Cephalopod Biodiversity, Ecology and Evolution
Payne, A. I. L., Lipiński, M. R., Clarke, M. R. and M. A. C. Roeleveld (Eds). *S. Afr. J. mar. Sci. 20: 323–336*

LOLIGO SPP. IN UNITED KINGDOM WATERS

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A Geographic Information System (GIS) was used to test hypotheses regarding the spatial distribution of the squid *Loligo forbesi* and *Loligo vulgaris vulgaris* in the northern North-East Atlantic during the years 1989-1994. *Loligo* spp. were present throughout coastal waters of the United Kingdom, but distribution was patchy and highly variable over space and time. The relationship between squid distribution and sea temperature and salinity in the North Sea was examined by overlaying maps of squid abundance (landings per unit effort *lpue*) and oceanographic variables, and using correlation and multiple regression analysis. Bottom temperature was most frequently correlated with *lpue*, with correlations between squid and oceanographic parameters occurring most often in January and February of a given year. Monthly changes in distribution patterns are consistent with squid undertaking seasonal migrations around the coast of the U.K. It is at present unknown whether temperature and salinity influence squid distribution directly (e.g. reflecting physiological tolerance limits), through effects on recruitment, growth or mortality, or indirectly as a result of passive movement of squid into the North Sea during inflow of warmer Atlantic water.

Cephalopod stocks are of relatively recent importance to international commercial fisheries, often being regarded as "non-conventional" resources (Boyle 1990). In the northern North-East Atlantic, cephalopods are caught primarily as a bycatch of the demersal trawl and seine whitefish fishery (Pierce *et al*. 1994b, Collins *et al*. 1995). Of particular interest are the loliginid (myopsid) squid *Loligo forbesi* and *L. vulgaris vulgaris* (Boyle and Pierce 1994). Squid of the genus *Loligo* are caught throughout waters of the United Kingdom, Scottish fishery catches consisting almost entirely of *L. forbesi* (Pierce *et al*. 1994a, b) and both species being caught in the English Channel (Robin and Boucaud-Camou 1995). *L. v. vulgaris* has a more southerly distribution than *L. forbesi* and, in areas of overlap, the former species is generally found closer inshore than the latter (Tinbergen and Verwey 1945, da Cunha *et al*. 1995).

Loligo forbesi and *L. v. vulgaris* have an annual life cycle (Holme 1974, Lum-Kong *et al*. 1992, Guerra and Rocha 1994, Pierce *et al*. 1994a, Arkhipkin 1995) and a coastal neritic habitat (Holme 1974). Both species breed mainly during winter (December – March) and generally recruit to the fishery in autumn (Holme 1974, Lum-Kong *et al*. 1992, Pierce *et al*. 1994a, Boyle *et al*. 1995). Landings from United Kingdom coastal waters are usually largest in autumn (September – November) of a given year (Holme 1974, Pierce *et al*. 1994b, Collins *et al*. 1995), and generally decline from December onwards (Pierce *et al*. 1994b).

Links between seawater temperature and distribution have been shown for a number of squid species (Summers 1969, Holme 1974, Worms 1983, Andriguetto and Haimovici 1991, Augustyn 1991, Sauer *et al*. 1991, Pierce *et al*. 1998) and in cuttlefish (Augustyn *et al*. 1995). The causal links underlying such relationships are difficult to establish. There may be limited physiological tolerance to colder waters (Summers 1969, Augustyn 1991), or effects on maturation and growth (Worms 1983, Forsythe 1993), migration (Summers 1969, Holme 1974) or seasonality of the life cycle (e.g. Laughlin and Livingston 1982). Squid distribution may also be influenced by temperature variations associated with ocean frontal systems (e.g. Andriguetto and Haimovici 1991). Variations in salinity within the normal range found in marine systems are unlikely to have much biological significance for squid. However, indirect links could arise between distribution and salinity because different water masses may be characterized by small differences in salinity.

It is important to distinguish between temporal (month to month or interannual) and spatial relationships. Investigations of the latter have been facilitated by the development of Geographic Information Systems (GIS) and geostatistics. To date, there have been few attempts to utilize GIS in the analysis of marine fisheries data (see Simpson 1992, 1994, Castillo *et al*. 1996, Fox and Starr 1996), and there appears to be much scope for future work in this field.

In the present study, a GIS was used to describe and analyse patterns in squid distribution and oceanographic parameters in waters around the United Kingdom

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Manuscript received: September 1997

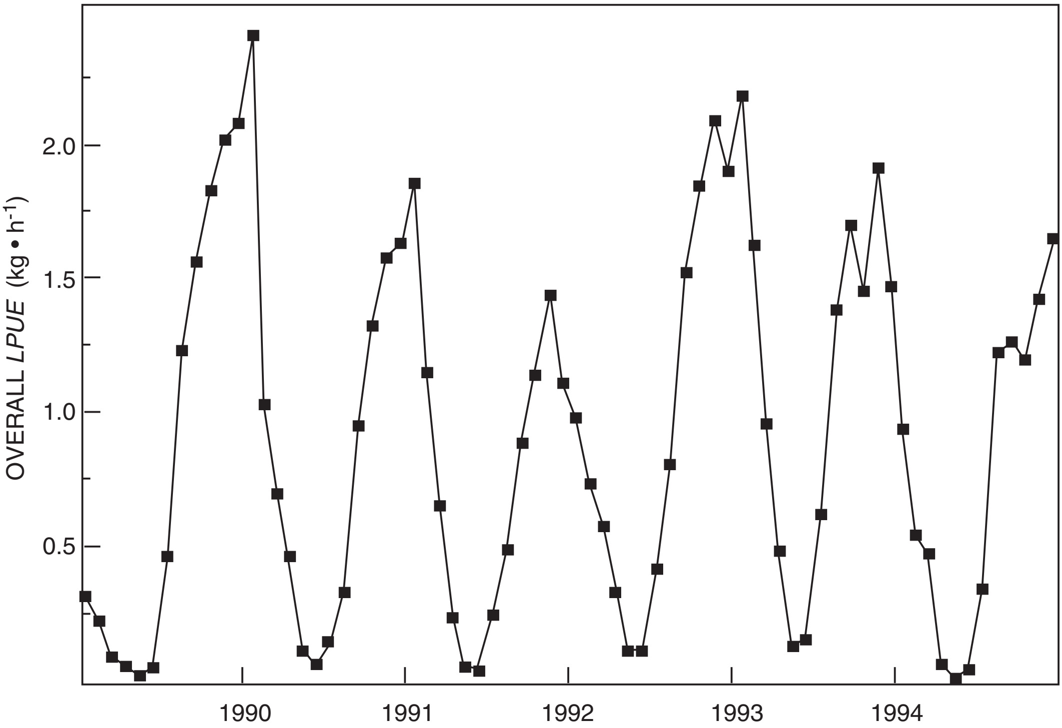

Fig. 1: Overall monthly *lpue* of *Loligo* spp. from U.K. waters (January 1989 – December 1994)

on a spatial basis. The main questions addressed were:

(a) what spatial patterns can be identified in *Loligo* distribution?
(b) how do these patterns vary from month to month and from year to year?
(c) is *Loligo* distribution related to oceanographic conditions?

METHODS

A GIS (PC Arc/Info: Environmental Systems Research Institute Inc. [ESRI]) was used to test hypotheses on the spatial distribution of *Loligo* spp. in the North Sea and northern North-East Atlantic. The study area was the region 48 – 63°N, 12°W – 10°E. This area encompasses most fishing effort by the UK demersal fleet and includes the west coast of Scotland, the North Sea and the English Channel.

Fishery data for the area (monthly landings of *Loligo* spp. in kg and fishing effort in hours) were available from three fishing fleets for the period January 1989 – December 1994, on a monthly basis by ICES (International Council for the Exploration of the Sea) statistical rectangle (i.e. with a spatial resolution of 0.5° of latitude by 1° of longitude). Data from U.K.-registered vessels landing in Scotland (henceforth referred to as the "Scottish" fleet) were obtained from the Fishery Research Services Marine Laboratory in Aberdeen. Data from the English/Welsh fleet were supplied by the Ministry of Agriculture, Fisheries and Food. Data for the French fleet were supplied by the University of Caen and are derived from the database of l'Institut Francais de Recherche pour l'Exploitation de la Mer (IFREMER). The French data extend back to the start of 1989 and that date was therefore chosen as the starting point for this study. In 1995, the Scottish Office introduced a new system of recording fishery data and the end of 1994 was therefore chosen as a sensible cut-off point. In the present study, data are used from all gear types (trawl and seine), and fleet and gear selectivity are not examined. As the two *Loligo* species are not separated in official landings statistics, they are treated together here.

Fishery data must always be treated with caution, being subject to a range of errors, e.g. misreporting. Official data on fishing effort are generally restricted to those vessels required by law to report effort (i.e.

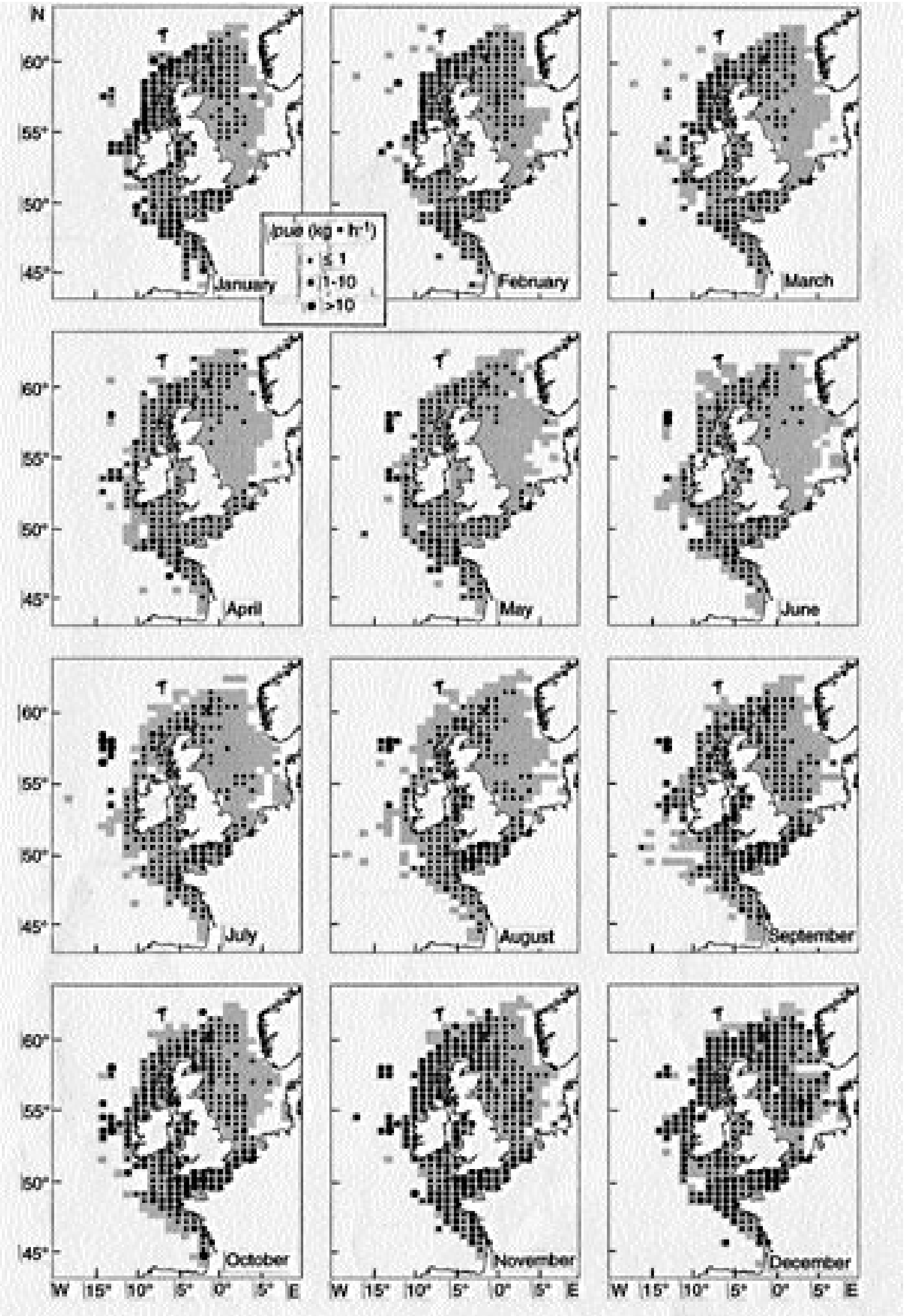

Fig. 2: *Loligo* spp. distribution and abundance in 1989. Circles represent landings per unit effort, *lpue*. Shaded areas represent areas in which fishing by the demersal fleet took place. *Loligo* are widely distributed over the entire region between September and December, but restricted to waters in the north-west and English Channel between January and August

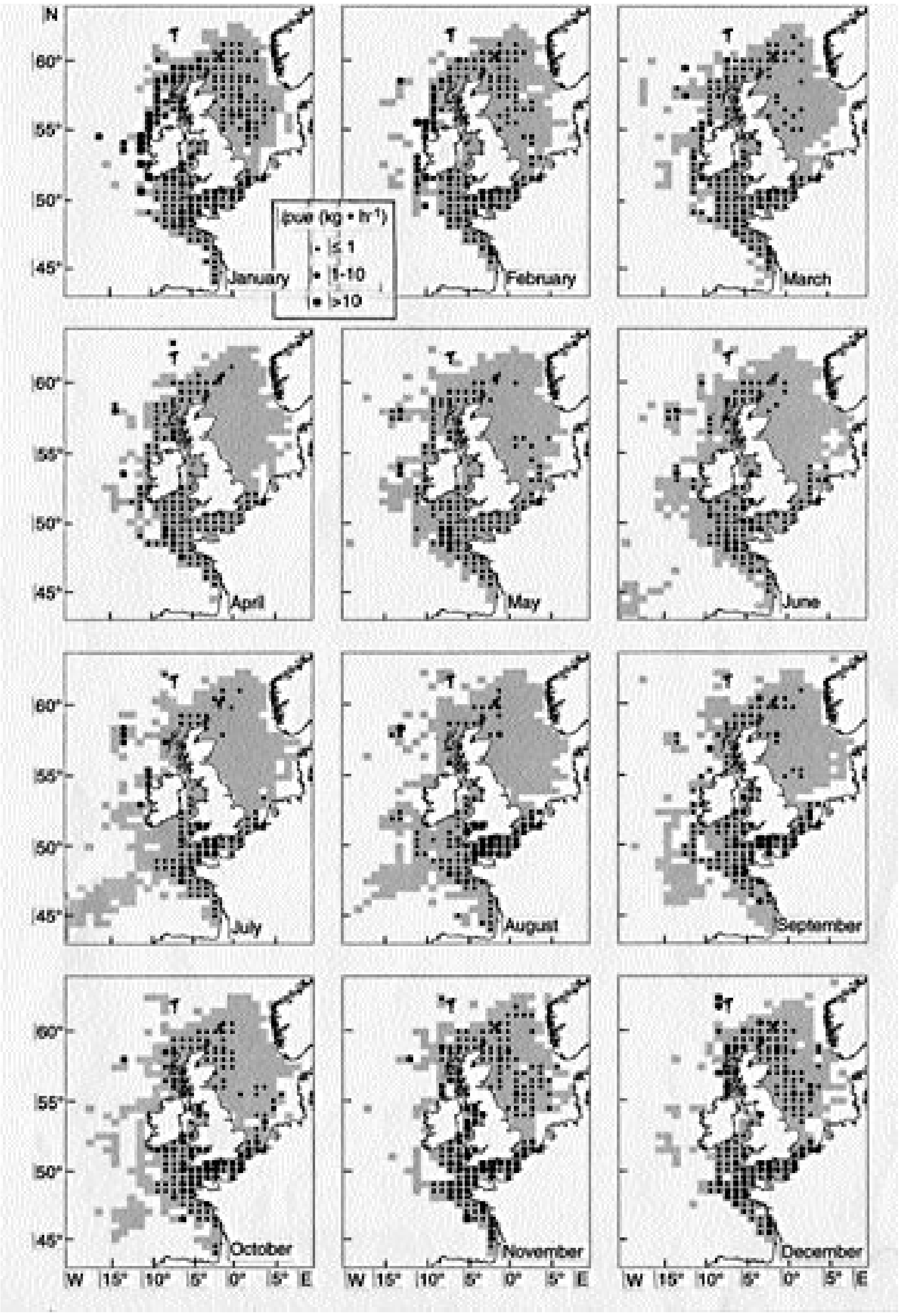

Fig. 3: *Loligo* spp. distribution and abundance in 1994. Circles represent landings per unit effort, *lpue*. Shaded areas represent areas in which fishing by the demersal fleet took place. *Loligo* are widely distributed over the entire region between September and December, but restricted to waters in the north-west and English Channel between January and August

Table I: Summary of results of correlation analysis. Number of months over the period 1989–1994 in which data on *lpue* and oceanographic variables were available for more than 20 rectangles and significant correlations were seen. Significant correlations are classified as positive with $p < 0.01$, positive with $p < 0.05$, negative with $p < 0.01$ and negative with $p < 0.05$. For approximately 60 repeats of a two-tailed test, significant correlations (±) would be expected to occur by chance alone in no more than one month (for $p < 0.01$) or three months ($p < 0.05$)

Correlation analysis classification	Number of months with significant correlations			
	Surface temperature	Bottom temperature	Surface salinity	Bottom salinity
$r_s > 0, p < 0.01$	24	31	27	12
$r_s > 0, p < 0.05$	28	38	33	19
$r_s > 0, p < 0.01$	2	0	0	3
$r_s > 0, p < 0.05$	4	0	0	6
Number of months of data > 20 rectangles	68	60	69	63

excluding very small boats). Fishery data were used to estimate landings per unit effort (*lpue*) in kilogrammes per hour, and these values were used as a relative index of squid abundance. As squid are not generally targeted by the whitefish fishery nor subject to quota restrictions, but are nevertheless sufficiently valuable to ensure that most catches are landed, it is assumed that *lpue* gives a reasonable estimation of abundance (see Pierce *et al*. 1994b). A composite *lpue*, by month and rectangle, was calculated by summing the landings by all three fleets and dividing them by the sum of the effort by all three fleets. Data on landings and effort by other European fleets fishing in the area (notably Ireland) are not available with the same spatial resolution and therefore could not be included. As the fishery data are used only as an index of abundance, this is not thought to be a serious shortcoming.

Oceanographic data (sea surface and bottom water temperature in °C, and sea surface and bottom water salinity $\times 10^{-3}$) for the same period were supplied by the ICES Oceanographic Data Centre as mean monthly values per ICES rectangle. All data (fishery/oceanographic) were assumed to refer to the latitude and longitude at the midpoint of each rectangle.

A series of maps (examples of which are given in Figs 4 – 6 later) were created on a month-by-month basis in order to observe the correspondence of areas of high and low *lpue* with areas of high and low values of the oceanographic variables. Because the coverage of salinity and temperature was most complete on the east coast, with more-limited coverage of the west coast of the U.K., the former presentation is restricted to the area east of 4°W. Similar maps, but for the whole area, were used to observe inter- and intra-annual trends in *lpue*.

To provide a simple formal test of the relationship between *lpue* and each of the four oceanographic variables, Spearman's rank correlation coefficients were calculated for each month in which data on *lpue* and an oceanographic variable coincided in at least 20 grid squares (i.e. the sample size was at least 20). For the purpose of that analysis, each ICES rectangle was treated as an independent data point. The prospects for using linear regression and discriminant analysis to predict *lpue* from surface temperature were explored using data from February 1993 (the month in which the strongest correlations between *lpue* and surface temperature were seen). In that month, there were 130 squares with data available for both variables.

RESULTS

Loligo were widely distributed around the coast of the United Kingdom, although distribution and abundance, as inferred from *lpue*, varied from month to month and between years, and was often patchy. The monthly patterns of overall *lpue* is similar for all six years studied (Fig. 1), falling to a minimum around June and rising to a peak at the end of the year. Squid were caught in similar abundance in the English Channel throughout the year. In contrast, catches in the North Sea, and to a lesser extent on the west coast of Scotland, were more seasonal, with *lpue* highest in the months November – January and lowest from May to August (Figs 2, 3).

The area covered by the fishery over the period 1989 – 1994 appears to be relatively consistent (Figs 2, 3), and changes in the distribution of *lpue* from month to month, which could be interpreted as attributable to migration, were seen in most of the years studied. From September onwards, squid appear to move into the North Sea from the vicinity of Orkney and Shetland to the north and possibly also via the Straits of Dover from the south. The distribution contracts again from January through July (Figs 2, 3). Identification of putative movements in the southern North Sea is complicated by the presence of two species in the data.

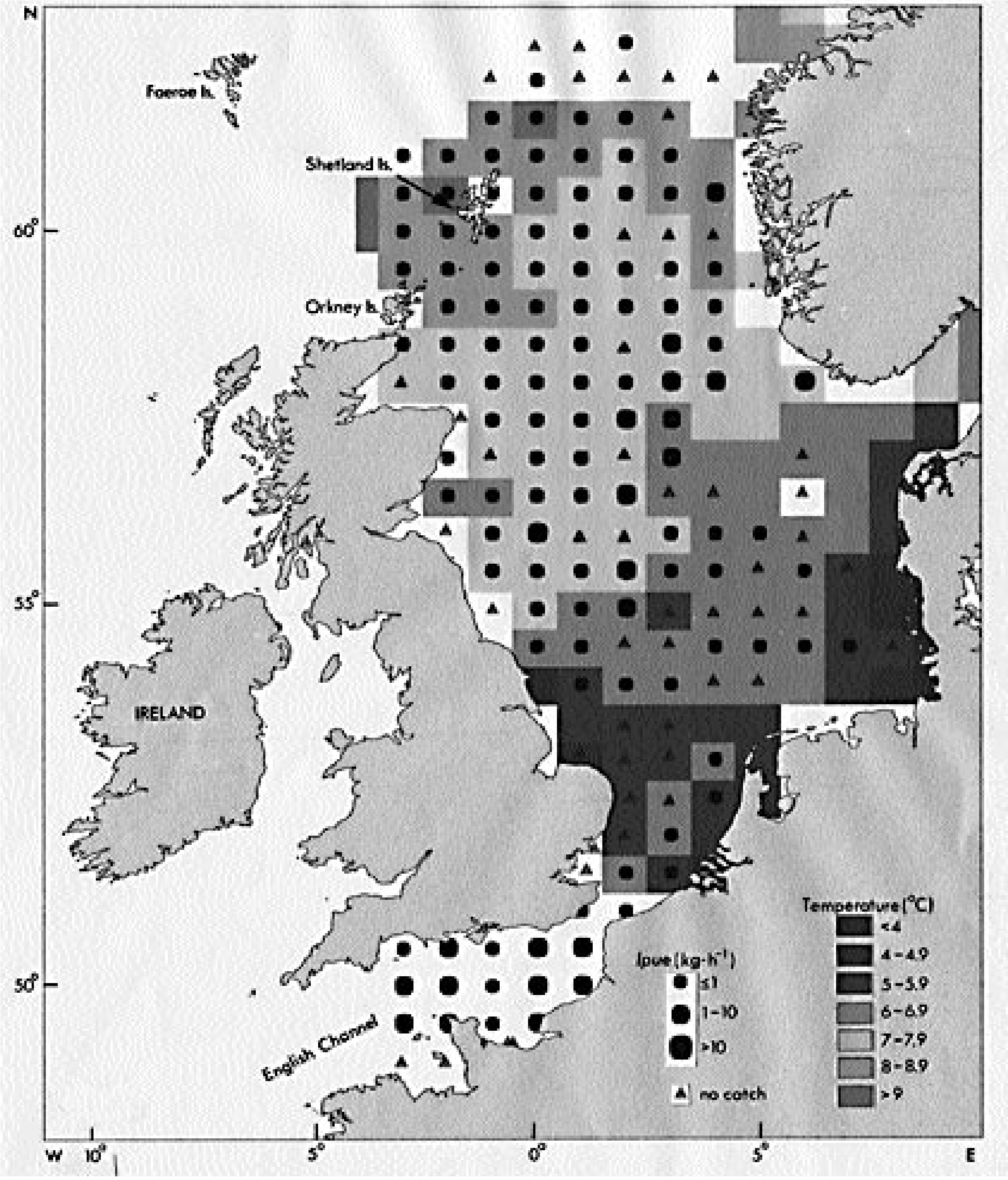

Fig. 4: Squid distribution in relation to bottom temperature, February 1992. Data are referenced to a base grid of ICES squares with a resolution of 0.5° latitude by 1° longitude. Circles represent landings per unit effort, *lpue*. Triangles represent areas where fishing took place but no squid were caught. Coloured polygons represent sea surface temperature, with red shaded areas being the warmest and blue areas the coldest. White squares represent a lack of temperature data in that area. During this period, *Loligo* spp. appear to be most common in the warmer waters of the northern North Sea

Sea temperatures were generally higher in the northern North Sea than farther south during winter, particularly from December to February, at which time squid *lpue* tended to be higher in warmer waters (Fig. 4). Temperatures were higher in the southern North Sea and English Channel during summer and autumn. Squid *lpue* was higher in warmer waters in autumn, but the relationship disappeared in summer (Fig. 5). Salinity values followed a similar trend, with high salinity and high *lpue* tending to be associated in winter (Fig. 6).

Squid were caught in statistical rectangles with bottom temperatures from 4°C (February and March 1991) to 19°C (August 1989) and surface temperatures from 5°C (February 1991) to 20.5°C (July 1989). Salinity values rarely fell below 33×10^{-3}, with a maximum surface salinity of 35.88×10^{-3} and bottom salinity of 35.68×10^{-3} recorded in July 1989 and March 1992 respectively.

Significant positive correlations between *lpue* and the four oceanographic variables were seen more frequently than would be predicted from chance alone (Table I). Bottom temperature was most frequently correlated with *lpue*. There were some significant negative correlations between *lpue* and both bottom salinity and surface temperature. When the data are examined in more detail (Table II), it is clear that positive relationships between *lpue* and oceanographic parameters were most often seen in January and February. Sample sizes for December and March were generally small, reducing the likelihood of correlations being detected. Some positive correlations between *lpue* and at least one of the four oceanographic variables were seen in all months. Statistically significant negative correlations between *lpue* and surface temperature were found for June and July only. In both those months *lpue* was, however, strongly positively associated with surface salinity. Negative correlations between *lpue* and bottom salinity were found in each month from July to November 1993 (accounting for five of the six negative correlations seen).

As is apparent from Figure 7, use of linear regression to predict *lpue* in February 1993 from surface temperature is not appropriate owing to the large number of zero *lpue* values: *lpue* is not normally distributed and cannot be transformed to normal. Nevertheless, it is clear that non-zero *lpue* values are seen more frequently at higher temperatures, with very low or zero *lpue*s found in temperatures <6°C. The average surface temperature in rectangles with non-zero *lpue* is significantly higher than in rectangles with zero *lpue* (medians 5.71 and 6.75°C respectively, Kruskal-Wallis $H = 31.75$, $df = 1$, $p < 0.0005$). However, presence/absence of squid catches can be predicted with only 69% success using a discriminant function based solely on surface temperature. If all four oceanographic variables are used (reducing the sample size from 130 to 118 owing to missing data), discrimination increases to 72%.

DISCUSSION

Spatial and temporal patterns of distribution

During the period 1989–1994, *Loligo* spp. were present throughout the North Sea, particularly in the north (57–62°N), on the west coast of Scotland and in the English Channel (between 48 and 51°N). Squid distribution and abundance were both spatially patchy and variable from year to year. Augustyn (1991) observed a similarly patchy spatial distribution for *Loligo vulgaris reynaudii* in the waters off the west coast of South Africa. Squid populations tend to consist entirely of a single year group and are highly responsive to inter-annual fluctuations in biological and physical variables. There is usually little overlap between adult generations, and this means that there is no (or very little) buffer against fluctuations in recruitment or the excessive mortality of breeding adults. Population size and distribution patterns can therefore vary widely from year to year (Caddy 1983, Pierce and Guerra 1994, Boyle and Boletzky 1996).

Squid *lpue* was highest during autumn (October – December) of a given year, corresponding with the recruitment of young squid to the fishery (Boyle *et al.* 1995), young recruits and pre-breeding squid being caught at the start of autumn and more-mature squid caught later. The consistent abundance of squid in the English Channel may in part reflect the presence of both species (*L. v. vulgaris* and *L. forbesi*) there. There was evidence of a summer/autumn migration of squid into both ends of the North Sea. An influx of squid into the southern North Sea from the English Channel via the Straits of Dover was recorded by Holme (1974) for *Loligo forbesi* and by Worms (1983) for *L. vulgaris*. The distribution in the northern North Sea contracts during the months January – April, which could represent northward migration or differential timing of post-spawning mortality.

Temperature and salinity

Of the four physical variables considered, bottom temperature was most strongly related to *Loligo lpue*, as indicated by the highest number of months with positive correlations. Nevertheless, the four variables examined all tend to co-vary, which suggests that this may be indicative of a given water mass, e.g. the

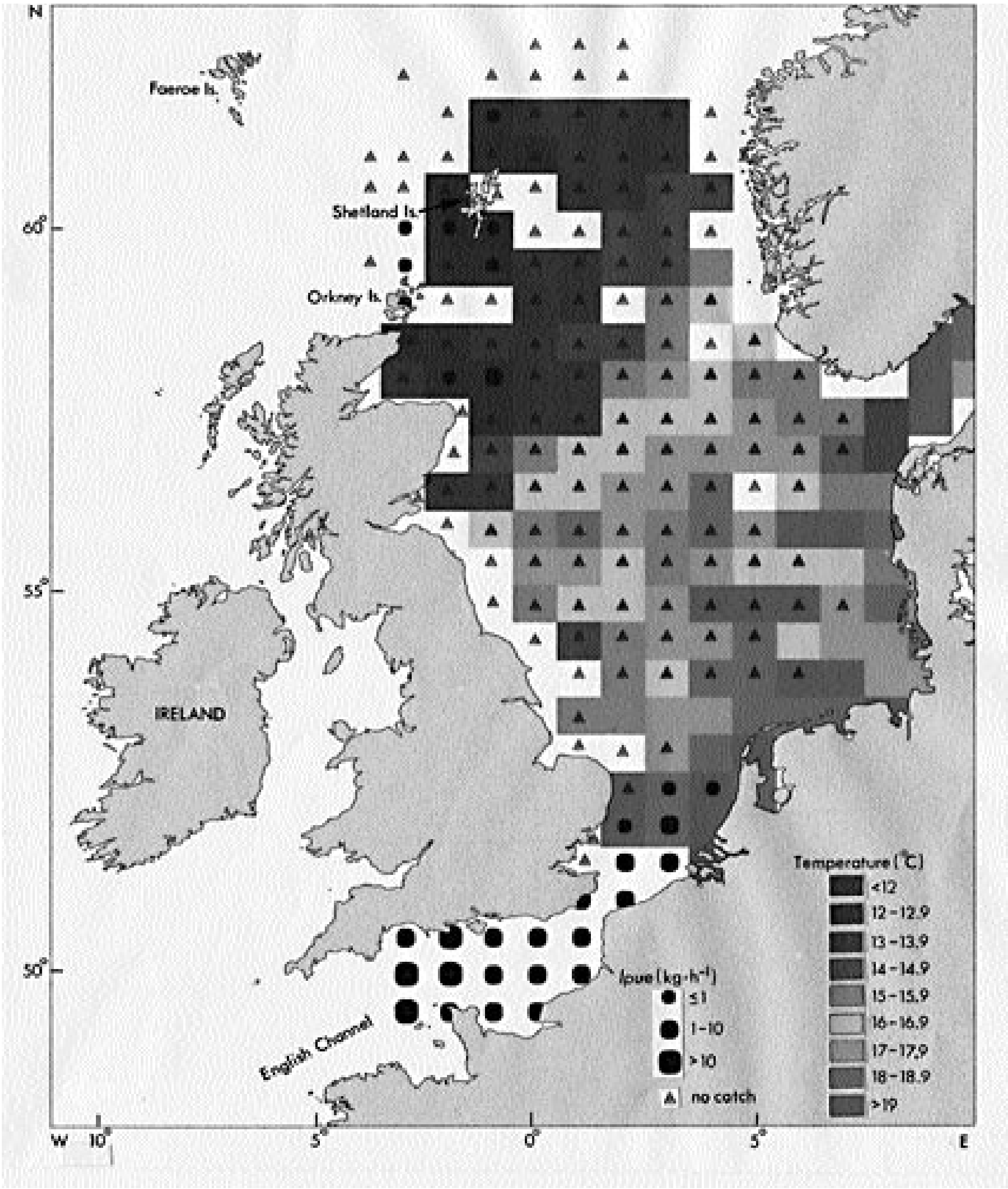

Fig. 5: Squid distribution in relation to surface temperature, August 1994. For a description of the key, see Figure 4. Higher temperatures were observed in the south of the region during summer. Squid are almost absent from the North Sea but remain in the vicinity of the English Channel, in areas of higher temperature

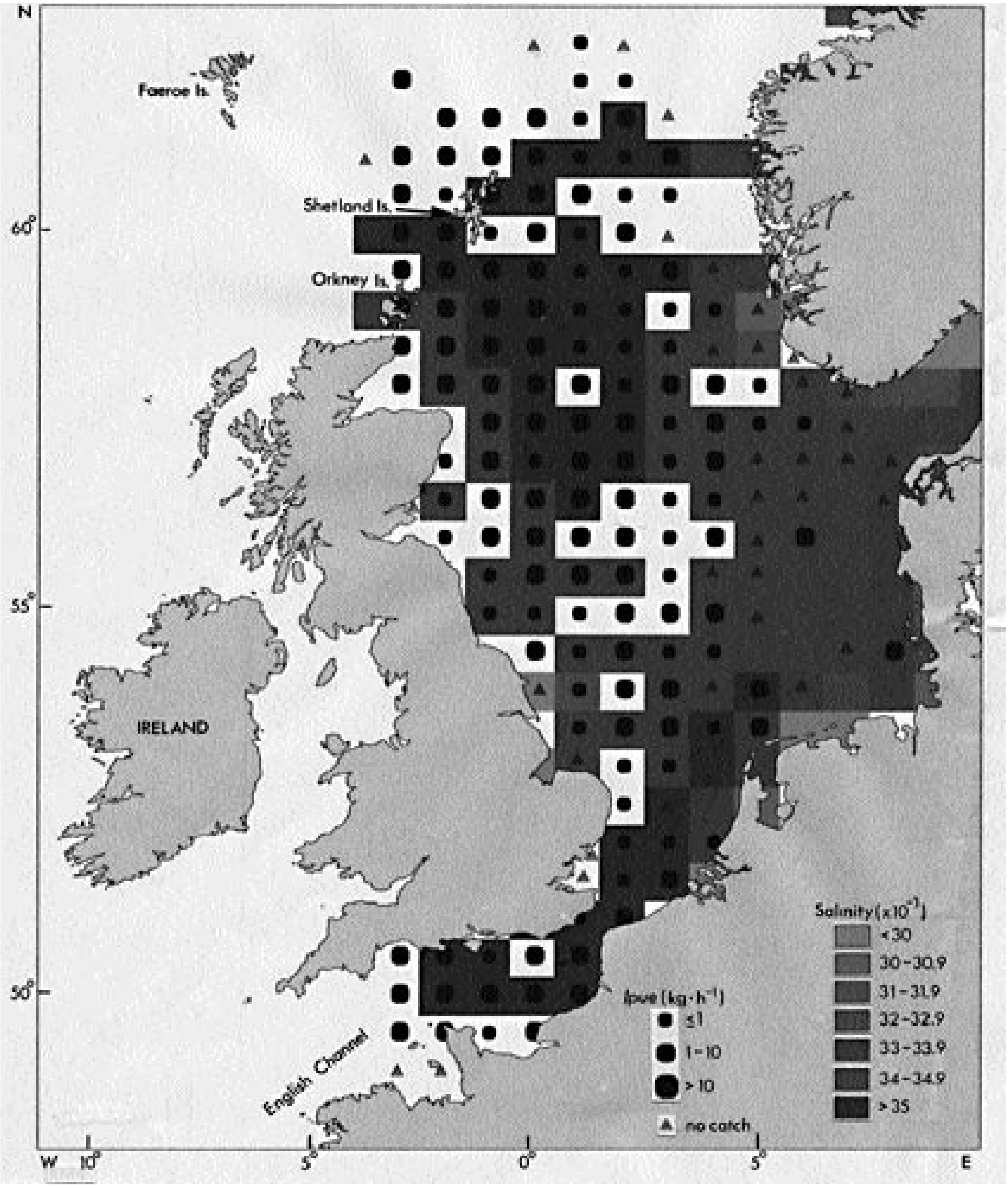

Fig. 6: Squid distribution in relation to surface salinity, November 1990. Higher salinity (shaded dark blue) is seen in both the north and the south of the North Sea, and squid are abundant and widely distributed throughout the whole area, particularly close to the U.K. coast and in waters of salinities of at least 34×10^{-3}

Table II: Results of correlation analysis. For each month, Spearman's rank correlation coefficients were calculated between overall *lpue* and each of the four oceanographic variables. Coefficients (r_s), sample sizes (n) and probabilities (p) are tabulated. Probabilities are based on a two-tailed test, * indicating $p < 0.05$ and ** indicating $p < 0.01$

Month	Results of correlation analysis											
	Surface temperature			Bottom temperature			Surface salinity			Bottom salinity		
	r_s	n	p	r_s	n	p	r_s	n	p	r_s	n	p
January 1989	0.410	85	**	0.425	73	**	0.333	79	**	0.355	71	**
1990	0.044	47		0.330	43	*	0.345	58	**	0.099	43	
1991	0.548	102	**	0.520	98	**	0.448	97	**	0.391	97	**
1992	0.315	70	**	0.457	67	**	0.499	83	**	0.378	69	**
1993	0.458	56	**	0.506	54	**	0.511	52	**	0.412	49	**
1994	0.224	62		0.285	54	*	0.135	70		−0.039	54	
February 1989	0.480	114	**	0.520	111	**	0.305	122	**	0.273	115	**
1990	0.225	97	*	0.363	104	**	0.314	97	**	0.262	104	**
1991	0.626	124	**	0.620	120	**	0.536	138	**	0.442	124	**
1992	0.487	127	**	0.501	127	**	0.439	128	**	0.445	128	**
1993	0.679	130	**	0.721	129	**	0.454	125	**	0.431	119	**
1994	0.563	91	**	0.453	89	**	0.338	93	**	0.236	89	*
March 1989	0.433	39	**	0.327	36		−0.015	40		0.094	37	
1990	0.588	10		0.655	6		−0.008	12		−0.393	6	
1991	0.655	16		0.000	4		0.740	30	**	0.000	4	
1992	−0.072	16		0.535	7		0.029	16		−0.445	7	
1993	0.167	20		0.247	8		0.059	22		0.083	8	
1994	−0.035	30		0.028	44		0.014	35		−0.121	47	
April 1989	0.500	56	**	0.465	53	**	−0.051	56		0.010	50	
1990	0.014	75		0.026	69		0.176	76		0.102	69	
1991	0.392	44	**	0.088	27		0.421	54	**	0.484	27	*
1992	0.043	80		0.201	63		0.108	81		0.064	63	
1993	0.319	66	**	0.390	64	**	0.154	69		0.371	65	**
1994	0.372	71	**	0.349	68	**	0.199	71		0.334	68	**
May 1989	0.283	65	*	0.377	60	**	0.205	65		0.255	61	*
1990	0.424	48	**	0.204	43		0.130	49		0.032	43	
1991	0.113	70		0.311	62	*	0.254	83	**	0.183	62	
1992	0.013	63		0.088	52		0.221	63		0.117	52	
1993	0.075	68		0.441	63	**	0.019	68		−0.081	63	
1994	0.356	73	**	0.336	66	**	−0.067	72		−0.122	65	
June 1989	−0.201	102	*	0.248	98	*	0.361	124	**	0.033	98	
1990	−0.195	76		0.502	74	**	0.425	92	**	0.131	82	
1991	−0.244	84	*	0.361	29		0.435	80	**	0.258	35	
1992	−0.460	80	**	0.444	64	**	0.249	92	*	0.182	64	
1993	−0.269	51		0.252	37		0.379	71	**	0.199	45	
1994	0.188	29		0.187	12		0.393	32	*	0.343	12	
July 1989	0.070	65		0.075	60		0.362	65	**	0.215	60	
1990	−0.012	74		0.133	63		0.157	75		−0.008	63	
1991	−0.426	49	**	0.166	16		0.546	32	**	0.194	20	
1992	0.435	21		−0.393	12		0.420	44	**	0.043	16	
1993	0.137	65		0.240	45		0.244	85	*	−0.397	48	**
1994	0.200	71		0.103	47		0.071	72		0.074	50	
August 1989	0.299	43	*	0.494	38	**	−0.027	48		−0.105	38	
1990	0.432	56	**	0.506	47	**	0.523	57	**	0.351	44	*
1991	0.290	21		0.000	11		0.424	21		0.000	11	
1992	−0.196	65		0.165	62		0.334	81	**	0.114	71	
1993	0.062	85		0.434	81	**	−0.051	102		−0.291	80	*
1994	−0.090	112		0.330	111	**	−0.023	124		−0.157	114	

(Continued)

Table II: (*continued*)

Month	Results of correlation analysis											
	Surface temperature			Bottom temperature			Surface salinity			Bottom salinity		
	r_s	n	p	r_s	n	p	r_s	n	p	r_s	n	p
September 1989	0.048	47		−0.076	40		0.551	52	**	0.372	40	*
1990	0.051	70		0.203	67		0.253	78	*	0.143	67	
1991	0.021	29		−0.175	19		0.235	33		0.269	21	
1992	−0.074	62		0.376	58	*	0.160	64		0.027	59	
1993	0.210	72		0.601	68	**	−0.015	73		−0.330	68	**
1994	0.200	46		0.283	46		−0.207	50		−0.155	46	
October 1989	0.235	54		0.168	42		0.157	54		0.230	42	
1990	0.262	31		0.465	23	*	0.383	34	*	−0.122	23	
1991	0.265	68	*	0.013	30		0.020	55		−0.181	42	
1992	0.345	77	**	0.531	73	**	−0.074	80		−0.401	76	**
1993	0.395	104	**	0.523	99	**	0.111	105		−0.259	100	*
1994	0.500	103	**	0.470	99	**	0.166	103		0.246	99	*
November 1989	0.285	89	**	0.303	79	**	0.037	106		−0.171	87	
1990	0.167	111		0.155	85		0.345	116	**	0.136	90	
1991	0.077	78		0.302	37		0.133	64		0.108	60	
1992	0.052	89		0.308	84	**	0.464	91	**	0.049	84	
1993	0.383	79	**	0.318	71	**	0.007	99		−0.241	78	*
1994	0.275	114	**	0.302	109	**	0.185	114		−0.036	109	
December 1989	0.236	60		0.300	53	*	−0.001	60		−0.003	53	
1990	−0.459	15		−0.274	9		0.564	32	**	0.616	26	**
1991	0.305	35		0.204	7		0.411	18		0.612	7	
1992	−0.099	36		0.069	27		0.421	44	**	0.142	27	
1993	0.504	51	**	0.441	47	**	0.200	65		0.299	49	*
1994	0.318	22		0.418	15		−0.013	38		−0.100	19	

influx of North Atlantic water. As loliginid squid are more commonly taken by demersal gear (Pierce *et al.* 1994a), bottom conditions might be expected to have a greater direct physiological influence on squid than conditions at the surface.

Squid were usually markedly more abundant in warmer than in colder areas, as reflected by the high proportion of months in which *lpue* and temperature were positively correlated. *Lpue* was also positively associated with surface and bottom salinity. Positive correlations between squid and oceanographic parameters (temperature and salinity) were most common during January and February, which corresponds with the breeding phase of the life cycle (e.g. Pierce *et al.* 1994a, b). This period is also characterized by temperature being generally higher in the northern North Sea than in the south, whereas temperatures were often higher in the south during summer and autumn. Significant negative correlations between *lpue* and one or more oceanographic parameters were seen in only four months (surface temperature) and six months (bottom salinity). This is slightly more frequent than expected by chance alone. Surface temperature was negatively correlated with *lpue* only in summer. It might be speculated that, in those months, temperature was never low enough to be limiting, but they are not the warmest months. Most negative correlations with bottom salinity were in one year of the study, 1993, which is apparently anomalous.

Relationships between oceanographic parameters and squid distribution and abundance have been widely reported in the literature. Some studies identify putative physiological limits whereas most report correlations, either on a temporal or spatial basis, between abundance and one or more physical variables. The underlying causal relationship is usually unknown, but several types of explanation may be suggested: physiological tolerance limits; effects on growth and mortality, possibly mediated by changes in prey abundance; adaptive behavioural preferences; effects on catchability, e.g. increased metabolic activity at higher temperatures; indirect relationships related to changes in current systems.

In February 1993, *lpue* was very low or zero at temperatures below 6°C. Several authors have proposed that squid distribution is limited by temper-

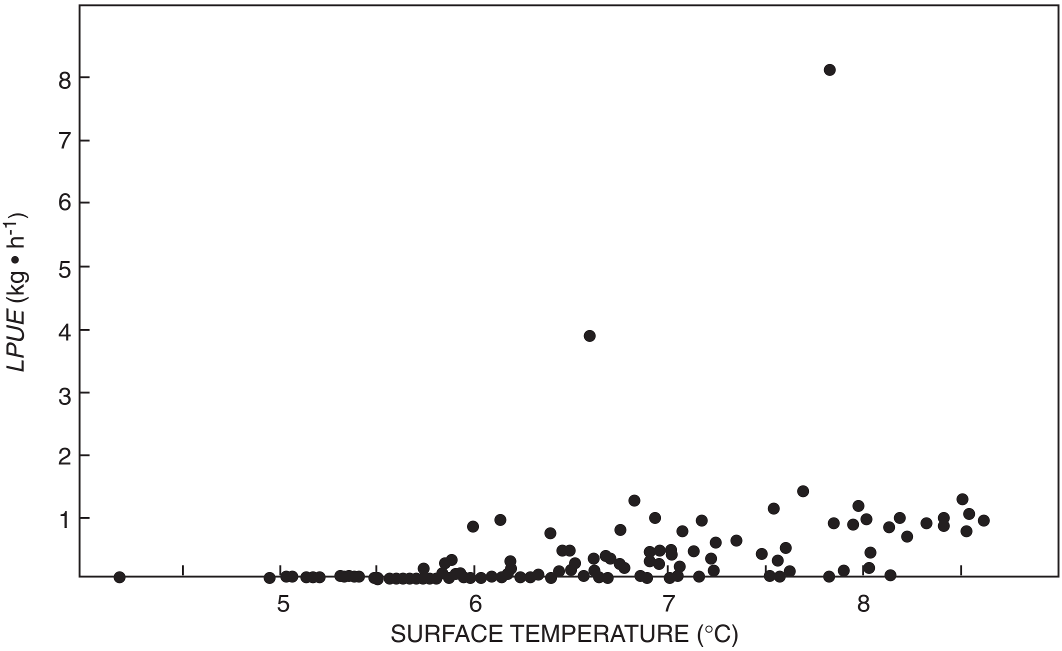

Fig. 7: Use of a linear regression to predict *lpue* of *Loligo* spp. from surface temperature. Non-zero *lpue* values are more common at temperatures >6°C

ature. Augustyn (1990) suggests that the majority of loliginids prefer a temperature range of 12 – 20°C, although limits undoubtedly vary between species and between areas. Holme (1974) found *Loligo forbesi* to be present in the western English Channel in areas of relatively warmer water, with the distribution apparently limited by temperatures <8.5°C. Pierce *et al*. (1998) found that *Loligo* were absent from survey catches from the North Sea in February below a lower limit of approximately 7°C. Augustyn (1991) suggested that *Loligo vulgaris reynaudii* off the west coast of South Africa are limited by sea-bed temperatures of 8°C, and Summers (1969) reached a similar conclusion for *Loligo pealei* in the mid-Atlantic bight.

Temperature tolerance and preferences change through the life cycle. Temperature may be particularly important during the paralarval and juvenile stages, when growth is characterized as "exponential" and is highly temperature-dependent (Forsythe 1993). Slow early growth may result in delayed maturation (Worms 1983). O'Dor (1992) suggests that squid commonly seek warm water to spawn. Southward (1960) proposed that *L. forbesi* spawn in water of 9 – 11°C. In the present study, the strongest link between abundance and temperature coincided with the breeding season (especially January and February).

Although it seems unlikely that variation in salinity, within the normal range found in seawater, should have any direct biological consequence for cephalopods, variation in salinity has been cited as a factor influencing the distribution of a number of species. Pierce *et al*. (1998) demonstrated that, after the effect of bottom temperature had been taken into account, there was still a (positive) relationship between salinity and survey abundance of *Loligo* in the North Sea, with abundance increasing sharply at bottom salinity $>35.2 \times 10^{-3}$. Augustyn (1991) showed the distribution of *Loligo vulgaris reynaudii* off the west coast of South Africa to be correlated with bottom salinity, although the distribution was more strongly related to bottom temperature. Salinity has also been shown to influence the distribution of *Illex illecebrosus* in the North-West Atlantic (Coelho 1985) and *Lolliguncula brevis*, a euryhaline species able to tolerate a wide range of salinities (Laughlin and Livingston 1982).

Several studies have demonstrated the influence of the strength of inflow of (warmer) Atlantic water on interannual (as opposed to spatial) variation in marine species. For example, Bailey and Steele (1992) showed that herring recruitment in the North Sea is dependent on oceanic inflow. Water flows into the northern North Sea from the North-East Atlantic via three persistent, stable inflows (see Turrell 1992) and enters the southern North Sea via the English Channel. Year-to-year variability in the inflow of Atlantic water may be a major influence on squid spatial distribution, especially if migratory routes are limited to a relatively narrow range of temperature and salinity (Summers 1969, Holme 1974, Laughlin and Livingston 1982). The influence of the North Atlantic Drift may also be important on the west coast of Scotland, for instance in transporting squid from Irish waters.

If squid movement into the North Sea corresponds with the inflow of North Atlantic water, with higher temperature and salinity, the correlation between squid *lpue* and temperature/salinity may be an incidental consequence. Regardless of the underlying causal relationships, empirical relationships between oceanographic variables and distribution/abundance offer potential indices of the availability of squid to fisheries (Fogarty 1989, Pierce and Guerra 1994).

The ultimate goal is to use marine GIS in fishery management. Further work will include the use of additional physical, oceanographic and biological datasets and the incorporation of statistical techniques such as geostatistics/spatial statistics (Cressie 1991, Cressie and Ver Hoef 1993) and General Additive Models (GAMs)/regression trees (e.g. Maravelias 1997, Pierce *et al.* 1998) to examine the spatial structure of the data and the complex relationships between fishery and environmental data respectively.

ACKNOWLEDGEMENTS

Financial support was provided by the Aberdeen University Research Committee and the EC (Contracts AIR 1 CT92 0573 and FAIR CT96 1520). FRS Marine Laboratory in Aberdeen supplied fishery data and the digitized base map, and mediated acquisition of English fishery data. Dr J-P. Robin of the University of Caen provided French fishery data, with the permission of IFREMER. M. Gorman, J. Thom, S. Northridge and R. Donald assisted with the use of ARC/INFO and some useful discussions. G. Hopwood and H. Dooley at ICES, Denmark, supplied oceanographic data to a range of specifications and we particularly valued their patience in helping to solve technical problems with data transfer! Prof. P. R. Boyle of the University of Aberdeen, Dr C. J. Augustyn (Sea Fisheries, Cape Town) and an anonymous reviewer provided helpful comments on the manuscript.

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