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Spatial and temporal patterns of cuttlefish (*Sepia officinalis*) abundance and environmental influences – a case study using trawl fishery data in French Atlantic coastal, English Channel, and adjacent waters

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The spatial and temporal distribution patterns of cuttlefish abundance and the relationships between cuttlefish abundance and environmental variables in the French Atlantic coast, the English Channel, and adjacent waters were studied using both geographical information system and statistical methods. Cuttlefish have a clear general annual migration pattern, consistently occurring in broadly the same areas in different years. The strength of the Atlantic currents into the west part of the English Channel and the south part of the Celtic Sea may be the dominant influence on the timing of cuttlefish migration to these areas. Local abundance shows a positive correlation with SST, although it is difficult to determine if this reflects any causal link. Cuttlefish expand their distribution further north in the spawning season in warm years and shift south in cool years. The centre of high abundance in offshore deep water shifts north in warm winters and south in cool winters.

Keywords: cuttlefish, environment, GIS.

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Introduction

Cuttlefish are an important cephalopod fishery resource in the Northeast Atlantic waters. In this area, over 80% of cuttlefish landings are taken by France and the UK, and catches are mainly located in the English Channel and adjacent waters, the French Atlantic coast, and the Bay of Biscay (Denis and Robin, 2001). In the English Channel, French Atlantic coast, and adjacent waters, cuttlefish landings were dominated by the common cuttlefish *Sepia officinalis*, although other species such as *Sepia elegans* occur, the landings records do not distinguish between them (Dunn, 1999; Denis and Robin, 2001). Over the period 1989–1998, cuttlefish comprised approximately 2.7% by weight of all French fishery landings (IFREMER, unpublished data).

Cuttlefish have a short life span of around 2 years. The spawning season is from early spring to mid-summer, followed by mass adult mortality, and hatching follows from mid-summer to autumn (Boletzky, 1983; Le Goff and Daguzan, 1991; Dunn, 1999). Previous studies of the spatial and temporal patterns of cuttlefish abundance show that there is an annual migration in this area, and large inter-annual fluctuations in landings (Boucaud-Camou and Boismery, 1991; Dunn, 1999; Denis and Robin, 2001). In early spring, adult cuttlefish concentrate in coastal spawning grounds, mainly along both sides of the English Channel and on the French Atlantic coast. In late autumn, the juveniles migrate from inshore nursery grounds to deeper waters in the west part of the English Channel and further west, and to offshore deep waters off the north part of French Atlantic coast, where they stay for the winter.

Given the short life span, large inter-annual fluctuations in landings, and the regular annual migration cycle, it is expected that marine environment conditions have an important impact on cuttlefish recruitment and distribution (Boletzky, 1983). This paper reports a new study, using historical data, on the spatial and temporal patterns of cuttlefish abundance, in which we attempt to (a) provide a more detailed picture of intra- and inter-annual variations in cuttlefish distribution and abundance and (b) quantify sea surface temperature (SST) influences on cuttlefish distribution and migration in the French Atlantic coast, the English Channel, and adjacent waters. The study area is located within parts of the International Council for the Exploration of the Sea (ICES) fishery Subdivisions 7 and 8, as shown in Figure 1, from which more than 80% of UK and French cuttlefish landings are taken.

Data and methods

Data on fishery landings of cuttlefish at English (including Welsh) and French ports from 1989 to 1998 were used. English cuttlefish landings data were provided by the Centre for the Environment, Fisheries and Aquaculture Science, Lowestoft (CEFAS). French cuttlefish landings data were provided by Centre Administratif des Affaires Maritimes St Malo (CAAM). French landings data prior to 1989 are not available at the same resolution, hence we start the data series in 1989. Figure 2 shows monthly total cuttlefish landings by UK and French trawls from 1989 to 1998.

Fishery landings per unit effort (LPUE, $kg\,h^{-1}$) by ICES statistical rectangles (1° longitude by 0.5° latitude) were used as a cuttlefish abundance index in the analysis. LPUE was calculated by summing the catches from all demersal trawls and dividing by the sum of fishing hours. Demersal trawl LPUE was chosen as the abundance index since indices for individual gear-types are not easily comparable between those of UK and France, due to differences in classifications of fishing activity.

Due to lack of the data, boat power and gear differences (within the "demersal trawl" category) were not considered in the calculation of LPUE. However, comparisons for squid *Loligo* spp. between LPUE calculated from fishery data in the same way and CPUE (catch per unit effort, $kg\,h^{-1}$) derived from trawl survey data suggest that trawl LPUE is an adequate abundance index (Pierce *et al.*, 1998; Robin *et al.*, 1998).

Reynolds SST data were downloaded from the National Center for Atmospheric Research, USA (NCAR) website. The data are monthly average model results from remotely sensed data, survey temperature data, and sea ice distribution, with a spatial resolution of 1° longitude by 1° latitude (Reynolds and Smith, 1994). The data were re-sampled to the spatial resolution of 1° longitude by

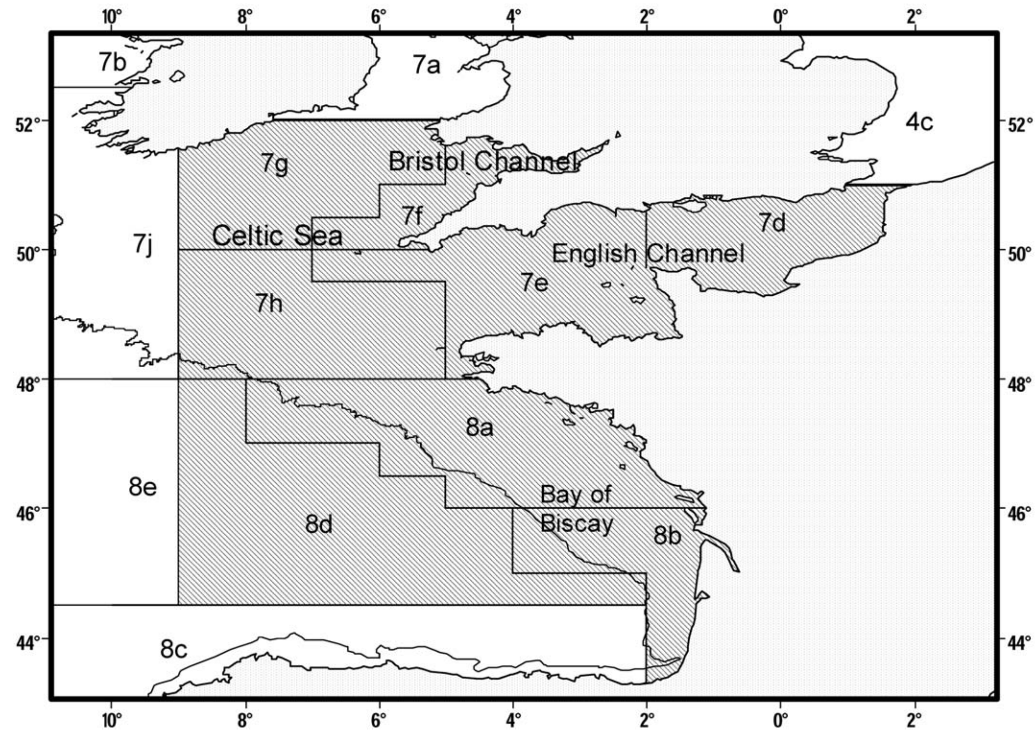

Figure 1. The study area (shadowed) that includes the English Channel, Celtic Sea, and the French West coast. It covers ICES Subdivisions 7d, 7e, 7g, and 7h, and ICES Subdivisions 8a, 8b, 8c, and 8d.

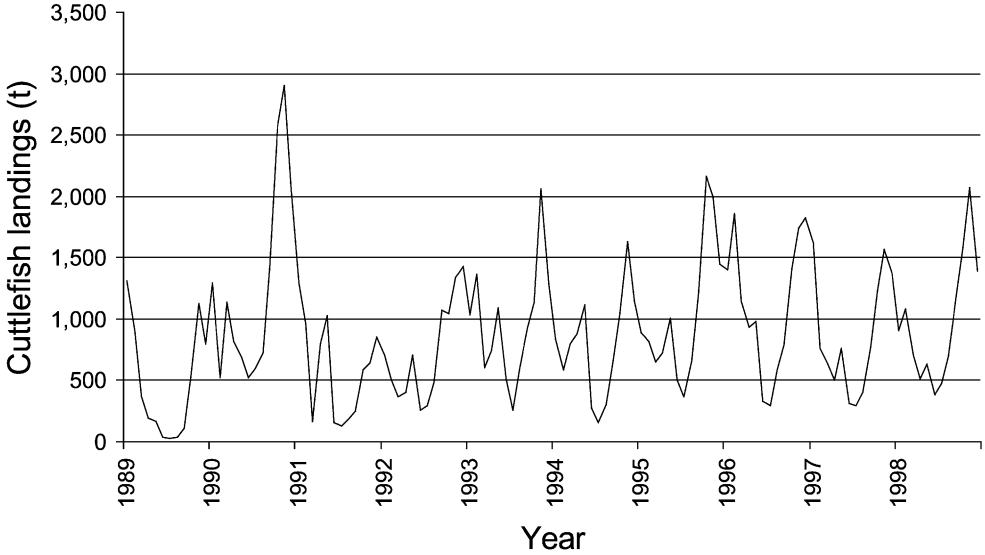

Figure 2. Monthly total cuttlefish landings by UK and French trawls in the study area from 1989 to 1998.

0.5° latitude, the same as the ICES statistical rectangles. The ICES provided sea bottom temperature (SBT) data. The SBT data are monthly averages by ICES statistical rectangles, but do not cover every ICES statistical square or every month, reflecting the opportunistic nature of data collection.

Sea depth data were downloaded from the website of the National Geographical Data Center, National Oceanic and Atmospheric Administration (NOAA, USA). The original data are gridded with 5′ by 5′ resolution. The mean depth of each single ICES rectangle was calculated and used in the analysis.

A geographical information system (GIS) was developed and used for visual analyses (Pierce *et al.*, 2001). It is based on Environmental Systems Research Institute, Inc (ESRI) GIS software ArcView®. Fishery and environmental data were imported from the Access database, and integrated in the GIS as shapefiles. Time-series maps of cuttlefish abundance with background of SST for the same time period or previous (time-lagged) period were created to visually analyse and depict spatial and temporal patterns of cuttlefish abundance, and the changes in abundance in relation to the changes in SST.

The spatial relationships between cuttlefish abundance and SST were calculated using Spearman's rank correlation and single month records of abundance, SST, from 1989 to 1998. Data for each ICES rectangle were treated as independent data points.

Different locations may experience different mechanisms of environmental change in the study area, at least, the spatial pattern of SST on the French Atlantic Coast is different from that in the other areas. Therefore, we divided the area into two subareas – one is the French Atlantic coast area in ICES Subdivision 8, the other is the English Channel and adjacent area in ICES Subdivision 7 (Figure 1) – and carried out statistical analysis for both subareas separately.

Results

Spatial and temporal patterns of cuttlefish abundance

Figure 3 displays the long-term monthly average LPUE. In this figure, long-term average monthly LPUE is displayed as a grid (interval $= 5\,\mathrm{kg\,h^{-1}}$) with a background of long-term monthly average SST (isotherms, interval $= 0.5°\mathrm{C}$). This illustrates the general spatial and temporal distribution patterns of cuttlefish abundance. The shift of high abundance centres in successive months shows the migration path. Cuttlefish concentrate in the west part of the English Channel during October to December, apparently move offshore in January to March, and are found at low densities through until September.

Time-series maps of single monthly average LPUE in each year from 1989 to 1998 show the spatial distribution of cuttlefish abundance in a single month and the month-to-month changes during 1989–1998. As examples, Figures 4 and 5 show LPUE in each single month in 1990 and 1991, respectively, representing a year of high LPUE (1990) and a year of low LPUE (1991) in this area. It can be seen that the seasonal pattern of distribution is broadly similar in these 2 years, although the density of cuttlefish in the English Channel was much lower in the second half of 1991 than in the second half of 1990.

On the French Atlantic coast, a centre of high LPUE appears in late autumn and winter. The high LPUE area expands from September, covering the largest area and

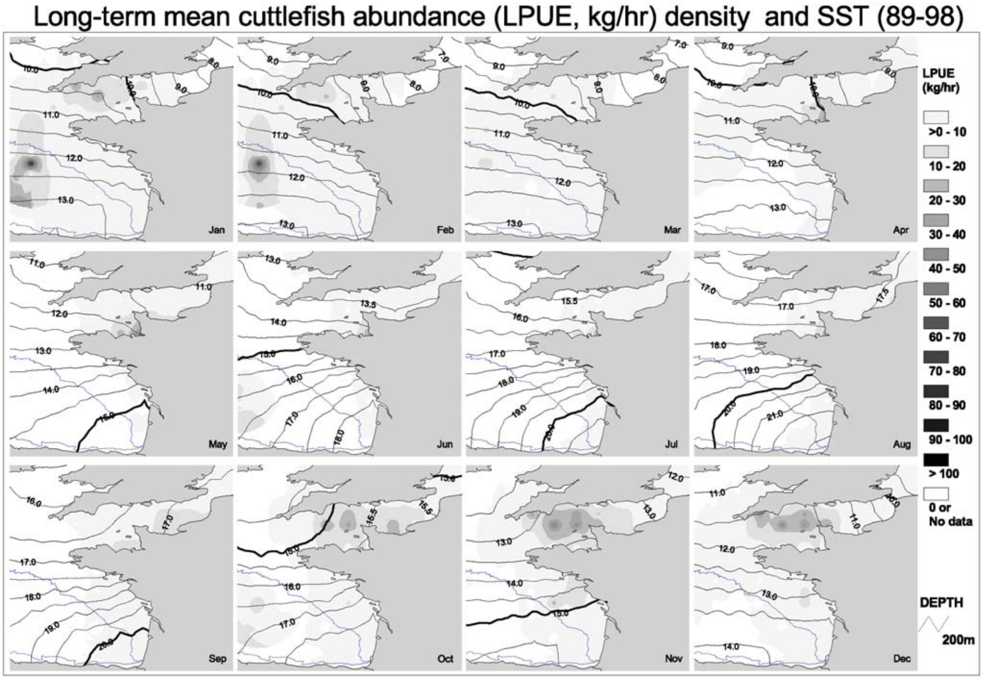

Figure 3. Long-term monthly average cuttlefish abundance was converted from point format into grid format and displayed with intervals of 5 kg h^{-1}, with a background of long-term monthly average SST, which was converted from point data into isotherms with intervals of 0.5°C.

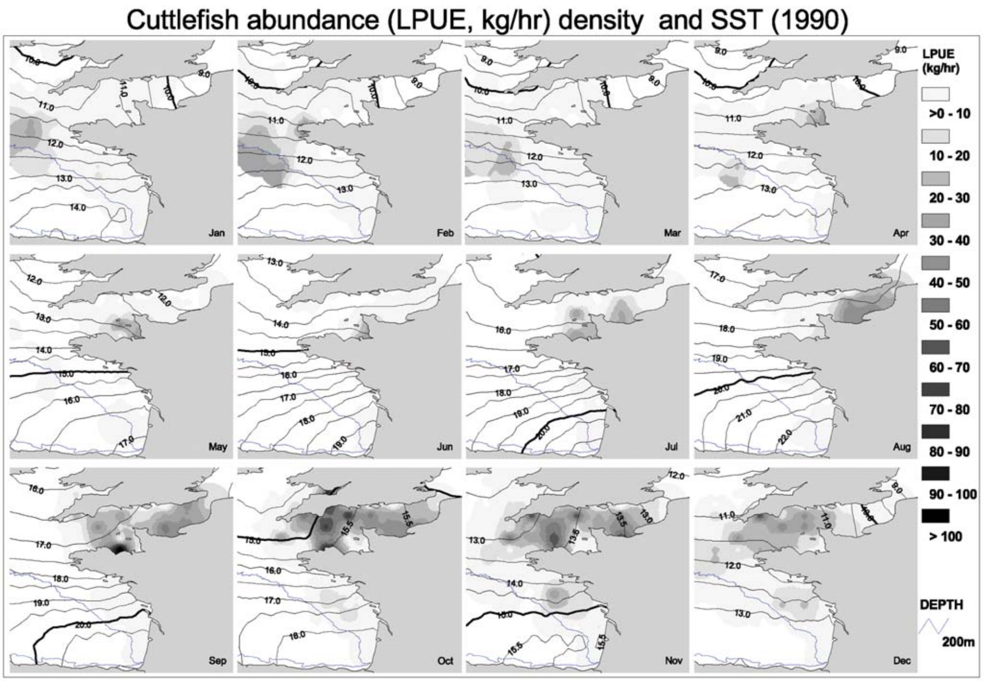

Figure 4. Monthly cuttlefish abundance in 1990 was converted from point format into grid format and displayed with intervals of 5 kg h^{-1}, with a background of SST, which was converted from point data into isotherms with intervals of 0.5°C.

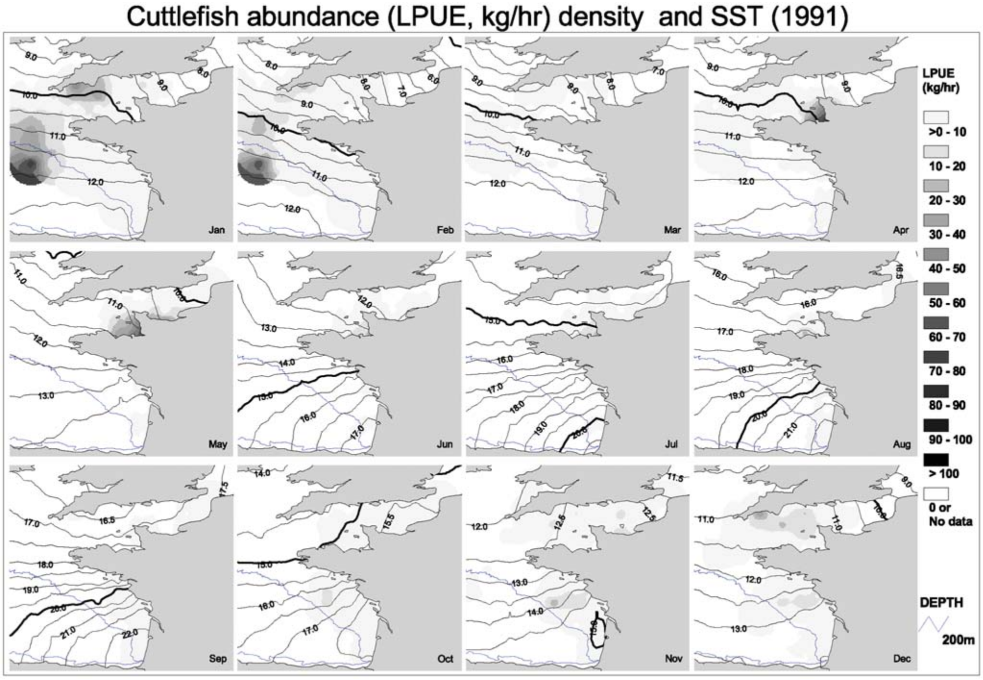

Figure 5. Monthly cuttlefish abundance in 1991 was converted from point format into grid format and displayed with intervals of 5 kg h^{-1}, with a background of SST, which was converted from point data into isotherms with intervals of 0.5°C.

reaching highest abundance in November. The centre shrinks from December, and disappears from March to April. In the English Channel and adjacent waters, cuttlefish show an annual north–south and west–east shift in distribution. During the spawning season from early spring to mid-autumn, cuttlefish concentrate in the shallow areas of both sides of the English Channel. From late autumn, the juveniles migrate from inshore nursery grounds to deeper waters in the west and middle part of the English Channel. From November, cuttlefish move further west, to the offshore deep waters off the north part of the French Atlantic coast, and stay there until March.

The influence of SST, depth, and oceanic circulation on cuttlefish abundance and distribution

SST data displayed as background in the time-series maps (e.g., Figures 3–5) show that, from October to May, SST varies spatially mainly in the east–west direction in the English Channel. At the west end of the English Channel and further west, SST spatial variation in SST is mainly in the north–south direction. During this period, the high cuttlefish LPUE centre is always located in a high temperature zone in the English Channel or further west in deep waters (Figures 3–5).

The spatial variation in SST along the Bay of Biscay shows a different pattern compared with that in the English Channel. During November–April, there is a consistent spatial trend in SST – SST decreases from south to north. The SST in the inshore area along the French Atlantic coast is lower than the SST in the offshore area at the same latitude. This may reflect the influence of cold weather on the European Continent on the inshore area and the influence of Atlantic currents on the offshore area. During May–October, as shown in Figures 3–5, there is a consistent

Table 1. Results of temporal correlation (ρ) between monthly total cuttlefish landings over the study area and the monthly mean SST in the middle of English Channel between 2.5°W and 0.5°W longitude from 1989 to 1998 (sample size is 10), using Spearman's rank correlation method. Significant correlations ($p < 0.05$) are indicated in bold.

		July	August	September	October	November	December
SST in April	ρ	0.58	0.72	0.58	0.63	0.65	0.48
	p-Value	0.10	0.05	0.10	0.08	0.07	0.18
SST in May	ρ	0.45	**0.83**	0.62	0.68	0.58	0.50
	p-Value	0.21	0.02	0.09	0.06	0.10	0.16
SST in June	ρ	0.38	0.72	0.58	0.70	0.38	0.42
	p-Value	0.29	0.05	0.10	0.05	0.29	0.25

Table 2. Results of spatial correlation (ρ) between cuttlefish LPUE and SST, using Spearman's rank correlation method for (a) the whole study area, (b) the area in ICES Subdivision 7, and (c) the area in ICES Subdivision 8. Single month LPUE and SST from 1989 to 1997 for single ICES rectangles were used in the calculation. n = Sample size. Significant correlations ($p < 0.05$) are indicated in bold.

		January	February	March	April	May	June	July	August	September	October	November	December
Whole area	ρ	**0.36**	**0.39**	**0.45**	**0.13**	0.01	**0.13**	**0.19**	**0.22**	**0.25**	**0.27**	**0.22**	**0.10**
	p-Value	0	0	0	0	0.70	0	0	0	0	0	0	0
	n	909	875	897	898	898	876	866	**878**	**892**	**908**	**910**	**909**
ICES Subdivision 7	ρ	**0.36**	**0.39**	**0.46**	**0.24**	−0.06	−0.06	−0.05	**0.09**	**0.25**	**0.39**	**0.31**	**0.17**
	p-Value	0	0	0	0	0.14	0.12	0.21	0.03	0	0	0	0
	n	621	600	605	614	612	603	597	606	614	622	625	615
ICES Subdivision 8	ρ	0.07	−0.02	0.04	0.01	**0.35**	**0.50**	**0.52**	**0.49**	**0.26**	**0.23**	**0.14**	−0.02
	p-Value	0.25	0.74	0.49	0.92	0	0	0	0	0	0	0.02	0.76
	n	288	275	292	284	286	273	269	272	278	286	285	294

spatial trend in SST – SST decreases in a north-westerly direction from the southeast coastal area of the Bay of Biscay. This suggests that the European Continent has great influence on the SST in the Bay of Biscay. The high cuttlefish LPUE centre is located in the French Atlantic coast in winter, disappears in summer, and does not show any clear relationship with SST.

Both visual analyses based on time-series maps and correlation results show that, in general, SST seems to be associated with cuttlefish abundance. For example, in 1990, SST in the months from April to June was higher than the long-term mean (Figures 3 and 4), and the LPUE in the following autumn and winter was higher than the long-term mean LPUE. In contrast, in 1991, SST in the months from April to June was lower than the long-term mean (Figures 3 and 5), and the LPUE in the following autumn and winter was lower than the long-term mean LPUE. The temporal correlations between monthly mean SST in the middle area of the English Channel in the months from April to June and the monthly total landings from July to December are overwhelmingly positive (Table 1).

The spatial correlation between LPUE and SST at the single ICES rectangle scale also shows that, in the English Channel and adjacent waters, the correlation between LPUE and SST is positive and significant from August to April (Table 2). During this period, as shown in Figures 3–6 and as mentioned above, juveniles migrate from inshore nursery grounds to deeper waters in the west part of the

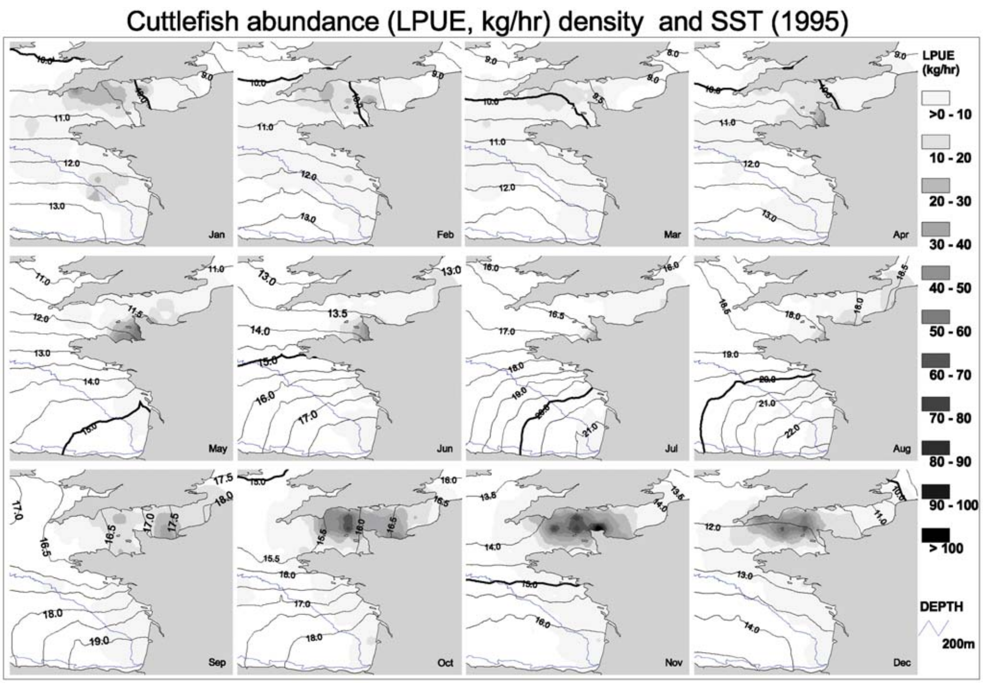

Figure 6. Monthly cuttlefish abundance in 1995 was converted from point format into grid format and displayed with intervals of 5 kg h^{-1}, with a background of SST, which was converted from point data into isotherms with intervals of 0.5°C.

Table 3. Results of correlation (ρ) between cuttlefish LPUE and sea depth, using Spearman's rank correlation method (a) for the whole study area, (b) the area in ICES Subdivision 7, and (c) the area in ICES Subdivision 8. Single month LPUE from 1989 to 1997 for each single ICES rectangle were used in the calculation. n = Sample size. Significant correlations ($p < 0.05$) are indicated in bold.

		January	February	March	April	May	June	July	August	September	October	November	December
Whole area	ρ	**0.27**	**0.34**	**0.27**	**−0.15**	**−0.43**	**−0.47**	**−0.49**	**−0.53**	**−0.54**	**−0.54**	**−0.38**	**−0.18**
	p-Value	0	0	0	0	0	0	0	0	0	0	0	0
	n	909	875	897	898	898	876	866	878	892	908	910	909
ICES Subdivision 7	ρ	**0.35**	**0.42**	**0.33**	**−0.12**	**−0.42**	**−0.48**	**−0.53**	**−0.59**	**−0.57**	**−0.55**	**−0.31**	−0.02
	p-Value	0	0	0	0	0	0	0	0	0	0	0	0.65
	n	621	600	605	614	612	603	597	606	614	622	625	615
ICES Subdivision 8	ρ	−0.05	0.01	**−0.12**	**−0.28**	**−0.58**	**−0.68**	**−0.72**	**−0.72**	**−0.68**	**−0.64**	**−0.66**	**−0.61**
	p-Value	0.39	0.82	0.03	0	0	0	0	0	0	0	0	0
	n	288	275	292	284	286	273	269	272	278	286	285	294

English Channel and offshore deep waters, and stay there for winter, where SST is higher than in both west and east parts of the English Channel and inshore areas. In ICES Subdivision 8, the spatial correlation between LPUE and SST is significant and positive from May to November (Table 2). This is consistent with cuttlefish concentrating in the spawning grounds along the French Atlantic coast and juveniles staying there until early winter. Spatial correlations between cuttlefish abundance and SST over the whole study area are overwhelmingly positive, and significant except in May (Table 2).

Table 3 lists the spatial correlation between cuttlefish abundance and sea depth. In the English Channel and adjacent waters (ICES Subdivision 7), the correlation between cuttlefish abundance and depth is significant and negative from April to November. On the French West coast (ICES Subdivision 8), the correlation between cuttlefish abundance and depth is significant negative from March to December.

Although the spatial distribution pattern of SST cannot fully reflect the water circulation mentioned above, it generally shows the distribution of frontal zones and the near-surface water movement path, which could reflect current strength and the influence of wind. As depicted by the SST isotherms in Figures 3–5, when cold water from the north dominates the south part of the Celtic Sea, cuttlefish stay in the frontal zone area in the west part of the English Channel where SST is higher than further west and further east. When cold water retreats, cuttlefish follow the frontal zone and migrate westwards. In the years, e.g. 1995, in which the Atlantic current was strong, cold water from the north Celtic Sea covered the areas of the south Celtic Sea, the west part of the English Channel, and the north part of the French Atlantic coast. SST in this area was lower than in the middle part of the English Channel (Figure 6), and the frontal zone in the English Channel also shifted further east. As a result, juveniles concentrated in the middle part of the English Channel (Figure 6).

The analysis of the influence of SBT on cuttlefish abundance was not carried out due to the lack of adequate pairs of LPUE and SBT data records. However, as shown in Figure 7, SBT is linearly and positively related to SST in shallow waters (<100 m depth) and the relationship remains generally positive for deeper waters. Therefore, it can be assumed that SBT has similar relationship to cuttlefish abundance as that of SST.

Discussion

Within the study area, spatio-temporal shifts in cuttlefish abundance indicate a clear general annual migration pattern, with cuttlefish seasonally concentrated within

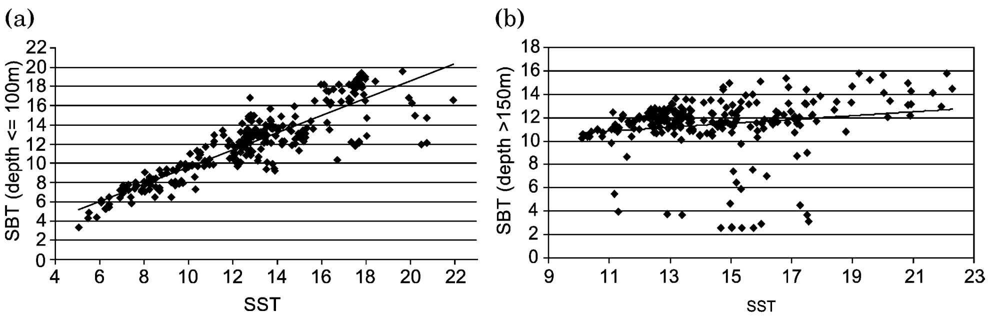

Figure 7. Pair plots of SST and SBT show that SBT is linearly related to SST: (a) in the English Channel area and (b) in the Celtic Sea area with depth >150 m.

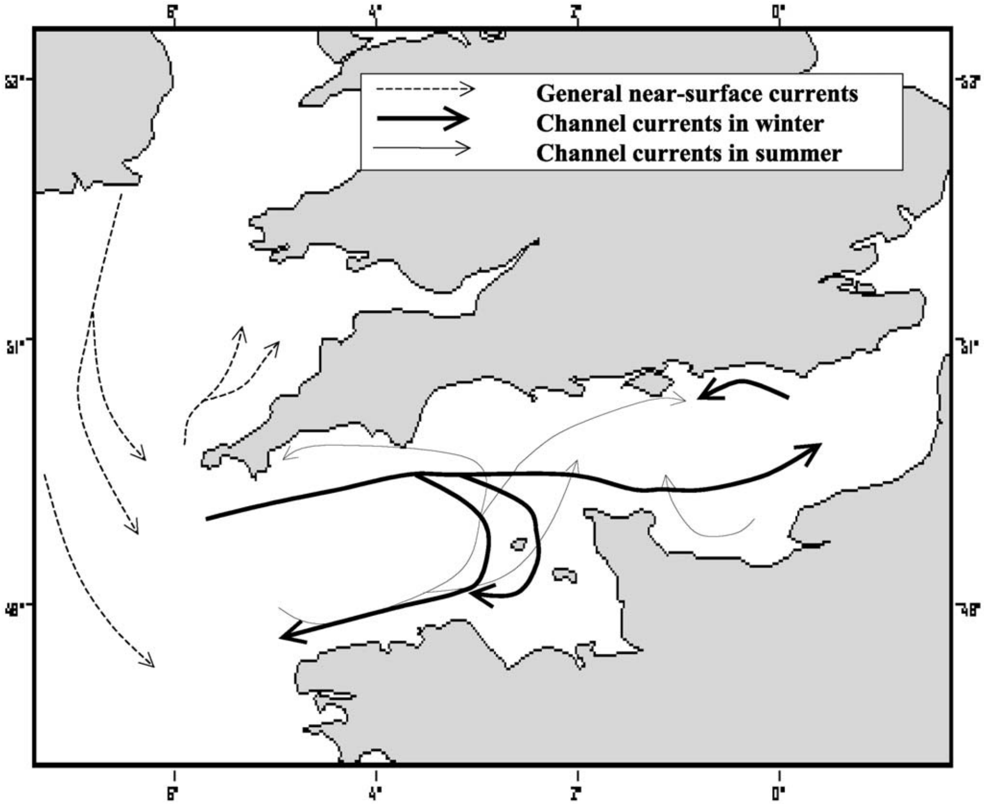

Figure 8. The general near-surface water movement in the English Channel and Celtic Sea (BODC, 1998).

a group of limited areas. In some winters, high LPUE centres in the English Channel and adjacent waters, and in offshore deep waters along the north part of the French Atlantic coast, merge. However, the high abundance centre along the French Atlantic coast in the inshore area seems always to be isolated from the high abundance centre in the offshore deep waters on the north part of the French Atlantic coast. This may indicate that the cuttlefish population in the offshore deep waters of the north part of the French Atlantic coast originates from the English Channel. This is consistent with the findings of Le Goff and Daguzan (1991), Pawson (1995), and Dunn (1999), who suggested that the cuttlefish in the English Channel are probably a separate population from those in the Bay of Biscay.

Relationships between environmental variables and cephalopod abundance and biology have been widely reported in the literature (Jackson and Choat, 1992; Jackson, 1995; Pierce and Boyle, 2003). Sea temperature and currents are likely to be the most important variables influencing cephalopod recruitment (Walsh and Martin, 1986; Turrell, 1992; Moltschaniwskyj and Martúnez, 1998; Waluda *et al.*, 1999). During the spawning and hatching season, high temperature accelerates egg hatching in cephalopods (Boyle, 1999). During the juvenile phase, survivorship plays an important role in determining the number of individuals that can recruit to the adult population (Calow, 1987; Moltschaniwskyj and Martúnez, 1998). Both low temperatures and poor nutrition will reduce growth rates and increase mortality (Van Heukelem, 1979; Berrigan and Charnov, 1994; Moltschaniwskyj and Martúnez, 1998). This may be the reason why high abundance appears after warm temperatures during the hatching season and juvenile phase.

The correlation pattern between cuttlefish abundance and depth is consistent with the annual pattern of movement described for cuttlefish in the English Channel and adjacent waters (ICES Subdivision 7). Any relationship with depth may be an indirect consequence of local abundance being related to SST.

Water circulation at local and meso-scales could have a strong influence on the annual migration of cuttlefish and local abundance in the English Channel and adjacent waters. In the English Channel and adjacent waters, it is reported that, as shown in Figure 8, there is a general near-surface current which flows from the Atlantic, Irish Sea, and the north Celtic Sea to the south part of the Celtic Sea and the west end of the English Channel (BODC (British Oceanographic Data Centre), 1998). In winter, Atlantic water from the Celtic Sea enters the English

Channel along the north side. Part of the water makes a clockwise "U" turn in the west part of the English Channel, and exits the English Channel along the south side (Figure 8). In contrast, during summer, Atlantic water enters the English Channel along the south side, part of it makes an anti-clockwise "U" turn in the west part of the English Channel, and then leaves the English Channel from the north side. The water circulation in the west part of the English Channel may cause water turbulence, and frontal zones in the English Channel and further west. As fish larvae accumulate and primary productivity increases in frontal areas (Koubbi *et al.*, 1991; Brunet *et al.*, 1992; Bruce and Short, 1993; Grioche and Koubbi, 1997), high abundance of many marine resource species, such as squid, cod, whiting, and hake, appeared in frontal zones (Turrell, 1992; Rodhouse *et al.*, 1996; Kimura *et al.*, 1998; Murphy *et al.*, 1998; Cole, 1999; Waluda *et al.*, 1999; Reid, 2001; Zheng *et al.*, 2001). The high mixing and circulation in the frontal zone could enhance food availability for cuttlefish. This may be another reason why cuttlefish stay in the frontal zone area and migrate following the frontal zone westward.

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