reserves for maturation are derived from food rather than stored reserves in both loliginid and ommatrephid squids (Hatfield et al. 1992; Ho et al. 2004). As noted above, spermatophore production may contribute to a progressive reduction in male body weight. Maturation may also lead to increased energy costs. By analogy with *Loligo vulgaris*, large males may guard females on the spawning grounds (see Hanlon and Messenger 1992) and males may also incur

courtship costs long before reaching the spawning areas, since many females carry sperm in the buccal pouch before reaching full maturity (Pierce et al. 1994b; Boyle et al. 1995).

A limitation of the present analysis is that it implicitly assumes that all individual males tend to follow the same growth trajectory whereas it remains possible that animals maturing at larger sizes are also heavier at a given size. Thus the two or more microcohorts that make up the Scottish “population” of *Loligo forbesi* (Collins et al. 1999) could have different growth patterns, e.g. because they hatch at different sizes (see Pecl et al. 2004) or experience different temperature regimes during their early life (Forsythe 1993).

4.3 Maturity at length

The analysis of maturity-at-length is, in effect, an investigation of variation in size at maturity, while avoiding the need to reduce this to a single parameter. In fact, maturity-at-length is best represented by a non-parametric smoother rather than a parametric function (such as the traditionally applied logistic curve). The contrasting shapes of these curves for males and females are consistent with the existence of more than one size at maturity in males (see Pierce et al. 2004a) – and this phenomenon was more obvious when dealing with data for December alone.

Raya et al. (1999) confirmed that there were size and seasonal components to maturation in *L. vulgaris*. The present analysis for *L. forbesi* confirms that there is a distinct seasonal effect on maturity, with the probability of an animal of a given size being mature being much higher in January to March than in August to October.

Regarding the summer breeding component of the population, examination of raw data on proportions of mature animals indicates that the proportion of mature animals in samples can be high in May and June (see Pierce et al. 1994b). However, as seen from Figure 4, during most years CPUE is generally low at this time of year, so that the absolute abundance of mature animals in summer is low (see Collins et al. 1997). Exceptions were the years of 1984, 1986 and 1989 and there was also a discernible secondary peak of abundance in May during 1998–2000 (see Fig. 4).

4.4 Environmental effects and relationships with population size

Before considering the environmental and stock size effects on biological parameters, it is worth reviewing the relationships between these biological parameters: high weight at length appears to have a negative relationship with the proportion of mature males present in December, while high maturity at length has a negative relationship with the proportion of mature males present in June. Thus there appears to be a relationship between growth strategy and timing of breeding.

Sims et al. (2001) showed that the timing of migration in *Loligo forbesi* in the English Channel could be related to the NAO index, with earlier migration in warmer years. Our data suggest that warm years favour precocious maturation in *Loligo forbesi* in Scottish waters, in that maturity at size

was positively related to winter NAO. Furthermore, following warmer years, a higher proportion of mature animals is seen in June and a lower proportion of mature animals is present in December (although in both cases the trend was evident for only one sex, females and males respectively). Thus a possible interpretation is that, following warm years, summer breeding is favoured.

A number of different abundance indices were derived, so that some caution is needed in interpreting the large number of correlation coefficients arising. Nevertheless, some consistent patterns appear to emerge. Firstly high squid abundance on the west coast in July was correlated with lower weights at length in the *following* year. Secondly, high abundance on the west coast in autumn (specifically October, in the case of fishery data) led to lower proportions of mature animals in samples from the *following* December. Results also confirmed a positive relationship between the NAO and squid abundance on the West coast (cf. Zuur and Pierce 2004). Low weight at length and low proportions of mature animals present in December could be due to increased intraspecific competition following high spawning success, although Young et al. (2004) suggested that *Loligo forbesi* rarely reaches very high abundance levels.

The third trend, for which the strongest evidence was seen, was for increased maturity at length (i.e. a lower size at maturity), especially in females, in years of high autumn abundance (in particular, high fishery abundance on the West coast in September). Lastly, high maturity at length (i.e. lower size at maturity) was positively related to squid abundance in the following year. High food availability might favour both high abundance and precocious maturation; precocious maturation in turn appears to favour high abundance in the following year.

It is difficult to fully reconcile these various trends. What is clear is that there is a complex interplay between environmental conditions, abundance, and the growth and maturation strategies of the present – and next – generation of squid. High autumn/winter temperatures (high winter NAO values) are associated with high abundance and precocious maturation. This tends to favour high abundance in the following year, along with increased body weight at length and reduced maturity in December in the following year’s population. High abundance in summer, conversely, leads to a fall of body weight at length in the following year. Thus there may be alternation of precocious and slow maturation, and/or summer and winter breeding, driven – at least in part – by a combination of environmental conditions and intraspecific competition. Given that the life-cycle of *Loligo forbesi* very likely often exceeds one calendar year (see, e.g. Challier et al., in press), interannual shifts in the timing of breeding may be almost inevitable; indeed, it is probably more difficult to explain the apparent general consistency in the timing of the main winter peak of breeding.

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References

- Bellido J.M., Pierce G.J., Wang J., 2001, Modelling intra-annual variation in abundance of squid *Loligo forbesi* in Scottish waters using generalised additive models. *Fish. Res.* 52, 23–39.
- Boyle P.R., Ngoile M.A.K. 1993a, Assessment of maturity state and seasonality of reproduction in *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. In: Okutani T., O'Dor, R., Kubodera, T. (Eds.), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, pp. 37–48.
- Boyle P.R., Ngoile M.A.K. 1993b, Population variation and growth in *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. In: Okutani T., O'Dor, R., Kubodera, T. (Eds.), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, pp. 49–60.
- Boyle P.R., Pierce G.J., Hastie L.C., 1995, Flexible reproductive strategies in the squid *Loligo forbesi*. *Mar. Biol.* 121, 501–508.
- Challier L., Pierce G.J., Robin J.P., Spatial and temporal variation in age and growth in juvenile *Loligo forbesi* and relationships with recruitment in the English Channel and Scottish (UK) waters. *J. Sea Res.*, in press.
- Collins M.A., Boyle P.R., Pierce G.J., Key L.N., Hughes S.E., Murphy J., 1999, Resolution of multiple cohorts in the *Loligo forbesi* population from the west of Scotland. *ICES J. Mar. Sci.* 56, 500–509.
- Collins M.A., Burnell G.M., Rodhouse P.G., 1995a, Age and growth of the squid *Loligo forbesi* (Cephalopoda: Loliginidae) in Irish waters. *J. Mar. Biol. Assoc. UK* 75, 605–620.
- Collins M.A., Burnell G.M., Rodhouse P.G., 1995b, Recruitment, maturation, and spawning of *Loligo forbesi* (Cephalopoda: Loliginidae) in Irish waters. *ICES J. Mar. Sci.* 52, 127–137.
- Collins M.A., Burnell G.M., Rodhouse P.G., 1995c, Reproductive strategies of male and female *Loligo forbesi* (Cephalopoda: Loliginidae). *J. Mar. Biol. Assoc. UK* 75, 621–634.
- Collins M.A., Pierce G.J., Boyle P.R., 1997, Population indices of reproduction and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish and Irish waters. *J. Appl. Ecol.* 34, 778–786.
- Dawe E.G., Colbourne E.B., Drinkwater K.F., 2000, Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*). *ICES J. Mar. Sci.* 57, 1002–1013.
- Forsythe J.W., 1993, A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. In: Okutani T., O'Dor, R., Kubodera, T. (Eds.), *Recent Advances in Cephalopod Fisheries Biology*. Tokai University Press, Tokyo, pp. 133–143.
- Forsythe J.W., 2004, Accounting for the effect of temperature on squid growth in nature: From hypothesis to practice. *Mar. Freshw. Res.* 55, 331–339.
- Guerra A., Castro B.G., 1994, Reproductive-somatic relationships in *Loligo gahi* (Cephalopoda: Loliginidae) from the Falkland islands. *Antarctic Sci.* 6, 175–178.
- Hanlon R.T., Messenger J.B., 1992, *Cephalopod behaviour*. Cambridge University Press, Cambridge.
- Hatfield E.M.C., Rodhouse P.G., Barber D.L., 1992, Production of soma and gonad in maturing female *Illex argentinus* (Mollusca: Cephalopoda). *J. Mar. Biol. Assoc. UK* 72, 281–291.
- Ho J.D., Moltschanivskyj N.A., Carter C.G., 2004, The effect of variability in growth on somatic condition and reproductive status in the southern calamary *Sepioteuthis australis*. *Mar. Freshw. Res.* 55, 423–428.
- Holme N.A., 1974, The biology of *Loligo forbesi* Steenstrup (Mollusca: Cephalopoda) in the Plymouth area. *J. Mar. Biol. Assoc. UK* 54, 481–503.
- Jackson G.D., Forsythe J.W., Hixon R.F., Hanlon R.T., 1997, Age, growth, and maturation of *Lolliguncula brevis* (Cephalopoda: Loliginidae) in the northwestern Gulf of Mexico with a comparison of length-frequency versus statolith age analysis. *Can. J. Fish. Aquat. Sci.* 54, 2907–2919.
- Lum-Kong A. 1989, The reproductive biology of female *Loligo forbesi* Steenstrup (Cephalopoda: Myopsida). PhD. University of Aberdeen.
- Lum-Kong A., Pierce G.J., Yau C., 1992, Timing of spawning and recruitment in *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Scottish waters. *J. Mar. Biol. Assoc. UK* 72, 301–311.
- Mangold K., 1987, Reproduction. In: Boyle P.R. (Ed.) *Cephalopod Life Cycles. Comparative Reviews*, Vol. II. Academic Press, London, pp. 157–200.
- Moltschanivskyj N.A., Semmens J.M., 2000, Limited use of stored energy reserves for reproduction by the tropical loliginid squid *Photololigo* sp. *J. Zool.* 251, 307–313.
- Ngoile M.A.K. 1987, Fishery biology of the squid *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae) in Scottish waters. PhD Thesis. University of Aberdeen.
- Pecl G.T., Steer M.A., Hodgson K.E., 2004, The role of hatching size in generating the intrinsic size-at-age variability of cephalopods: extending the Forsythe Hypothesis. *Mar. Freshw. Res.* 55, 387–394.
- Perez, JAA, de Aguiar, DC, Oliveira, UC, 2002, Biology and population dynamics of the long-finned squid *Loligo plei* (Cephalopoda: Loliginidae) in southern Brazilian waters. *Fish. Res.* 58, 267–279.
- Pierce G.J., Bailey N., Stratoudakis Y., Newton A., 1998, Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data. *ICES J. Mar. Sci.* 55, 14–33.
- Pierce G.J., Boyle P.R., Hastie L.C., Shanks A.M., 1994a, Distribution and abundance of the fished population of *Loligo forbesi* in UK waters: analysis of fishery data. *Fish. Res.* 21, 193–216.
- Pierce G.J., Boyle P.R., 2003, Empirical modelling of interannual trends in abundance of squid (*Loligo forbesi*) in Scottish waters. *Fish. Res.* 59, 305–326.

- Pierce G.J., Boyle P.R., Hastie L.C., Key L., 1994b, The life history of *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. *Fish. Res.* 21, 17-41.
- Raya C.P., Balguerías E., Fernández-Núñez M.M., Pierce G.J., 1999, On reproduction and age of the squid *Loligo vulgaris* from the Saharan Bank (north-west African coast). *J. Mar. Biol. Assoc. UK* 79, 111-120.
- Robin J.P., Denis V., 1999, Squid stock fluctuations and water temperature: temporal analysis of English Channel Loliginidae. *J. Appl. Ecol.* 36, 101-110.
- Rocha F., Guerra A., 1996, Signs of an extended and intermittent terminal spawning in the squids *Loligo vulgaris* Lamarck and *Loligo forbesi* Steenstrup (Cephalopoda: Loliginidae). *J. Exp. Mar. Biol. Ecol.* 207, 177-189.
- Shaw P.W., Pierce G.J., Boyle P.R., 1999, Subtle population structuring within a highly vagile marine invertebrate, the veined squid *Loligo forbesi*, demonstrated with microsatellite DNA markers. *Mol. Ecol.* 8, 407-417.
- 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. Lond. B Biol.* 268, 2607-2611.
- Smith J.M., Pierce G.J., Zuur A., Boyle P.R., 2005, Seasonal patterns of investment in reproductive and somatic tissues in the squid *Loligo forbesi*. *Aquat. Living Resour.* 18, 341-351.
- Thomas H.J. 1969, Some observations of the exploitation and distribution of squid around Scotland. *Int. Counc. Explor. Sea CM* 1969/K:29.
- 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.
- Waluda C.M., Trathan P.N., Rodhouse P.G., 2004, Synchronicity in southern hemisphere squid stocks and the influence of the Southern Oscillation and Trans Polar Index. *Fish. Oceanogr.* 13, 255-266.
- Young I.A.G., Pierce G.J., Daly H.I., Santos M.B., Key L.N., Bailey N., Robin J.-P., Bishop A.J., Stowasser G., Nyegaard M., Cho S.K., Raserio M., Pereira J.M.F., 2004, Application of depletion methods to estimate stock size in the squid *Loligo forbesi* in Scottish waters (UK). *Fish. Res.* 69, 211-227.
- Zuur A.F., Pierce G.J., 2004, Common trends in Northeast Atlantic squid time series. *Neth. J. Sea Res.* 52, 57-72.