ICES Journal of Marine Science, 55: 14–33. 1998

Distribution and abundance of the fished population of *Loligo forbesi* in Scottish waters: analysis of research cruise data

G. J. Pierce, N. Bailey, Y. Stratoudakis, and A. Newton

Pierce, G. J., Bailey, N., Stratoudakis, Y., and Newton, A. 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.

Length-frequency data on squid (*Loligo forbesi*) collected during trawling surveys in Scottish waters from 1980 to 1994 were analysed to describe temporal and spatial patterns in abundance and to examine the prospects for using survey abundance to forecast fishery abundance. *Loligo* was patchily distributed in space and time. Distribution patterns in the North Sea in February appeared to be strongly related to bottom temperature (squid avoided waters <7°C) and, to a lesser extent, salinity (more squid in more saline water). For other areas and times, no temperature or salinity data were available, but there were trends for squid on the west coast to be more abundant in westerly areas and higher latitudes, and for squid at Rockall to be more abundant in shallow water. Inter-annual trends in abundance differed between the North Sea, west coast and Rockall, but average survey abundances for the North Sea and west coast tended to be positively correlated. For the North Sea and west coast, survey abundance was positively correlated with fishery abundance for the same month and area, and average abundance for the February North Sea survey was a reasonable predictor of commercial CPUE in the autumn of the same year (the peak of the fishery). Some of the observed trends were consistent with the existence of a stock-recruitment relationship but may indicate that abundance in a given calendar year is linked to climatic factors.

Key words: squid, *Loligo forbesi*, distribution, abundance, stock assessment, temperature.

Received 7 December 1995; accepted 14 April 1997.

G. J. Pierce: Department of Zoology, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK. N. Bailey, Y. Stratoudakis and A. Newton: Scottish Office, Agriculture, Environment and Fisheries Department (SOAEFD) Marine Laboratory, PO Box 101, Victoria Road, Torry, Aberdeen AB11 9DB, UK. Correspondence to G. J. Pierce: tel: +441224272459; fax: +441224272396.

Introduction

Squid are an important by-catch in UK whitefish and *Nephrops* fisheries in European waters (Howard, 1979; Howard *et al.*, 1987; Pierce *et al.*, 1992, 1994a), worth approximately £4 400 000 at first sale in 1993 (Anon., 1995). The main species landed are veined squid *Loligo forbesi* Steenstrup, 1856 and European squid *L. vulgaris* Lamarck, 1798, of which only the former is normally caught in Scottish waters.

The life-cycle of *L. forbesi* is annual, with a clear peak of spawning in Scottish waters from January to March and recruitment mainly during the autumn, although some recruits and spawners are present in most months (Ngoile, 1987; Lum-Kong, 1989; Lum-Kong *et al.*, 1992; Boyle and Ngoile, 1993; Pierce *et al.*, 1994b; Boyle *et al.*, 1995). It is apparently mainly demersal in distribution, since the majority of landings arise from demersal gears (Pierce *et al.*, 1994a).

Fishing for squid in UK waters is unregulated apart from the imposition, by the European Union, of a minimum mesh size (40 mm from 1/1/96). Nevertheless, fishery data (landings and effort) are collected. Analysis of such data from 1980–1990 indicated that *L. forbesi* was widely distributed on the continental shelf and also occurred on offshore banks, notably Rockall. The fishery showed a consistent seasonal pattern, with peak landings from Rockall in June–August and from coastal waters in October and November. There were, however, considerable between-year fluctuations in total landings (Pierce *et al.*, 1992, 1994a).

Another potentially important source of information on squid distribution and abundance in Scottish waters is provided by research cruise surveys. Survey data have

1054–3139/98/010014+20 $25.00/0/jm970257

been widely used in other areas to examine the distribution and biology of *Loligo forbesi* (Holme, 1974; Moreno *et al.*, 1994; Collins *et al.*, 1995) and other squid species (Summers, 1969; Kristensen, 1984; Hatfield *et al.*, 1990; Andriguetto and Haimovici, 1991; Augustyn, 1991; Hatfield and Rodhouse, 1994) but there has been little such analysis of survey data for Scottish waters. Lum-Kong *et al.* (1992) inferred the seasonal pattern of recruitment in *Loligo forbesi* in Scottish waters from survey length-frequency data, and Yau (1994) used survey data to examine the distribution and abundance of cephalopods on the west coast of Scotland in 1989 and 1990.

Survey data are used for stock assessment in some squid fisheries, e.g. to provide recruitment indices, real time indices of adult abundance, or direct estimates of adult stock size (Lange and Sissenwine, 1983; Okutani and Watanabe, 1983; Sato and Hatanaka, 1983; Murata, 1989; Augustyn *et al.*, 1992; see Pierce and Guerra, 1994 for a recent review) but no such work has been done on *L. forbesi*.

The present paper contains an exploratory analysis of patterns in squid distribution and abundance using survey data for Scottish waters (1980–1994). We ask:

(1) Do surveys at different times of year and in different areas show the same inter-annual trends in squid abundance?
(2) Do survey data reveal a stock-recruitment relationship (correlation between abundance in spring [peak breeding] and abundance in autumn [peak recruitment]) or a link between recruitment strength and the size of the resulting breeding stock in the following spring?
(3) Is survey abundance correlated with fishery abundance, either concurrently or during the peak months of the fishery?
(4) Can the observed distribution patterns be related to any specific environmental parameters?

Methods

The data analysed arise from 69 demersal trawling surveys undertaken during 1980–1994 (Table 1). These surveys were primarily aimed at collecting data on finfish but incidental squid catches were routinely recorded. In the North Sea (International Council for the Exploration of the Sea [ICES] fishery subdivision IV), surveys were carried out in February and July–August, with additional surveys in April–May (1981, 1987, 1991–1994) and October–November (1981–1983, 1987). On the west coast of Scotland, there were surveys during January–March each year. In 1990–1994 there were further surveys in November, extending southwards from the west coast of Scotland to the west coast of Ireland. The Rockall area was surveyed in September (1985–1994) but also in May 1982. Normally, within a series of surveys (i.e. surveys at a similar time of year and in the same area), the same gear was used every year (Table 1). The number of hauls excludes foul (incomplete) hauls. Two standard gears were deployed, the French designed Grande Overture Verticale (GOV) and the 48 foot (14.77 m) Aberdeen trawl. The GOV is now regarded as the standard survey trawl in the North Sea and is fitted with an internal liner with a stretched mesh of 20 mm. The normal ground gear consists of a combination of 100 and 200 mm rubber discs that are weighted to maintain good ground contact. The net is fished with an "Exocet" kite and this gives a headline height of approximately 4 m. The Aberdeen trawl is a smaller net, which is based on a traditional Scottish design and is still deployed on some Scottish surveys in order to maintain continuity with historic surveys. This net has a codend mesh of 75 mm and is fitted with an external cover with a stretched mesh of approximately 35 mm. The headline height of the Aberdeen trawl is markedly lower at approximately 2 m.

The spring west coast surveys in 1980 and 1981 both extended to Rockall: data for the Rockall area from these surveys were treated separately.

Each survey typically took place over 2–3 weeks. Hauls were taken at standard stations, although the precise locations varied from year to year. Although fishing occurred throughout the day, relatively few hauls were taken in the period 00.00 h to 04.00 h.

Loligo spp. were routinely distinguished from other squids (*Alloteuthis* spp., Ommastrephidae) and *Loligo* from Scottish waters can generally be assumed to be *L. forbesi* (Pierce *et al.*, 1994a,b).

All the survey data are held on a database at the Marine Laboratory, Aberdeen. For each completed haul (n=3674), data were extracted on the time and location of the vessel at shooting and hauling of the net, water depth, and the length-frequency distribution of *Loligo*. Mantle lengths (ML) were measured in centimetres and frequencies were standardized to numbers per hour. Mantle length data were missing for the spring 1980 west coast survey and for two hauls during the February 1983 North Sea survey. For the February North Sea survey series (1983 onwards) surface and bottom temperature and salinity data were also available for most hauls.

Numbers of squid caught were converted to estimated biomass using a weight-length relationship derived from measurements on 7024 specimens of *L. forbesi* caught in Scottish waters (Pierce *et al.*, 1994b; Collins *et al.*, in press, unpublished data):

$$W = 0.0009252 \times L^{2.3257}$$

where W is in grams and L in millimetres.

Table 1. SOAEFD Research cruise surveys 1980–1994. Surveys that yielded length-frequency data on *Loligo* are tabulated. Normally two standard gears were deployed, the GOV or the 48 foot (14.77 m) Aberdeen trawl (see text). The two surveys marked† used different nets: the JCB trawl is a smaller version of the standard GOV net, while BT168 is a light weight version of the JCB net. The number of hauls excludes foul (incomplete) hauls.

Area, month, year	Survey programme	Vessels	Gears used	No. of hauls each year (no. with *Loligo*)
North Sea, Feb., 80–94	International Young Fish/ Pre-recruit Surveys	Explorer (80–84), Scotia (85–94)	GOV	57 (0), 31 (0), 38 (3), 56 (12), 58 (1), 58 (4), 52 (0), 58 (0), 46 (7), 53 (17), *47 (27), *59 (25), 63 (18), 50 (15), 56 (4)
North Sea, Apr.–May, 81, 87, 91–94	Spring Groundfish Surveys	Explorer (81), Clupea (87), Scotia (91–94)	48′ (81), BT168 (87), GOV (91–94)	43 (2), 54 (9), 69 (29), 71 (9), †32 (0), *75 (1)
North Sea, Aug. 80–94	Demersal Fish/Groundfish/ Pre-recruit Surveys	Explorer (80–81), Scotia (82–94)	48′	54 (10), 63 (2), 77 (2), 79 (4), 82 (3), 83 (1), 80 (1), 73 (3), 85 (3), 86 (6), 85 (6), 90 (6), 87 (10), *87 (3), 87 (2)
North Sea, Oct. 81–83, Nov. 87	Demersal/Pre-recruit Surveys	Explorer (81–83), Dawn Sky (87)	48′ (81–83), JCB (87)	42 (8), 33 (6), 32 (12), †26 (24)
West Coast, Jan.–Mar. 80–94	Pre-recruit Surveys	Explorer (80), Scotia (81–94)	48′ (80), GOV (81–94)	24 (5), 34 (7), 30 (11), 47 (18), 12 (3), 59 (34), 38 (12), 50 (20), 52 (21), 46 (27), *44 (30), 56 (36), 40 (33), *41 (27), *44 (15)
West Coast, Nov. 90–94	Mackerel Recruitment Surveys	Scotia	GOV	46 (34), 50 (36), 38 (32), *44 (33), *33 (20)
Rockall, Mar. 80–81, May 82, Aug.–Sep. 85–94	Demersal Fish/Groundfish/ Pre-recruit and Haddock Surveys	Explorer (80), Clarkwood (85), GA Reay (86), Dawn Sky (87), Scotia (81, 82, 88–94)	GOV (80–81) 48′ (82–94)	4 (3), 4 (3), 25 (17), 23 (14), 31 (16), 19 (3), 40 (10), *39 (6), *36 (2), *40 (4), 40 (5), *46 (1), 42 (0)

*Subsamples of squid were retained for collection of reproductive data.

Average abundances

Since the catchrate data were skewed, with a substantial proportion of zeros, a Δ-distribution is assumed and the minimum variance unbiased estimators of the mean [c] and variance of the mean [$var_{est}(c)$] are used, defined as follows (from Pennington, 1996):

see equations at foot of page

where n is the number of observations, m is the number of non-zero values, y=ln(x), $\bar{y}$, and s^2 are the sample mean and variance of the logged non-zero values, x_1 denotes the single untransformed value when m=1, and $g_m(t)$, which is a function of m and t (where t is any expression), is defined by:

$$g_m(t)=1+\frac{m-1}{m}t+\sum_{j=2}^{\infty}\frac{(m-1)^{2j-1}}{m^j(m+1)(m+3)\ldots(m+2j-3)}\frac{t^j}{j!}.$$

For large n, approximate 95% confidence limits are $c \pm 2[var_{est}(c)]^{1/2}$ and this estimate is used here. Values were calculated using a purpose-written BASIC programme which was first tested using data sets given in Pennington (1996).

Temporal trends: correlations between survey and fishery abundance indices

For four of the survey series (North Sea, February and August; west coast, spring; Rockall, September) there were data for at least 10 consecutive years. For each survey, the minimum variance unbiased estimater of mean catch rate (c, as defined above) across all hauls (squid h^{-1}) was used as an abundance index. Separate indices were also derived for different size (ML) classes: ⩽15 cm, >15 cm. Full recruitment to the fishery occurs at a mantle length of approximately 15 cm (Pierce *et al.*, 1994b; see also Hastie, 1996).

Fishery data for *Loligo* were obtained from a database held at the Marine Laboratory. Records of total landings in Scotland (units of 100 kg) and the associated hours fishing, by UK-registered vessels, for all fishing gears combined and for individual gear-types, are available categorized by month and by ICES statistical rectangle (1° longitude × 0.5° latitude). The unit of fishing effort, "hours fishing", is not corrected for vessel fishing power and refers to the total fishing activity of the fleet, very little of which is directed at squid. Nevertheless, the catch per unit of effort (CPUE) obtained by dividing total landings by total hours fishing is thought to be a reasonable estimator of fishery abundance (see Pierce *et al.*, 1994a for further details). From these raw data (all gears), overall monthly and peak season (October–December in coastal waters, June to August at Rockall) CPUEs were derived for the main ICES fishery subdivisions of Scottish waters (IVa, VIa, VIb). Relationships between different survey indices, and of survey indices with commercial CPUE were expressed as Spearman's non-parametric correlations. Given the potentially large number of comparison between abundance indices from survey and fishery data, the correlation analysis was restricted to addressing the specific questions, regarding inter-annual trends, previously listed above.

Biological data

During 1989–1994, subsamples of the squid catches were obtained from some surveys (see Table 1) and from surveys in the North Sea during May and June 1990. For all subsamples, the following data were routinely collected: wet weight, mantle length, sex, and maturity stage. Maturity was measured using a standard 5 point scale (Pierce *et al.*, 1994b) in which stage I is immature, stages II and III maturing and stages IV and V mature. These data were used to describe the seasonal pattern of maturity.

$$c=\begin{cases}\frac{m}{n}\exp(\bar{y})g_m(s^2/2), & m>1\\ \frac{x_1}{n}, & m=1\\ 0, & m=0\end{cases}$$

$$var_{est}c=\begin{cases}\frac{m}{n}\exp(2\bar{y})\left\{\frac{m}{n}g_m^2(s^2/2)-\left(\frac{m-1}{n-1}\right)g_m\left(\frac{m-2}{m-1}s^2\right)\right\}, & m>1\\ \left(\frac{x_1}{n}\right)^2, & m=1\\ 0, & m=0\end{cases}$$

Spatial distribution

For each series of surveys, the overall spatial distribution of untransformed *Loligo* catch rates was plotted using SURFER (Golden Software Inc.). For North Sea survey data, contours (number of squid h^{-1}) were calculated using the inverse distance method (power parameter=2), with 1 unit on the Y-axis (latitude) set to equal 1.84 units on the X-axis (longitude) to approximate actual distances. For the west coast and Rockall, catch rates are plotted as point samples since the patchiness of the distribution did not justify fitting contours.

Relationships between abundance, time, position, depth, temperature and salinity

To investigate the relationship between squid abundance and environmental variables, information on the fished locations (latitude, longitude, depth, time, temperature, and salinity) and squid biomass were screened in bivariate plots. The high correlation between potential explanatory variables, and the anticipation of significant interaction terms in the fitted effects, suggested that regression trees (Clark and Pregibon, 1993) would provide a more informative tool than traditional regression techniques for exploring such relations. Tree-based models are often simpler to interpret, can easily handle interaction terms and are more adept at capturing non-additive behaviour. They are fitted by binary recursive partitioning, whereby a response variable is successively split into increasingly homogeneous subsets, until it is unfeasible to continue. Despite the lack of formal procedures of inference, the method is gaining widespread popularity as a means of devising prediction rules for rapid and repeated evaluation, as a screening method for variables and for summarizing large multivariate data sets (Clark and Pregibon, 1993).

Trees were fitted with squid abundance (log[biomass+0.1]) as the response variable and the environmental (temperature, salinity, depth, time) and spatial variables (latitude and longitude) being the explanatory variables. Year was also included in the model as a continuous variable. Analysis mainly concentrated on the North Sea February survey (1983 onwards), for which information on bottom temperature and salinity were available. For the remaining data sets, the same model was fitted, excluding temperature and salinity. Trees were initially fitted with no constraints on the number of terminal nodes, leading to some overfitting. The optimal number of terminal nodes was then evaluated by cross-validation (Clark and Pregibon, 1993). The final trees were obtained by pruning the overfitted trees to the number of terminal nodes that provide the smallest residual deviance.

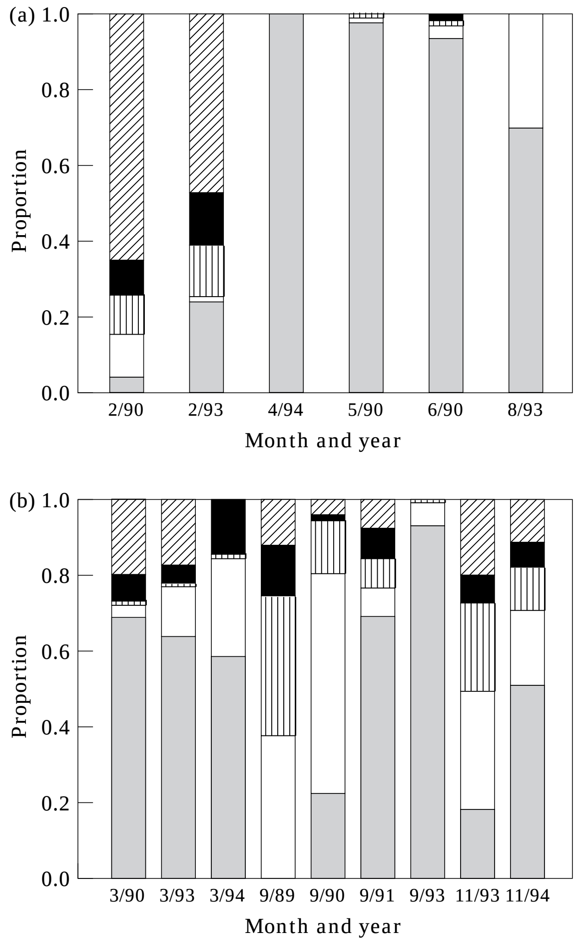

Figure 1. Maturity stages for squid samples taken from (a) the North Sea (sample sizes=46, 160, 186, 1101, 573, 16) and (b) the west coast and Rockall (sample sizes=386, 99, 175, 8, 188, 13, 102, 103, 61). Rockall samples are those from September. ▨ I; □ II; ▥ III; ■ IV; ▨ V.

Estimation of squid density at Rockall and in the North Sea

During various recent surveys a SCANMAR net monitoring system was attached to the net providing data on the spread of the wings and the headline height. In addition, data were logged from the ship's navigation system to provide information on the towing speed and the distance towed. The latter was calculated every 30 sec and then summed to provide the total distance moved during the tow. Data were available for surveys at Rockall (1988–1994) and in the North Sea in February (1989–1992). To estimate swept area, the towing distance was multiplied by the mean wing spread (individual wing spread measurements were screened for possible error by excluding any reading outside the range 12–30 m). Where incremental towing distance data were not available, normally due to spurious

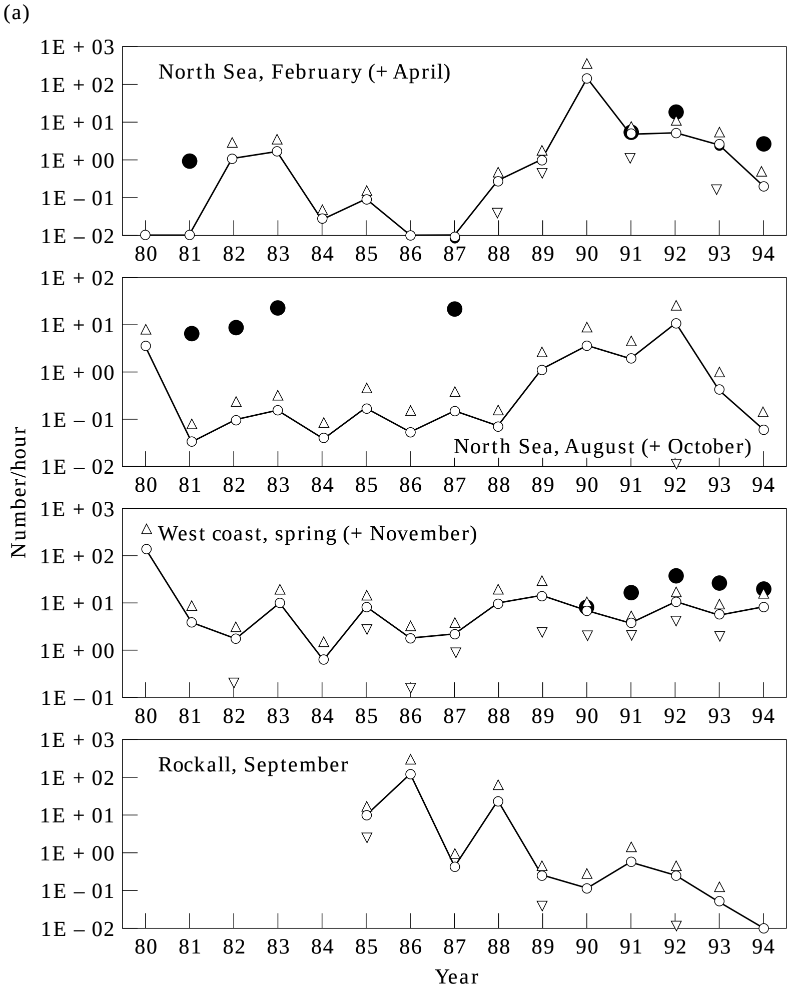

Figure 2(a).

readings from the GPS system, the towing distance was estimated as the shortest distance between the ship's position at "blocking up" (when it is decided that the gear has become stable on the bottom) and "knocking out" (when the gear is heaved back from the seabed). If no wing spread data were available, the average value for the survey was used. Ideally, hauls for which no SCANMAR data were obtained would be excluded but, since *Loligo* are of patchy occurrence, this could have a strong influence on the estimate of average density. Thus, in such cases, swept area was assumed to equal the average for the survey.

Most evidence suggests that post-recruit *Loligo* are demersal in distribution, for example the vast majority of *Loligo* landed commercially are caught by demersal gears (Pierce *et al.*, 1994a; SOAEFD, MAFF, unpublished data). Thus density for each haul may be estimated as:

Squid density (N/m^2)=(No. of squid/Swept area).

Averages and confidence limits for each survey are estimated using the method of Pennington (1996) as described above.

Results

Statistical distribution of catch rate

Loligo were caught during 63 of the 69 surveys and in 833 of the 3674 hauls. Catch rates (per haul) varied between 0 and 3200 squid h^{-1}. The statistical distribution of catch rate was positively skewed, indicating a patchy distribution. Numerical and biomass catch rates were strongly correlated (Pearson's $r=0.641$ for 825 non-zero hauls, $p<0.001$).

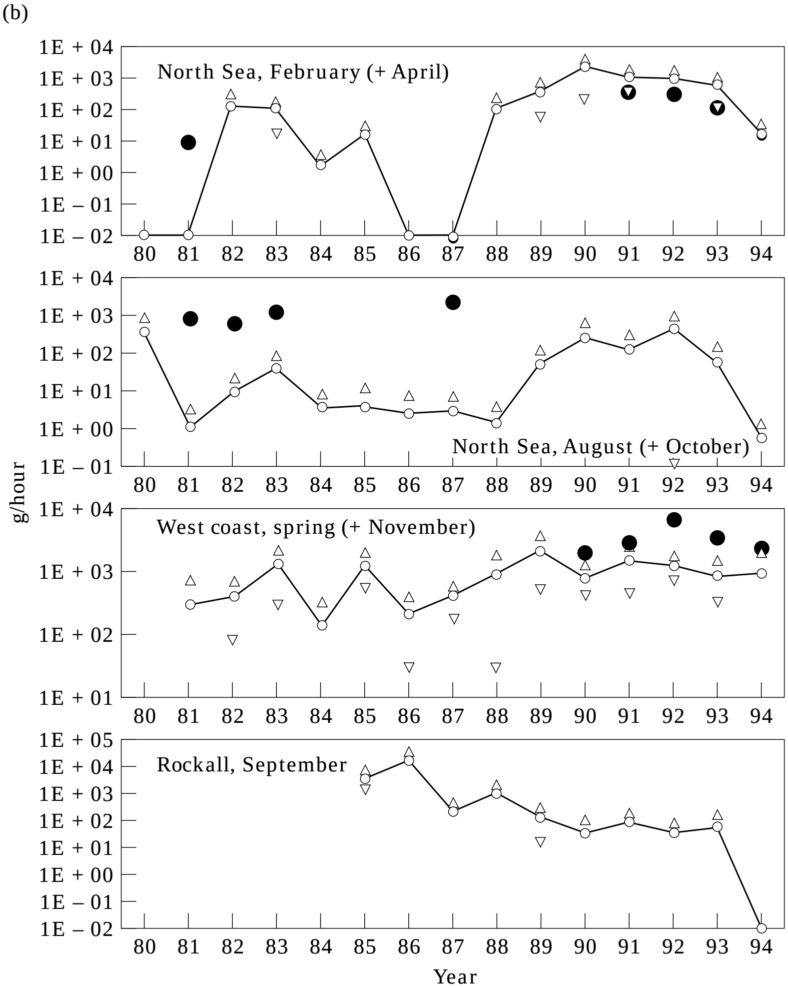

Figure 2. Inter-annual trends in average survey abundance. (a) Number caught per hour. Average (—○—) numerical survey abundances with lower (▽) and upper (△) 95% confidence limits. (b) Biomass (g) per hour. Average (—○—) biomass survey abundances with lower (▽) and upper (△) 95% confidence limits. Lower 95% limits <0 are not shown. Additional data sets are shown using ●. Note that abundance in the North Sea for February 1983 is underestimated due to absence of length-frequency data for two hauls.

Seasonal pattern of maturity

Squid in survey catches ranged in size (ML) from 3 cm to almost 60 cm. Squid of ML>35 cm were absent from the North Sea survey catches in April, August and October.

February subsamples from the North Sea (Fig. 1a) contained a high proportion of mature squid. In April, the subsample was entirely immature (stage I). Subsamples taken later in the year contained a small but increasing proportion of maturing (stage II) animals and a small number of mature animals was taken in June 1990.

On the west coast (Fig. 1b), subsamples from March and November included animals at all maturity stages. The proportion of Stage I animals in March subsamples was higher than in November and higher than in the North Sea in February. In two of the four years for which subsamples were taken at Rockall during September (1989, 1991), very few squid were caught. In 1990 and 1993 most squid caught at Rockall were immature.

Inter-annual variation in survey abundance

Trends in mean (c) numeric and biomass catch rates for the main series of surveys are given in Figure 2a,b. It can be seen that catch rates have fluctuated from year to year, although confidence limits are wide and many of the inter-annual differences are not therefore statistically significant. Trends in abundance in the North Sea, the west coast and at Rockall appear rather different.

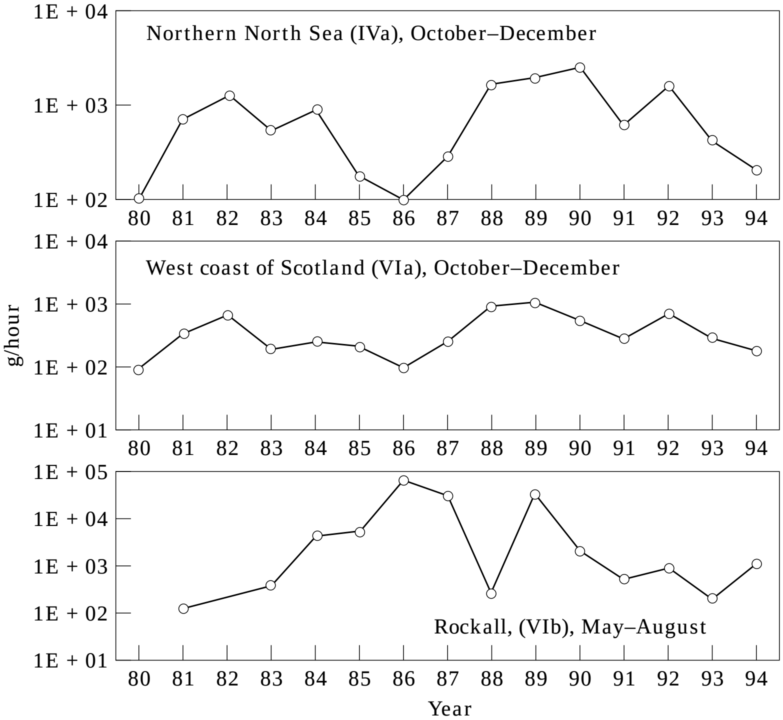

Figure 3. Inter-annual trends in overall catch per unit effort of *Loligo* by UK-registered boats landing in Scotland, for the northern North Sea (area IVa) and the west coast of Scotland (area VIa), October–December, and for Rockall (area VIb), May–August, 1980–1994.

Within the North Sea, the February and August surveys both showed peaks of abundance in the early 1990s. Numerical abundance in the April surveys was similar or slightly higher than in February whereas biomass was lower in April, consistent with April being a period of recruitment. Abundances in October were higher than in August.

Survey abundance on the west coast has been more stable over the period 1980–1994, while abundance at Rockall has declined markedly since peaks in 1986 and 1988.

Visual comparisons with commercial CPUE for UK registered vessels the peak of the fishing season (Fig. 3) indicate some degree of correspondence between inter-annual trends in survey and fishery abundance for all three areas. It is also interesting to note that average catch rates (g h^{-1}) for the commerical fleet and the research vessels reach maxima of similar orders of magnitude.

Correlation analyses for inter-annual trends

Correlation analyses were restricted to the longest running surveys (Table 2). Survey abundances for the North Sea in February and August were positively correlated, and also positively correlated with the west coast survey index. Abundance at Rockall was negatively, but non-significantly, related to other survey abundances. The correlations between February and August abundances in the North Sea are improved by using "big" squid abundance (instead of all squid) in February but are not improved by using "small" squid abundance in August. Correlations between February (North Sea) abundance and the previous year's August abundance were positive but non-significant.

In the North Sea in February, survey abundances were strongly correlated with fishery abundance. Similar but lower correlations were seen in August (Table 3). On the west coast in spring, survey abundance of large squid was correlated with fishery abundance for March. The correlations between survey and fishery abundance for Rockall in September were non-significant.

Of all the surveys, only the February North Sea survey provided significant correlations with fishery abundance at the peak of the fishing season, and was a reasonable predictor of fishery abundance both in the North Sea and on the west coast. Fishery abundance in the North Sea and on the west coast at the peak of the fishing season was highly correlated with survey abundance in the following year's February North Sea and spring west coast surveys.

Table 2. Correlations between abundance indices from different surveys. For each survey, average abundance is expressed by c (see text). Spearman's rank correlation coefficients are given, with significant values ($p<0.05$, 1-tailed test) indicated in bold type. In each part of the table, correlations for numbers of squid appear in the top right, correlations for biomass in the bottom left. Squid size classes are as defined in the text. For most data series, n=15 years. For Rockall surveys, n=10; for west coast spring survey biomass, n=14. For correlations between the current and previous year's data, sample size is reduced by one since there is no previous year's value for the first year in the sequence.

	Different surveys in the same year			
	N. Sea, Feb.	N. Sea, Aug.	W. Coast, spr.	Rockall, Sep.
N. Sea, Feb.		**0.616**	0.214	− 0.480
N. Sea, Aug.	**0.596**		**0.559**	− 0.358
W. Coast, spr.	**0.581**	0.486		− 0.200
Rockall, Sep.	− 0.523	− 0.358	− 0.115	
	February (North Sea) and August (North Sea), taking size into account			
	Feb., all squid	Feb., big squid	Aug., all squid	Aug., small squid
Feb., all squid		0.943	**0.616**	0.416
Feb., big squid	**0.980**		**0.644**	**0.498**
Aug., all squid	**0.596**	0.604		**0.912**
Aug., small squid	**0.550**	**0.538**	**0.882**	
	February (North Sea) and the previous August (North Sea)			
	Feb., all squid	Feb., big squid	Aug., all squid	Aug., small squid
Feb., all squid			0.345	0.378
Feb., big squid			0.368	0.451
Aug., all squid	0.245	0.278		
Aug., small squid	0.333	0.416		

Spatial patterns

The spatial pattern of catches was examined separately for each series of surveys. In the North Sea (ICES area IV), during February (Fig. 4) squid were caught mainly in two areas: on the shelf edge off Shetland; and in the Long Forties/North Dogger Bank grounds. In the latter area, there are a number of deep water "holes". In April–May (Fig. 5), the main concentrations of squid were further south: to the east of Shetland and in the outer Moray Firth, and to the south of Dogger Bank. However, there was no sampling on the shelf edge and there were only four years' data. In August (Fig. 6), squid abundance was much lower and the main concentrations were in and around the Moray Firth. However, no samples were taken at this time in the south-eastern North Sea. In October (Fig. 7), when sampling was restricted to the north-western North Sea, concentrations of squid were seen in the Moray Firth and the outer Firth of Forth.

On the west coast during January–March (Fig. 8) almost all squid were caught in deeper water on the shelf edge, at the western edge of the area sampled. In November (Fig. 9), sampling extended from Shetland in the North to the Grand Sole grounds south of Ireland. Most squid were caught in the northern part of this area, on the shelf edge north-west of Lewis but with the highest concentration on the shelf to the north of Ireland.

In August–September at Rockall (Fig. 10), most squid were caught at the north of the Bank, close to Rockall itself.

Figure 11 shows the fitted tree to the squid biomass from the North Sea surveys in February during the period 1983–1994. Bottom temperature is the most important explanatory variable, with mean squid abundance being much higher in temperatures close to or above 7°C. At these temperatures, bottom salinity is also significant and is positively correlated with squid abundance. The overall relationship is demonstrated in Figure 12 where squid biomass is plotted against temperature on a salinity gradient. It is apparent that for all levels of salinity, non-zero squid biomass occurs only for the highest temperatures and that the frequency of large biomass increases with salinity. The regression tree for the North Sea February survey also suggested that higher abundance can be associated with daylight (<1700 h) and with the period 1990–1991. However, these variables did not contribute much to the explanatory power of the fitted model and are not included in Figure 11.

When temperature and salinity are excluded from the model for the North Sea February surveys, latitude becomes the most important variable, having larger biomass associated with the northern parts of North Sea (>59°N). This reflects the area where warm and saline Atlantic water enters in the North Sea. For the

Table 3. Correlations between survey and fishery abundance indices. For each survey, average abundance is expressed by c (see text). Fishery abundance is expressed as overall CPUE (g h^{-1}) for the Scottish fleet for the period in question. The main fishing seasons are October–December (North Sea, west coast) and June–August (Rockall). Spearman's rank correlation coefficients are given, with significant values ($p<0.05$, 1-tailed test) indicated in bold type. For most data series, n=15 years. For Rockall, n=10; for west coast biomass, n=14. For correlations between the current and previous year's data, sample size is reduced by one since there is no previous year's value for the first year in the sequence.

	Survey abundance with fishery abundance in the same area and month			
Survey/fishery	N. Sea, Feb.	N. Sea, Aug.	W. Coast, Mar.	Rockall, Sep.
Numbers (all)	**0.685**	**0.511**	0.189	0.297
Numbers (big)	**0.777**	**0.463**	**0.473**	0.442
Numbers (small)	**0.690**	**0.529**	0.323	0.213
Biomass (all)	**0.754**	0.443	0.385	0.370
Biomass (big)	**0.781**	0.374	**0.534**	0.370
Biomass (small)	**0.704**	**0.507**	0.319	0.213

	Survey abundance (February and August North Sea, spring west coast, September Rockall) with fishery abundance at the peak of the fishing season in the same year					
	Fishery CPUE vs. survey numbers			Fishery CPUE vs. survey biomass		
Survey/fishery	N. Sea	W. coast	Rockall	N. Sea	W. coast	Rockall
Feb., all squid	**0.593**	**0.508**	− 0.147	**0.647**	**0.613**	− 0.086
Feb., big squid	**0.509**	**0.542**	− 0.151	**0.542**	**0.549**	− 0.129
Feb., small squid	**0.606**	**0.595**	− 0.060	**0.626**	**0.638**	− 0.073
Spr., all squid	0.150	0.171	− 0.186	0.182	0.270	− 0.020
Spr., big squid	0.328	0.354	− 0.002	0.174	0.398	− 0.020
Spr., small squid	0.328	0.429	0.090	0.354	0.257	0.090
Aug., all squid	0.222	0.223	− 0.043	0.267	0.193	− 0.143
Aug., big squid	0.267	0.183	− 0.323	0.249	0.105	− 0.338
Aug., small squid	0.171	0.264	− 0.020	0.246	0.293	0.013
Sep., all squid	− 0.273	− 0.139	0.321	− 0.382	− 0.212	0.442
Sep., big squid	− 0.293	− 0.176	0.539	− 0.382	− 0.212	0.442
Sep., small squid	− 0.356	− 0.226	0.045	− 0.356	− 0.226	0.045

	Survey abundance (February North Sea, spring west coast) with fishery abundance at the peak of the fishing season (North Sea and west coast) in the previous year			
	Fishery CPUE vs. survey numbers		Fishery CPUE vs. survey biomass	
Survey/fishery	N. Sea	W. coast	N. Sea	W. coast
Feb., all squid	**0.801**	**0.828**	**0.841**	**0.823**
Feb., big squid	**0.860**	**0.842**	**0.869**	**0.851**
Feb., small squid	**0.681**	**0.683**	**0.682**	**0.679**
Spr., all squid	0.297	0.433	**0.635**	**0.591**
Spr., big squid	**0.723**	**0.692**	**0.767**	**0.692**
Spr., small squid	0.160	0.341	0.196	0.490

remaining data sets (where the key explanatory variables temperature and salinity are not available), a similar analysis showed some significant results, although the presence of spatial variables render biological interpretation more difficult. In the North Sea surveys, the only other significant effect was in the August data, where mean biomass was larger in western waters (>2°W). In the spring survey on the west coast, much higher mean biomass is observed in westerly areas (>8°W) and in higher latitudes (>59°N). The latitudinal pattern is very similar to that of the North Sea February data set. Finally, in Rockall, mean squid abundance is much higher in the early years (before 1987) and most non-zero values are observed in shallower waters (<150 m).

Density and population size estimates

Absolute density of *Loligo* at Rockall was highest in 1988, the first year for which data are available and was at low levels in the other years (Table 4). No *Loligo* at all were caught in the 1994 survey. The average density at Rockall during the 1988 survey is equivalent to a Rockall population of 1.34 million.

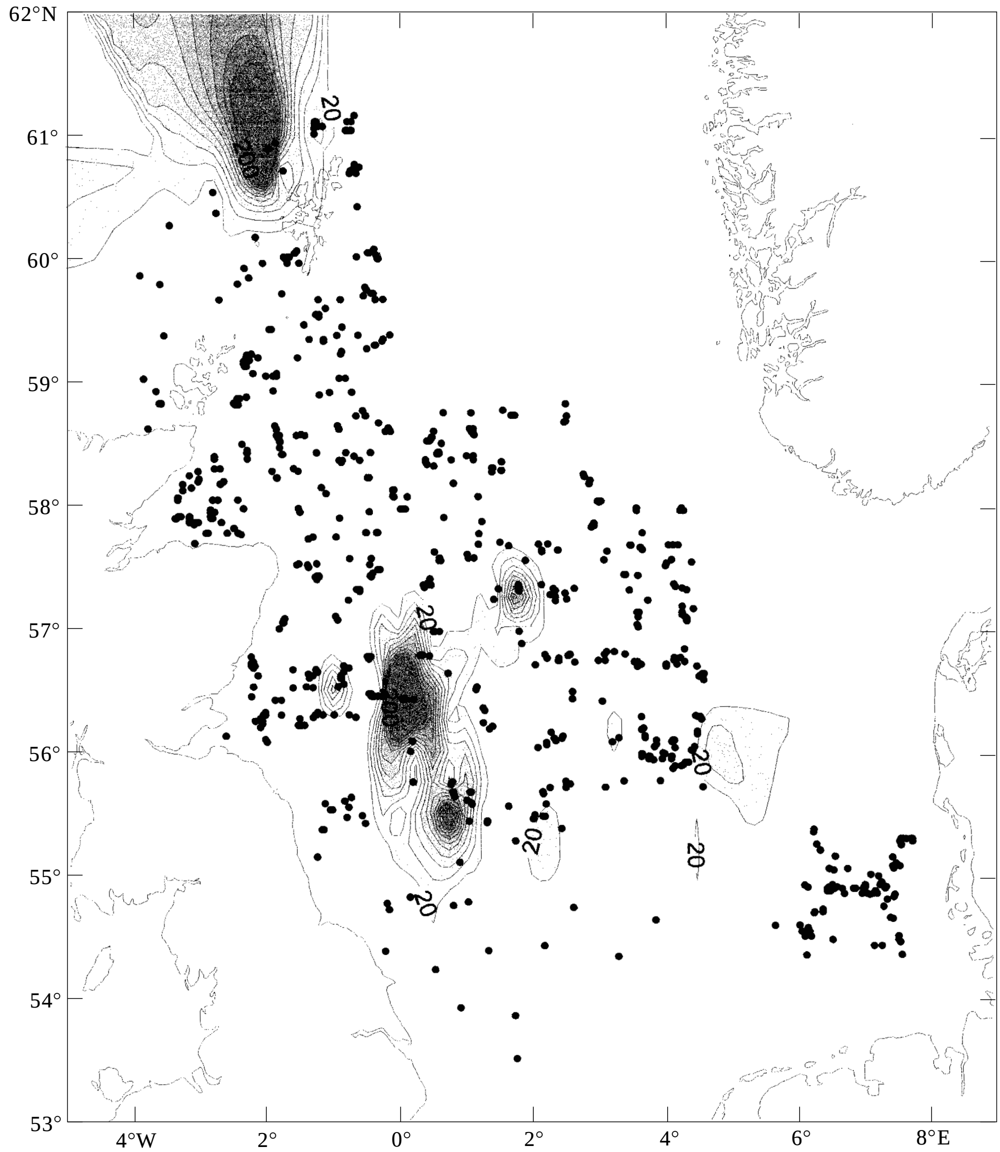

Figure 4. North Sea surveys, February (1980–1994): haul locations (●) and contours of *Loligo* abundance (contours at intervals of 20 squid h^{-1}).

Estimated densities for the February North Sea surveys were highest in 1990 (Table 5). Values for 1992 were the lowest but data for this year were less reliable (complete SCANMAR data were available for only 37 out of 63 hauls).

Discussion

Temperature and abundance

The most interesting result to emerge from this analysis was the strong relationship between survey abundance and sea bottom temperature in the February North Sea surveys, with squid avoiding areas with temperatures lower than 7°C. Several other studies on squids have suggested links between distribution and temperature. Holme (1974) suggested that *Loligo forbesi* in the English Channel occurs where bottom temperatures are at least 8.5°C. Distribution of adult chokka squid (*Loligo vulgaris reynaudii*) on the west coast of South Africa is thought to be strongly related to temperature, e.g. the species is associated with bottom temperatures above 8°C (Augustyn, 1991; Roberts and Sauer, 1994). Coelho and Rosenberg (1984) demonstrated a positive correlation

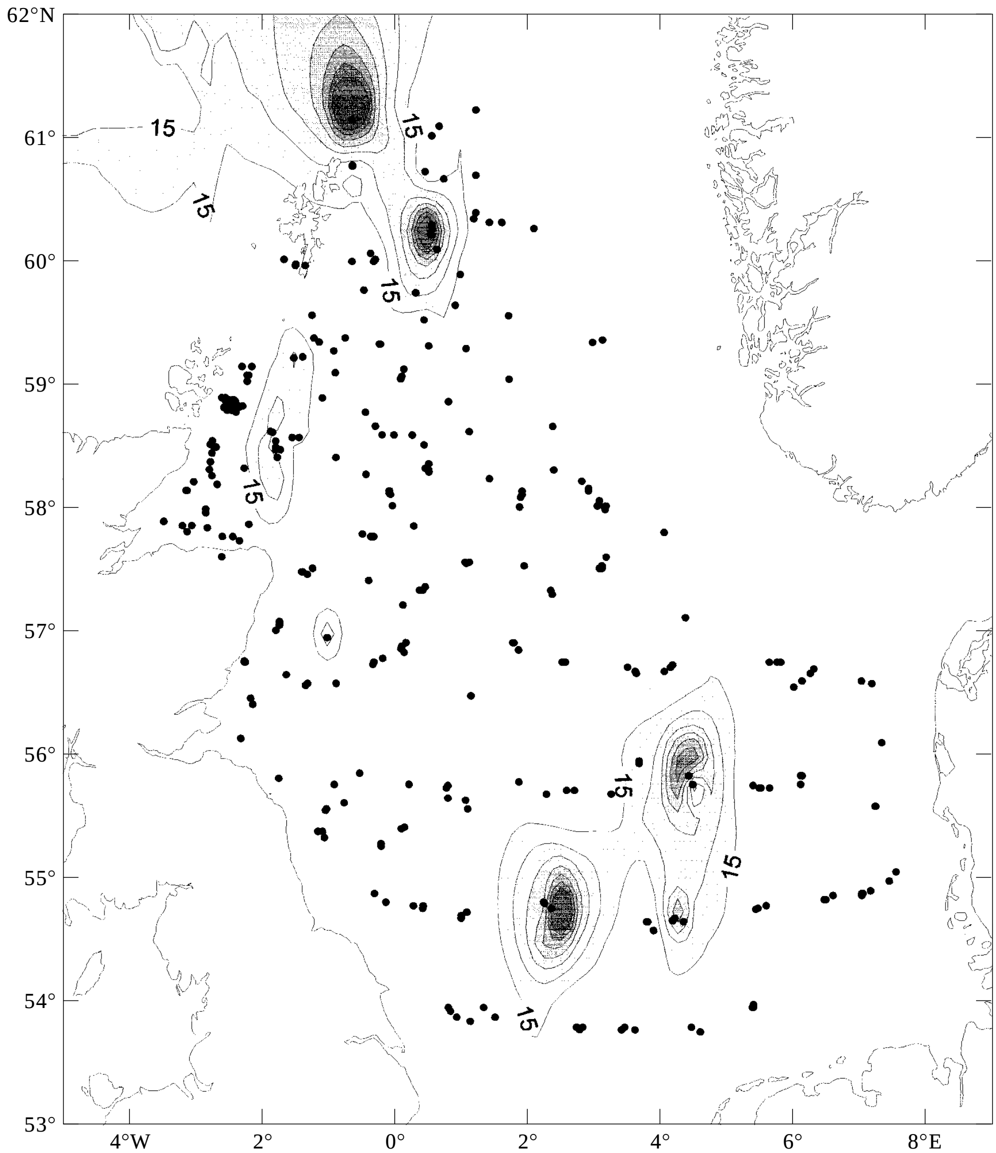

Figure 5. North Sea surveys, April (1991–1994): haul locations (●) and contours of *Loligo* abundance (contours at intervals of 15 squid h^{-1}).

between temperature and catches of *Illex illecebrosus* on the Scotian shelf. Conversely, Andriguetto and Haimovichi (1991) found that *Loligo sanpaulensis* tends to avoid water temperatures above 16°C.

A range of heuristic models, which use environmental parameters such as temperature and salinity to predict fishery abundance of molluscs is reviewed by Fogarty (1989). Rasero (1994) found survey abundance of *Todaropsis eblanae* in Spanish waters to be related to an "upwelling" index.

The present analysis also suggested that North Sea survey abundance was higher during daylight hours, which may relate to a diel cycle of vertical movement. Such diel variation in catchability are a general problem for survey indices of abundance (e.g. for Gadidae, Michalsen *et al.*, 1996). For the west coast, the regression tree analysis also confirmed the visual impression that *Loligo* was concentrated at the western edge of the survey area. At Rockall, survey catches were mostly in the shallowest water (<150 m).

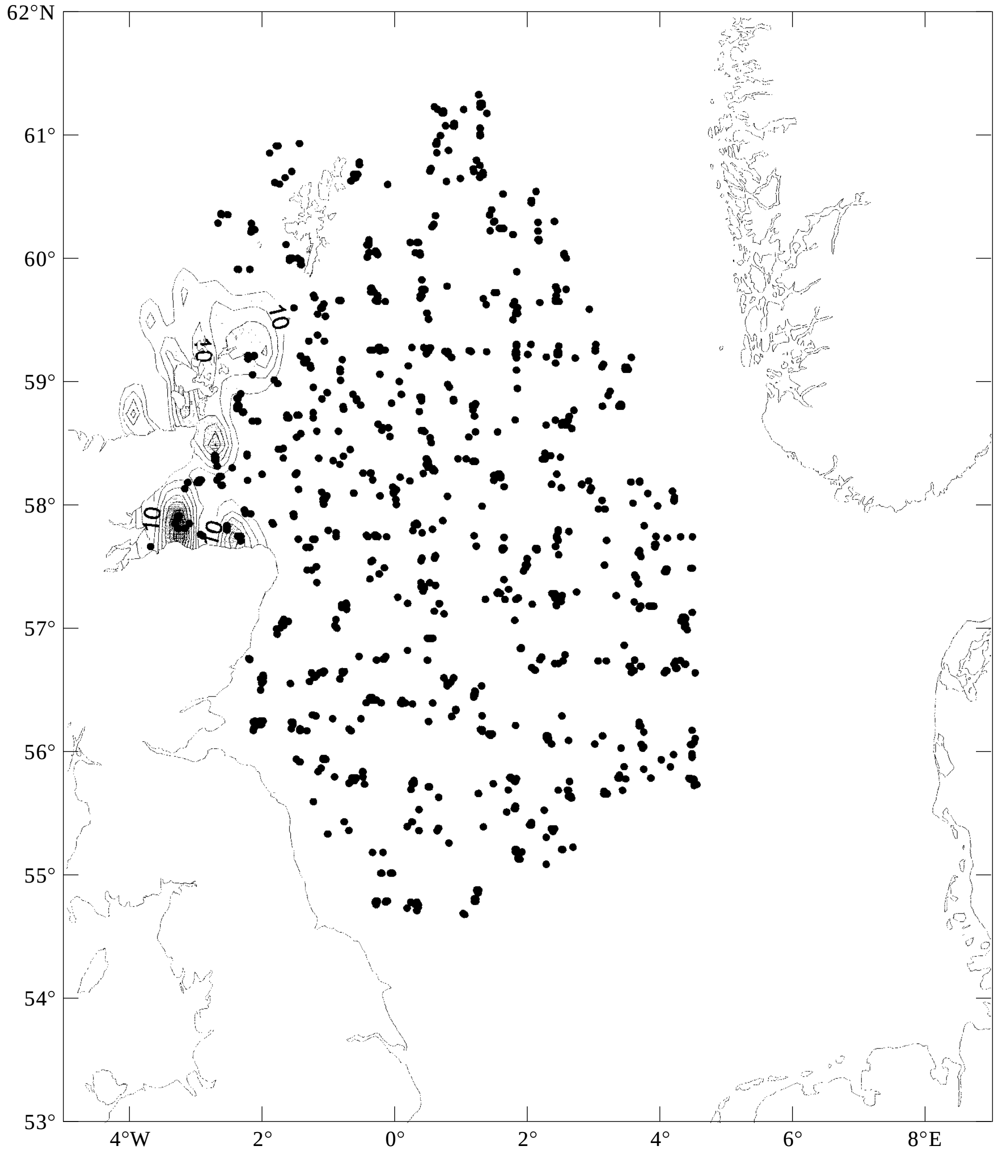

Figure 6. North Sea surveys, August (1980–1994): haul locations (●) and contours of *Loligo* abundance (contours at intervals of 10 squid h^{-1}).

Stock recruitment relationships

The analyses presented provide some evidence consistent with the existence of a stock recruitment relationship: this is seen in correlations between survey abundances in the North Sea for February and August, and the correlation between North Sea February survey abundance and commercial CPUE in October–December. Any relationship between spring and autumn abundance of *Loligo forbesi* spans two generations, since the February population will consist mainly of breeding adults and the autumn population of new recruits of the next generation (Pierce *et al.*, 1994b). Okutani and Watanabe (1983) found a correlation between abundance of winter-spawning *Todarodes pacificus* and larval density the following year, which could also be interpreted as a stock-recruitment relationship. However, it is generally thought that consistent stock-recruitment relationships are unlikely to be found in squids due to their apparent sensitivity to climatic fluctuations (Caddy, 1983).

The apparent link may be indirect, e.g. due to water temperature. High water temperature may contribute

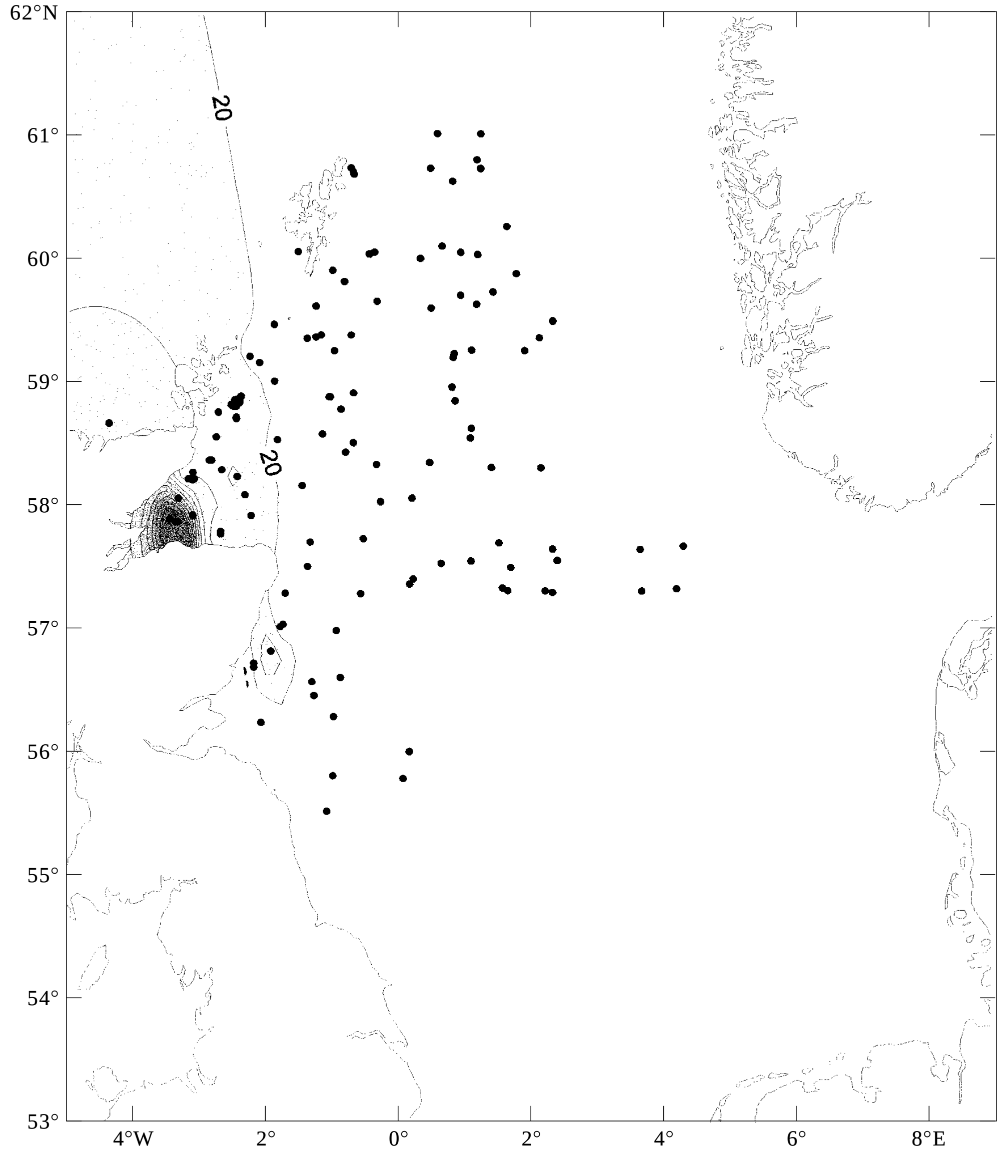

Figure 7. North Sea surveys, October (1981–1983): haul locations (●) and contours of *Loligo* abundance (contours at intervals of 20 squid h^{-1}). Note that contours extending to the edge of the map are artefacts caused by the absence of data.

(through increased metabolic rate and/or food supply) to growth rate and recruitment success of the juveniles of the year. Forsythe (1993) demonstrated that quite small changes in water temperature could, theoretically, result in large changes in growth patterns. It is less clear how temperature could influence the abundance of the February (spawning) population in the North Sea, although increased incursion of Atlantic water (associated with high temperature) could contribute to passive immigration from west coast stocks.

Surveys as predictors of fishery abundance

The only survey that provided a useful indication of fishery abundance in the main fishing season (October–December in coastal waters) was the North Sea survey in February. It is possible that the spring west coast survey fails to provide adequate prediction because its timing is too variable. The survey occurs at a time when abundance is expected to be declining due to post-spawning mortality and results may depend critically on exactly

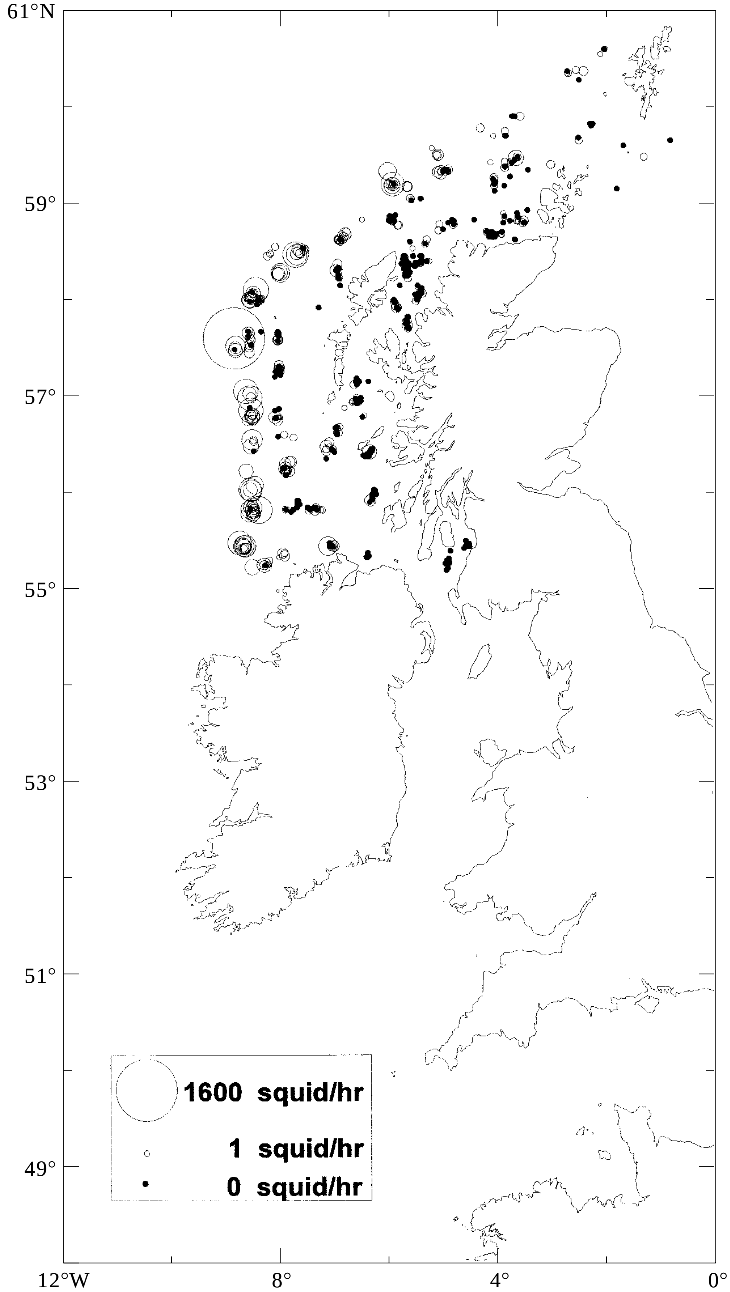

Figure 8. West coast surveys, January–March (1980–1994): haul locations and *Loligo* abundance. The closed circles (●) represent zero catches; the area of the open circles is proportional to the square root of the catch rate. Large open circle – 1600 squid h^{-1}; small open circles – 1 squid h^{-1}; small closed circles – 0 squid h^{-1}.

when the survey occurs. Given flexibility in the timing of life-cycle events, even a fixed survey timing would not guarantee success.

No evidence was obtained that the survey abundance of small squid in the North Sea in August could be used as a "recruitment index" to predict the adult stock size in the North Sea in the winter. The August survey takes place at a time of very low abundance and resulting abundance estimates may be sensitive to variation in the timing of recruitment.

Using average squid weight caught per hour (rather than average numbers) as the survey abundance index

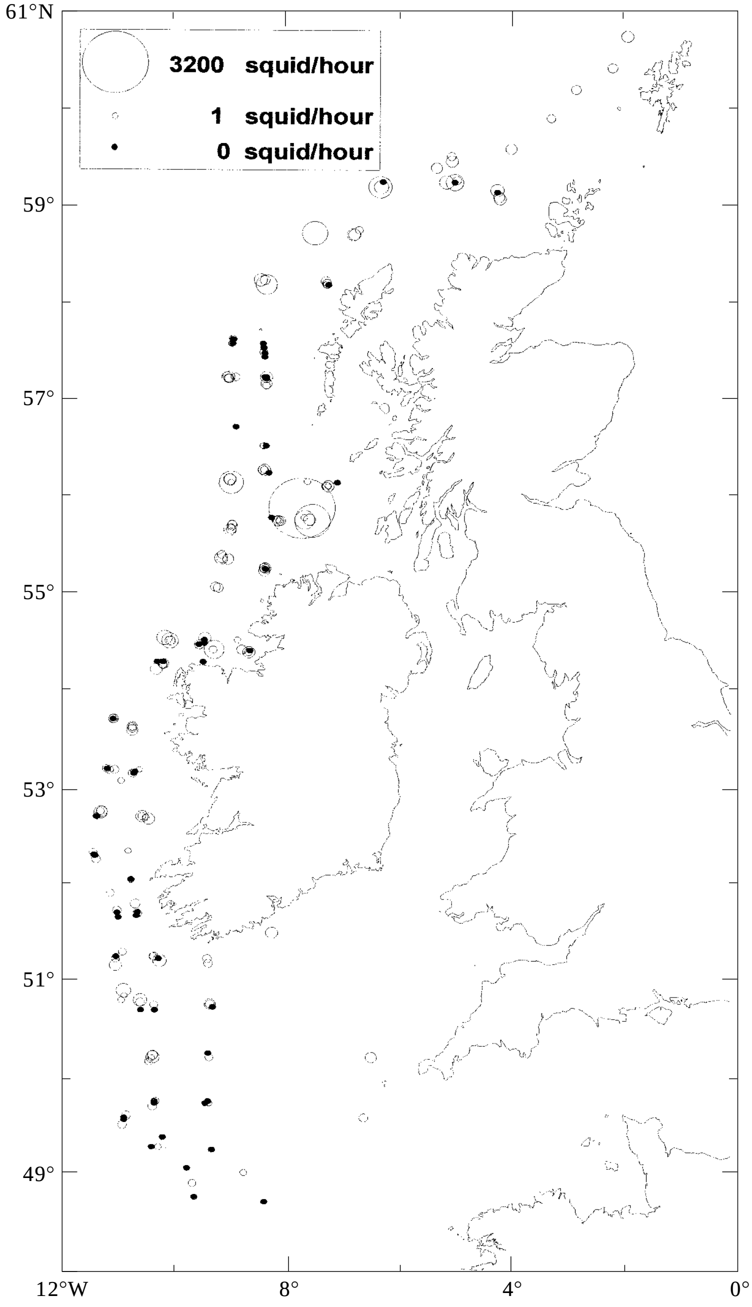

Figure 9. West coast surveys, November (1990–1994): haul locations and *Loligo* abundance. The closed circles (●) represent zero catches; the area of the open circles is proportional to the square root of the catch rate. Large open circle – 3200 squid h^{-1}; small open circles – 1 squid h^{-1}; small closed circles – 0 squid h^{-1}.

improved the quality of prediction. It would also have the advantage of being relatively robust to mis-identification of the very small loliginid *Alloteuthis* as *Loligo* (although such mis-identification is thought to be unlikely). Nevertheless, at best, variation in the average survey abundance explained only 42% of variation (r^2=0.42) in overall CPUE in the fishing season. It is possible that this could be improved by using a refined measure of CPUE (e.g. based on a smaller and more uniform sample of boats).

Fishery abundance at Rockall was not predicted by any of the survey indices and appears to follow quite

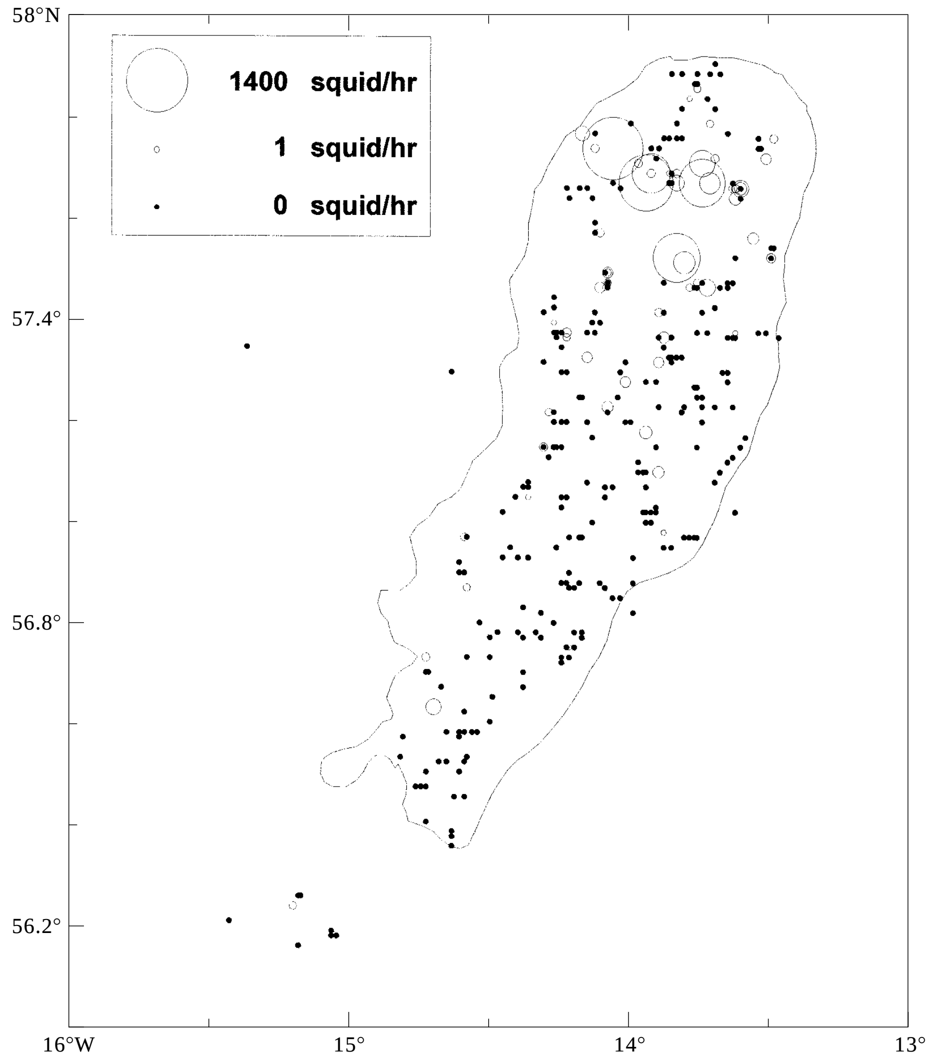

Figure 10. Rockall surveys, September (1985–1994): haul locations and *Loligo* abundance. The closed circles (●) represent zero catches; the area of the open circles is proportional to the square root of the catch rate. The outline represents 200 m depth contour. Large open circle – 1400 squid h^{-1}; small open circles – 1 squid h^{-1}; small closed circles – 0 squid h^{-1}.

separate trends to the coastal fishery. It is speculated elsewhere (Pierce *et al.*, 1994a,b) that the Rockall fishery may be based on a separate stock.

It should be noted that survey hauls do not exactly mimic commerical hauls, and the small mesh covers used on the survey gear are expected to retain more squids in the size range 10–20 mm ML than would commercial gears (Hastie, 1996).

Life cycle data

Results on the timing of the life-cycle obtained during this study largely support the established picture of winter/spring breeding and autumn recruitment (Boyle and Ngoile, 1993a,b; Pierce *et al.*, 1994b). Additionally, as reported by Lum-Kong *et al.* (1992), some smaller squids, presumably pre-recruit *Loligo*, are present all year round. It is interesting to note that the proportion of mature animals at Rockall in September samples was very variable between years.

Squid density

Estimates of absolute density and abundance at Rockall and in the North Sea were attempted using standard swept-area calculations. These calculations provide minimum estimates in that they assume *Loligo* has a strictly demersal habit and that there is zero escapement

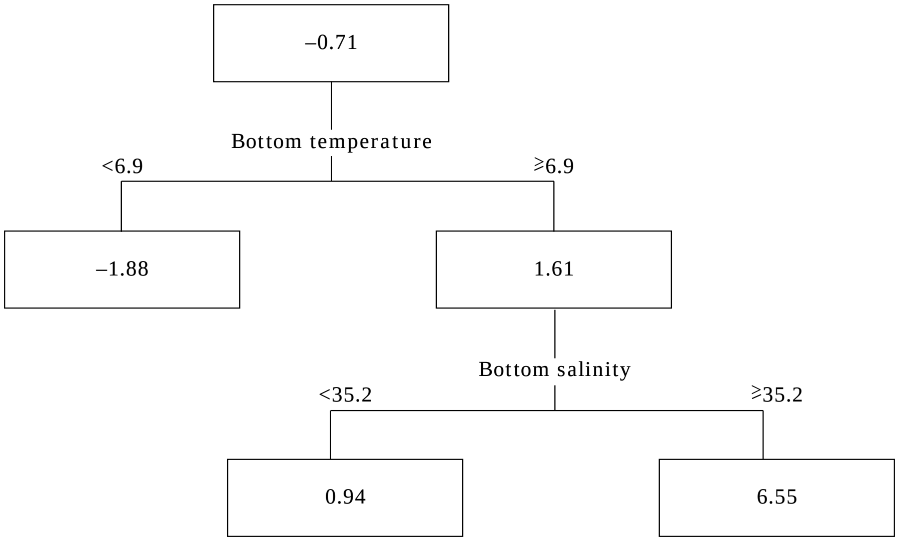

Figure 11. Regression tree for squid biomass (log) in the North Sea February survey. Values in boxes indicate mean predicted log (biomass) for each node. The variable that generates each significant binary partition and the cut-off levels are shown along the branches of the tree.

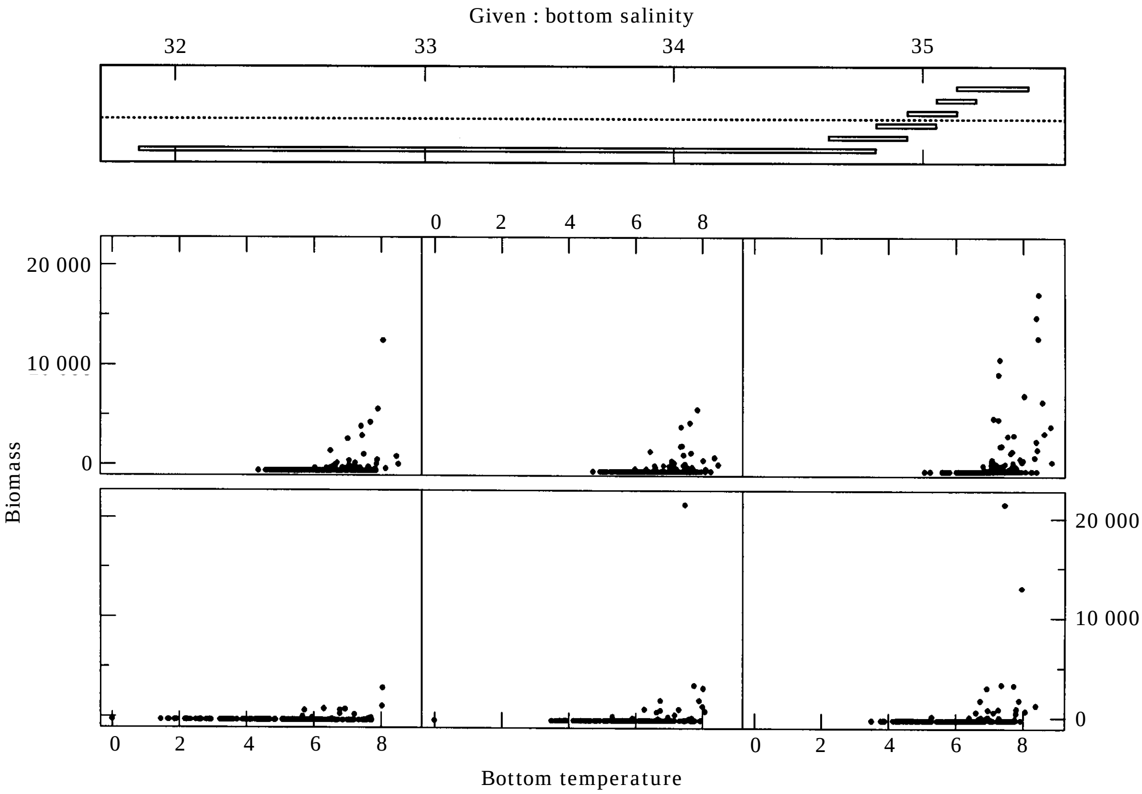

Figure 12. Conditional plot of squid biomass in the North Sea February survey against bottom temperature along a bottom salinity gradient. Salinity increases from bottom-left to top-right. The top graph demonstrates the salinity levels considered in each plot.

Table 4. Squid density from September Rockall surveys, 1988–1993. Average (c) densities (numbers and biomass of *Loligo* per unit swept area) ± 1 standard deviation of c. The averages are used to derive absolute numbers and biomass of *Loligo* at Rockall, assuming a total area of 9236.5 km^2. No squid were caught during the 1994 survey.

Year	1988	1989	1990	1991	1992	1993
No. of hauls	40	39	36	40	40	38
No. with full data	35	33	29	14	38	46
No. km^2	145.11	1.26	0.59	3.45	1.43	0.14
	± 106.93	± 0.53	± 0.46	± 2.44	± 0.68	± 0.14
kg/km^2	6.00	0.71	0.21	0.49	0.21	0.18
	± 4.30	± 0.32	± 0.18	± 0.29	± 0.14	± 0.18
Total no.	1.34×10^6	1.16×10^4	5.45×10^3	3.19×10^4	1.36×10^4	1.29×10^3
Total biomass (kg)	5.54×10^4	6.55×10^3	1.94×10^3	4.53×10^3	1.94×10^3	1.66×10^3

Table 5. Squid density from North Sea surveys, February 1989–92. Numbers and biomass of *Loligo* per unit swept area: averages (c) ± 1 standard deviation of c.

Year	1989	1990	1991	1992
No. of hauls	53	47	59	63
No. with full data	53	45	50	37
No. km^2	6.03	1065.47	26.36	3.86
	± 1.78	± 651.74	± 9.93	± 1.31
kg/km^2	2.41	15.17	6.65	1.10
	± 1.06	± 7.24	± 2.44	± 0.45

from the net. Also, the patchy distribution results in wide confidence limits to the estimates. Nevertheless, the figures represent the first attempt at assessment for this species and provide a basis for comparison with any future estimates.

Statistical problems

Loligo were routinely caught during demersal trawl surveys during 1980–1994. Surveys provide data unbiased by prior assortment into commercial size categories and, in particular, can indicate the distribution and abundance of pre-recruits, i.e. squid smaller than the minimum size normally appearing in commercial catches.

Nevertheless, the survey data used presented a number of statistical problems. Firstly, the survey design was non-random. Secondly, and more importantly, zero catches were frequent so that standard mean and variance estimates were unsuitable. The solution used here follows Pennington (1996) and assumes that catch size followed a Δ-distribution. The use of regression trees is also relatively new but offers a robust technique for developing predictive relationships.

Another question relates to the suitability of standard trawling gear for catching squid. Although most squid landed in the UK are trawled, during research surveys squid are often seen entangled in the net rather than in the codend (M. A. Collins, pers comm.). Video recordings of squid inside trawls show them holding station and, sometimes, swimming out. Many are probably caught when they attempt to escape sideways (SOAEFD, unpublished data).

Acknowledgements

This analysis was funded by the Commission of the European Communities under Contract No. AIR 1 CT92 0573). We would like to thank SOAEFD staff in the finfish and computing sections for access to unpublished data and assistance with data retrieval. Gayle Mackay helped transcribe the SCANMAR data. The manuscript benefited from comments by P. R. Boyle and M. A. Collins (University of Aberdeen), R. Fryer (SOAEFD), J. H. S. Blaxter, S. J. Smith and an anonymous referee.

References

Andriguetto Jr, J. M. and Haimovici, M. 1991. Abundance and distribution of *Loligo sanpaulensis* Brakoniecki, 1984 (Cephalopoda, Loliginidae) in southern Brazil. Sci. Mar., 55: 611–618.

Anon. 1995. United Kingdom Sea Fisheries Statistics 1993. Ministry of Agriculture, Fisheries and Food. HMSO, London.

Augustyn, C. J. 1991. The biomass and ecology of chokka squid *Loligo vulgaris reynaudii* off the west coast of South Africa. S. Afr. Tyderskr. Dierk., 26: 164–181.

Augustyn, C. J., Lipinski, M. R., and Sauer, H. H. 1992. Can the *Loligo* squid fishery be managed effectively? A synthesis of research on *Loligo vulgaris reynaudii*. *In* Benguela trophic functioning, Ed. by A. I. L. Payne *et al.* South African Journal of Marine Science, 12: 903–918.

Boyle, P. R., Pierce, G. J., and Hastie, L. C. 1995. Size modes at maturity in *Loligo forbesi*. Marine Biology, 121: 501–508.

Boyle, P. R. and Ngoile, M. A. K. 1993a. Assessment of maturity state and seasonality of reproduction of *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. *In* Recent advances in cephalopod fisheries biology, pp. 37–48.

Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.

Boyle, P. R. and Ngoile, M. A. K. 1993b. Population variation and growth in *Loligo forbesi* (Cephalopoda: Loliginidae) from Scottish waters. *In* Recent advances in cephalopod fisheries biology, pp. 49–59. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.

Caddy, J. F. 1983. The cephalopods: factors relevant to their population dynamics and to the assessment and management of stocks. *In* Advances in assessment of world cephalopod resources, pp. 416–449. Ed. by J. F. Caddy. FAO Fisheries Technical Papers, 231.

Clark, L. A. and Pregibon, D. 1993. Tree-based models. *In* Statistical models in S, pp. 377–419. Ed. by J. M. Chambers and T. J. Hastie, AT&T Bell Laboratories. Chapman and Hall, London.

Coelho, M. L. and Rosenberg, A. A. 1984. Causal analysis of some biological data for *Illex illecebrosus* from the Scotian Shelf. NAFO Scientific Council Studies, 7: 61–66.

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

Collins, M. A., Pierce, G. J., and Boyle, P. R., 1997 Population indices of reproduction and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish and Irish waters. Journal of Applied Ecology, 34: 778–786.

Fogarty, M. J. 1989. Forecasting yield and abundance in exploited invertebrates. *In* Marine invertebrate fisheries: their assessment and management, pp. 701–724. Ed. by J. F. Caddy. John Wiley and Sons, New York.

Forsythe, J. W. 1993. A working hypothesis of how seasonal temperature change may impact the field growth of young cephalopods. *In* Recent advances in cephalopod fisheries biology, pp. 133–143. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo.

Hastie, L. C. 1996. Estimation of trawl codend selectivity for squid (*Loligo forbesi*), based on Scottish research vessel survey data. ICES Journal of Marine Science, 53: 741–744.

Hatfield, E. M. C. and Rodhouse, P. G. 1994. Distribution and abundance of juvenile *Loligo gahi* in Falkland Island waters. Marine Biology, 121: 267–272.

Hatfield, E. M. C., Rodhouse, P. G., and Porebski, J. 1990. Demography and distribution of the Patagonian squid (*Loligo gahi* d'Orbigny) during the austral winter. ICES Journal of Marine Science, 46: 306–312.

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.

Howard, F. G. 1979. Recent trends in the Scottish fishery for *Loligo forbesi*, together with some notes on the biology of the species. ICES CM 1979/K: 36.

Howard, F. G., Ngoile, M. A., and Mason, J. 1987. *Loligo forbesi*: its present status in Scottish fisheries. ICES CM 1987/K: 5.

Kristensen, T. K. 1984. Biology of the squid *Gonatus fabricii* (Lichtenstein, 1818) from West Greenland waters. Meddelelser om Grønland Bioscience, 13: 3–17.

Lange, A. M. T. and Sissenwine, M. P. 1983. Squid resources of the Northwest Atlantic. *In* Advances in assessment of world cephalopod resources, pp. 21–54. Ed. by J. F. Caddy. FAO Fisheries Technical Papers, 231.

Lum-Kong, A. 1989. The reproductive biology of female *Loligo forbesi* Steenstrup (Cephalopoda: Myopsida). PhD thesis, University of Aberdeen.

Lum-Kong, A., Pierce, G. J., and Yau, C. 1992. Timing of spawning and recruitment in *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. Journal of the Marine Biological Association of the United Kingdom, 72: 301–311.

Michalsen, K., Godo, O. R., and Ferno, A. 1996. Diel variation in the catchability of gadoids and its influence on the reliability of abundance indexes. ICES Journal of Marine Science, 53: 389–395.

Moreno, A., Cunha, M. M., and Pereira, J. M. F. 1994. Population biology of the veined squid (*Loligo forbesi*) and European squid (*Loligo vulgaris*) from the Portuguese coast. Fisheries Research, 21: 71–86.

Murata, M. 1989. Population assessment, management and fishery forecasting for the Japanese common squid, *Todarodes pacificus*. *In* Marine invertebrate fisheries: their assessment and management, pp. 613–636. Ed. by J. F. Caddy. John Wiley and Sons, New York.

Ngoile, M. A. K. 1987. Fishery biology of the squid *Loligo forbesi* (Cephalopoda: Loliginidae) in Scottish waters. PhD thesis, University of Aberdeen.

Okutani, T. and Watanabe, T. 1983. Stock assessment by larval surveys of the winter population of *Todarodes pacificus* Steenstrup (Cephalopoda: Ommastrephidae), with a review of early works. Biological Oceanography, 2: 433–456.

Pennington, M. 1996. Estimating the mean and variance from highly skewed marine data. Fishery Bulletin, 94: 498–506.

Pierce, G. J., Boyle, P. R., Hastie, L. C., and Howard, F. G. 1992. The Scottish fishery for *Loligo forbesi*: current trends. ICES CM 1992/K: 6.

Pierce, G. J., Boyle, P. R., Hastie, L. C., and Shanks, A. 1994a. Distribution and abundance of the fished population of *Loligo forbesi* in UK waters: analysis of fishery data. Fisheries Research, 21: 193–216.

Pierce, G. J., Boyle, P. R., Hastie, L. C., and Key, L. 1994b. The life history of *Loligo forbesi* in Scottish waters. Fisheries Research, 21: 17–41.

Pierce, G. J. and Guerra, A. 1994. Stock assessment methods used for cephalopod fisheries. Fisheries Research, 21: 255–285.

Roberts, M. J. and Sauer, W. H. H. 1994. Environment: the key to understanding the South African chokka squid (*Loligo vulgaris reynaudii*) life-cycle and fishery? Antarctic Science, 6: 249–258.

Rasero, M. 1994. Relationship between cephalopod abundance and upwelling: the case of *Todaropsis eblanae* (Cephalopoda: Ommastrephidae) in Galician waters (NW Spain). ICES CM 1994/K: 20, 3 pp.

Sato, T. and Hatanaka, H. 1983. A review of assessment of Japanese distant-water fisheries for cephalopods. *In* Advances in assessment of world cephalopod resources, pp. 145–203. Ed. by J. F. Caddy. FAO Fisheries Technical Papers, 231.

Summers, W. C. 1969. Winter population of *Loligo pealei* in the Mid-Atlantic Bight. Biological Bulletin, 137: 202–216.

Yau, C. 1994. The ecology and ontogeny of cephalopod juveniles in Scottish waters. PhD thesis, University of Aberdeen.