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Environmental and stock effects on recruitment variability in the English Channel squid *Loligo forbesi*

Laurence Challier[1], Juliette Royer[1], Graham John Pierce[2], Nick Bailey[3], Beatriz Roel[4] and Jean-Paul Robin[1,a]

[1] Laboratoire de Biologie et Biotechnologies marines, Institut de Biologie Fondamentale et Appliquée, Université de Caen, esplanade de la Paix, 14032 Caen Cedex, France
[2] School of Biological Sciences (Zoology), University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK
[3] Fisheries Research Services, The Marine Laboratory, PO Box 101, Victoria Road, Aberdeen, AB11 9DB, UK
[4] CEFAS, The Centre for Environment, Fisheries and Aquaculture Science, Lowestoft Laboratory, Pakefield Road, Lowestoft, Suffolk NR33 0HT, UK

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Abstract – Recruitment variability is commonly attributed to variation in spawning stock size and environmental variability. Here, the abundance of *Loligo forbesi* in the English Channel was estimated using cohort analysis. Environmental and adult biomass effects on recruitment variation were then tested. A stochastic length-age key was included in the cohort analysis, considering inter-individual variability in age at length. The number of recruits and parental stock biomass per monthly age-class were computed for a series of 13 fishing seasons (1989-2002). Recruitment was examined in relation to adult biomass and environmental parameters (sea surface temperature, SST, and the North Atlantic Oscillation, NAO) at the time of hatching. Recruits were approximately 7 months old and recruitment for each annual cohort occurred between April and August. Squid bigger than the length at maturity were assumed to be spawners. In the spawning season (September December), spawners were 11–13 months old. Parametric stock-recruitment curves (Ricker, Beverton and Holt, Shepherd, etc.) fitted poorly, while SST was negatively correlated with recruitment in a simple linear model. Recruitment was unrelated to NAO. A model combining SST and adult biomass showed that recruitment is probably density-dependent when stock size is high, and negatively correlated with temperature. The study did not indicate obvious recruitment overfishing in the English Channel *L. forbesi* population.

Key words: Stock-recruitment / Environmental factor / Temperature / NAO / Cephalopod

Résumé – Effets de l'environnement et du stock sur la variabilité du recrutement chez le calmar, *Loligo forbesi*, en Manche. La variabilité du recrutement est généralement attribuée à la taille du stock de géniteurs et à l'environnement. Dans cette étude, les estimations de stock du calmar *Loligo forbesi* en Manche sont mises à jour et affinées. Cette nouvelle série d'estimation est utilisée pour tester l'influence du niveau de géniteurs et celle des conditions de milieu sur le recrutement. La modélisation des stocks est améliorée par l'utilisation d'une clé longueur-âge stochastique considérant ainsi la variabilité inter-individuelle de croissance. Le nombre de recrues et la biomasse des géniteurs sont estimés mensuellement, pour une série de 13 saisons de pêche (1989-2002). Pour chaque cohorte annuelle, l'abondance cumulée des recrues est étudiée en fonction de la biomasse de géniteurs de la cohorte précédente et des paramètres environnementaux (température de l'eau de surface de la mer, SST, et l'oscillation Nord Atlantique, NAO) observés lors de la période d'éclosion. Les recrues sont âgées de 7 mois et le recrutement annuel intervient entre avril et août. Pendant la période de reproduction (septembre-décembre), les animaux ayant atteint la taille de maturité sexuelle sont âgés de 11 à 13 mois. Les relations stock-recrutement (courbes de Ricker, Beverton et Holt, Shepherd, etc.) ne sont pas significatives. La température de l'eau de surface en automne est négativement corrélée avec le recrutement de l'année suivante alors que la relation NAO-recrutement n'apparaît pas significative. Un modèle combinant SST et biomasse de géniteurs montre que le recrutement est probablement "densité-dépendant" lorsque le stock de géniteurs est abondant, et est négativement corrélé avec la température. L'étude n'indique aucune surexploitation du recrutement de la population de *L. forbesi* en Manche.

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[a] Corresponding author: `jean-paul.robin@unicaen.fr`

1 Introduction

Understanding recruitment variability is important for good fisheries management. Recruitment is defined as the renewal of a stock via young classes that enter the fishery, and recruitment strength varies substantially from year to year in many exploited fish stocks worldwide, especially in squid stocks (Agnew et al. 1998; Waluda et al. 2001; Royer et al. 2002; Young et al. 2004). Because cephalopods are short-lived and generally comprise a single cohort, successful and sustainable exploitation depends heavily on recruitment. Changes in recruitment are commonly attributed to stock size variation, as described by various stock-recruitment models (Hilborn and Walters 1992). The density-dependence assumption underlying many hypothesized stock-recruitment relationships has been supported for several fish stocks (Myers and Barrowman 1996; Zheng 1996; Mackenzie et al. 2003), but more rarely in cephalopods. However, density dependence of recruitment has been documented for *Loligo gahi* around the Falkland Islands (Agnew et al. 2000, 2002), the Indian squid *Loligo duvauceli* (Mohamed and Rao 1997), and the Japanese flying squid *Todarodes pacificus* (Okutani and Watanabe 1983). Empirical support for such relationships is often weak, due in part to short time-series and the difficulties associated with accurately estimating of recruitment and stock size (Basson et al. 1996; Agnew et al. 1998; Royer et al. 2002).

Climate variability has also been recognized as a crucial factor in recruitment dynamics. Temperature is often the major environmental factor investigated, because it influences life-history parameters and, in practice, is easily measured and long time-series are available. In cephalopods, temperature has been used to explain variability in abundance (Brodziak and Hendrikson 1999; Robin and Denis 1999; Bellido et al. 2001; Pierce and Boyle 2003) and the onset of migrations (Sims et al. 2001; Wang et al. 2003). Because SST is influenced by larger ocean-climate effects, such as the North Atlantic Oscillation (NAO), we would anticipate that these latter indicators on their own might be reasonable predictors of recruitment (Agnew et al. 2000, 2002). The NAO is a large-scale index that reflects the atmospheric circulation pattern, and is considered as a proxy for climate variability in the North Atlantic (Hurrel 1995). The influence of the NAO on abundance has been demonstrated for Northeast Arctic cod and haddock (Solow 2002), for herring and cod in the Barents Sea (Hjermann et al. 2004), and for squid (Dawe et al. 2000; Sims et al. 2001; Zuur and Pierce 2004).

The focus of this study is the effect of the environment and stock size on recruitment strength of the squid *Loligo forbesi* in the English Channel. Assessment of this stock using depletion methods and cohort analysis has previously been reported (Royer et al. 2002). The stock has demonstrated clear interannual fluctuations in recruitment over the years that cannot be attributed solely to effects of fishing pressure (on spawning stock size). Recruitment takes place mainly in summer (Holme 1974; Robin and Boucau-Camou 1995). Population indices of reproduction and recruitment described by Collins et al. (1997) suggest when applied to English Channel data, that spawning takes place mainly in autumn (Royer 2002). In cephalopods, early life history is generally influenced by environmental conditions such as temperature (Boyle and Boletzky 1996; Forsythe et al. 2001; Hatfield et al. 2001). Waluda et al. (1999) suggest that temperature influences recruitment to the fished stock via effects on early life stages, and Cushing (1996) stresses that the effect of the NAO on recruitment is greatest at the larval stage. Therefore, we would expect environmental conditions, as indicated from temperature and/or NAO data, to play an important role in survival of early life stages and in subsequent recruitment of *Loligo forbesi*.

Spawning stock size and recruitment are first re-examined and updated to obtain a long time-series. We then test the hypothesis that recruitment is density-dependent, and investigate whether interannual changes in SST and NAO are influential in regulating recruitment variability.

2 Materials and methods

2.1 Updated population estimates

English Channel *Loligo forbesi* were assessed using the monthly cohort analysis procedure developed by Royer et al. (2002). The number of recruits and the spawning stock biomass (SSB) were calculated using fishery statistics collected from French (*Centre Administratif des Affaires Maritimes,* CAAM) and British (Centre for Environment, Fisheries and Aquaculture Science, CEFAS) databases and results of monthly biological sampling. The time-series in Royer et al. (2002) was extended to cover 14 years (1989-2002). Biological sampling carried out since autumn 1992 provided monthly estimates of the following variables per commercial category: the proportion of *Loligo forbesi* and *Loligo vulgaris,* mean body weight and length frequencies. To derive monthly estimates for the whole catch, these variables were combined with monthly landings statistics which were split by commercial category and by rectangle. Monthly averages of these variables estimated in the surveyed period were used to obtain population estimates for the period 1989-1992.

2.2 Population estimates

The usual procedure for deriving catch-at-age distributions for cohort analyses requires length-age keys to be applied to catch-at-length distributions. Recruitment and SSB estimates from Royer et al. (2002) have been improved by including a stochastic length-age key for *L. forbesi* in the English Channel. Instead of using raw age data to create the age-length key, thereby incorporating probably spurious sampling effects, we modelled growth using a quantile regression method. Age data were derived from reading statoliths for a whole fishing season, from June 1993 to May 1994, for animals 10–58 cm DML (Dorsal Mantle Length). Growth increments have been validated as daily in *L. forbesi* in Irish waters (Collins et al. 1995). Total increment number was determined from one count of 328 statoliths according to the protocol in Challier et al. (2002). We assumed that the stochastic length-age key was applicable to all fishing seasons. Cephalopod growth shows interannual variation in growth rates (Villanueva 1992; Arkhipkin and Laptikhovsky 1994) but it is also characterised by high inter-individual variability (Natsukari et al. 1988;

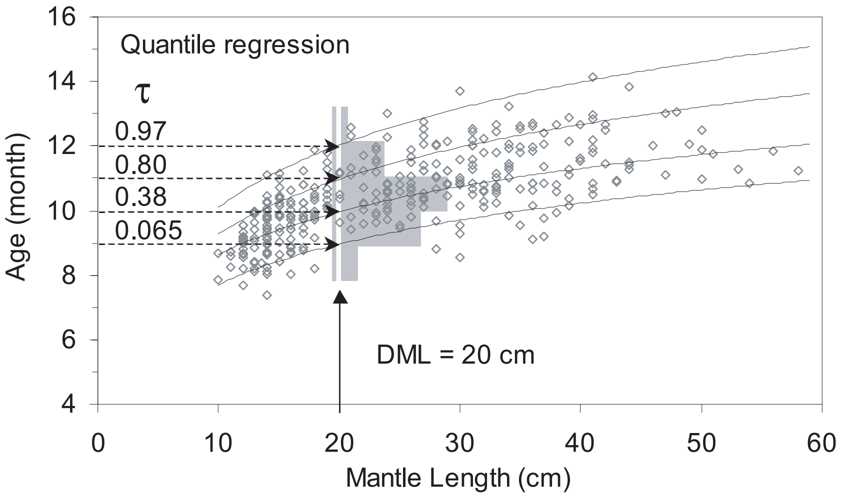

Fig. 1. Length-age relationships for *Loligo forbesi* in the English Channel for the 1993-cohort and example of application to the age-length key. Quantile-regression lines presented here are fitted for the case of animals 20 cm DML (Dorsal Mantle Length). For this length-class, proportions in each age (month) derive from quantiles $\tau \in \{0.065, 0.38, 0.80, 0.97\}$. The shaded histogram represents age proportions (in %: 6.5, 31.5, 42, 17, 3 respectively).

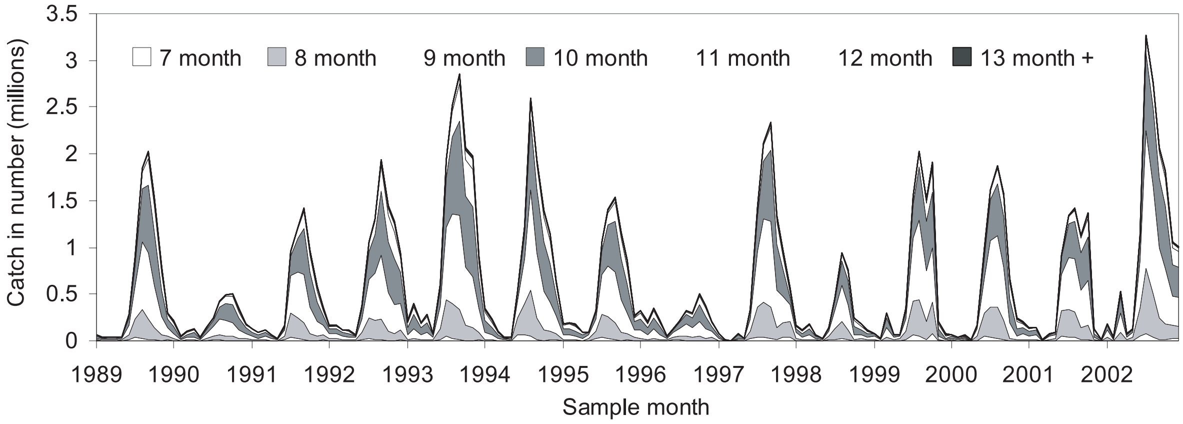

Fig. 2. Updated and refined catch-at-age estimates from the conversion of catch-at-length of *Loligo forbesi* in the English Channel.

Arkhipkin and Nekludova 1993). A logarithmic function was fitted to the data and inter-individual variability in age at any 1 cm length-class was simulated using the quantile regression technique (Koenker and Basset 1978; Cade and Noon 2003). Quantile regression allows one to fit relationships between variables for all portions of a probability distribution by minimizing the weighted sum of absolute deviations. Koenker and Hallock (2001) refer to "stochastic relationships" and so the derived age-length key was called a "stochastic key". Quantile regression is a semi-parametric method in the sense that it computes estimates without assuming any parametric error distribution (e.g. Gaussian, Poisson). In the present study, quantiles τ (ranging from the 1st to the 99th) were employed to represent the spread of the data and to generate slope and origin ordinate estimates (Fig. 1). Values for the local goodness of fit $R^1(\tau)$ of quantile lines, as described in Koenker and Machado (1999), were highly significant ($p < 0.001$) for $\tau \in \{0.01, 0.99\}$ and were approximately 0.30 in the range of quantiles $\tau \in \{0.1, 0.9\}$. It is worthwhile noting that local $R^1(\tau)$ values had to be tested because $R^1(\tau)$ are generally not comparable to the global R^2 used in least squares regression (Baur et al. 2004). The proportion of squid of age a in length-class l is derived from the quantiles of the boundaries of age-class a (Fig. 1). In the sample from 1993/4 very few squid were found of ages <7 or >13 months. Although there may well be significant inter-annual variation in growth rate, here we assume there is no such variation (or, rather, that it is masked by the high inter-individual variation). Using this method of age-length key construction, we estimated that most squid in the catches were 9−10 months old (Fig. 2).

2.3 Environmental data

Sea surface temperature (SST) information was derived from the National Oceanic and Atmospheric Administration (NOAA, US) database on a monthly basis for the period January 1988 to December 2002 (51°N to 48°S, 7°W to 2°E). The data were available with a spatial resolution of 0.5° latitude by 1° longitude. Monthly temperature from September to

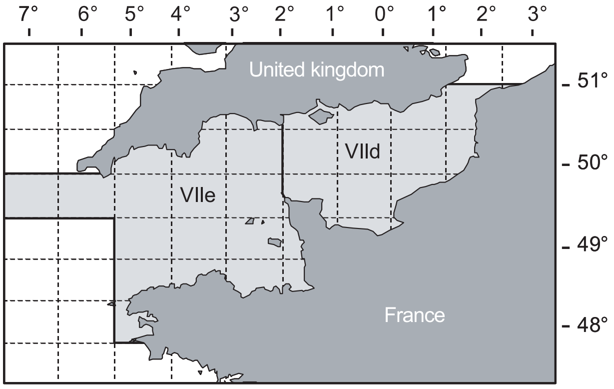

Fig. 3. The English Channel study area (shaded; ICES divisions VIIe and VIId).

December was averaged annually over the western part of the English Channel (ICES division VIIe, Fig. 3). The rationale for selecting this area is that it is a spawning ground (Holme 1974) and that it is also in this part of the English Channel that recruitment take place (Royer 2002). The period corresponds to hatching time back-calculated from 1993 statolith data.

Monthly NAO indices were available from National Center for Atmospheric Research (NCAR, `http://www.cgd.ucar.edu/~jhurrell/nao.stat.other.html`). They represent the difference in the normalized sea-level pressure between the Azores and Iceland (Hurrel 1995). "autumn" means were computed from September to December for the period 1989-2002.

2.4 Data analysis

Cohort analysis provided monthly estimates of population numbers-at-age. This data set was pooled on an annual basis to describe variation between annual cohorts. The annual recruitment is the sum of the number 7-month old animals estimated to be present during each month of the recruitment season. For each annual cohort, SSB is obtained by pooling estimated numbers of animals in the spawning season. Mature animals were here assumed to be a mixture of males and mature females, assuming a balanced sex ratio as described from biological sampling (Thomas et al. 2004). Mature age groups were determined from a previously determined length-at-maturity relationship (Thomas et al. 2004) and the length-age key (Fig. 1). Spawners represent the fraction of the stock from 11 to 13 months old. To provide an understanding of environmental and stock effects on recruitment variation in the *L. forbesi* stock, the relationship between SSB of the previous year and the number of recruits of the year was determined using the standard stock-recruitment models of Ricker (1954), Beverton and Holt (1957), Shepherd (1982), and the Saila-Lorda (in Needle 2002) non-linear model. A segmented regression (also known as hockey-stick) was also used to model the stock-recruitment relationship. The break-point indicates SSB values below which recruitment was weakened. Relationships between annual recruitment strength and (a) SST and (b) NAO were determined using a simple linear model.

Table 1. Descriptive statistics for recruits (in millions individuals) and spawning stock biomass (SSB; in 10^3 tonnes) of *Loligo forbesi* estimated from cohort analysis.

Statistic parameters	Recruits	SSB
Mean	11.39	0.90
Minima	3.21	0.38
Maxima	20.50	1.90
Standard deviation	5.55	0.45

3 Results

3.1 Population estimates

Cohort analysis produced monthly estimates of recruit numbers and SSB (Fig. 4). Results shown for the recruitment years 1990-1992 are based on average length-frequency data as no length frequency samples were available in those years. Over the period 1993-2002, the timing of the major peaks in recruitment and SSB (respectively, June and October) was constant, but peaks extended from April to August for recruits, and from September to December for SSB. In the English Channel *L. forbesi* stock, squid aged ≥11 months were considered to be mature. Annual values of recruitment and SSB varied by approximately 49% (coefficient of variation) (Table 1).

3.2 Stock-recruitment relationships

There was no clearly discernible relationship between stock size and recruitment (Fig. 5), high recruitment (e.g. in 1993, 1994 and 2002) being generated from both high and low values of SSB.

The Ricker, Beverton and Holt, Shepherd, and Saila and Lorda functions were fitted to the stock-recruitment data, but showed no significant correlation ($p > 0.05$, Table 2). The analysis based on segmented regression provides no evidence that recruitment would be impaired below of SSB of 377 tonnes, given that there are no data to the left of that point (Fig. 5).

3.3 Relationships between environmental variables and recruitment

There was no significant relationship between the NAO index and recruitment (Table 3). However, there was a negative relationship between annual recruitment and SST in the western part of the English Channel (Fig. 6). A simple linear regression of recruitment on SST in autumn of the previous year was significant (Table 3). In the range of mean SST between 13 and 15 °C, temperature negatively influences recruitment.

3.4 Temperature and stock effects on recruitment

The stock-recruitment data and the significant relationship of temperature with recruitment (Figs. 5 and 6) suggest that a high SSB can generate a high level of recruitment when SST

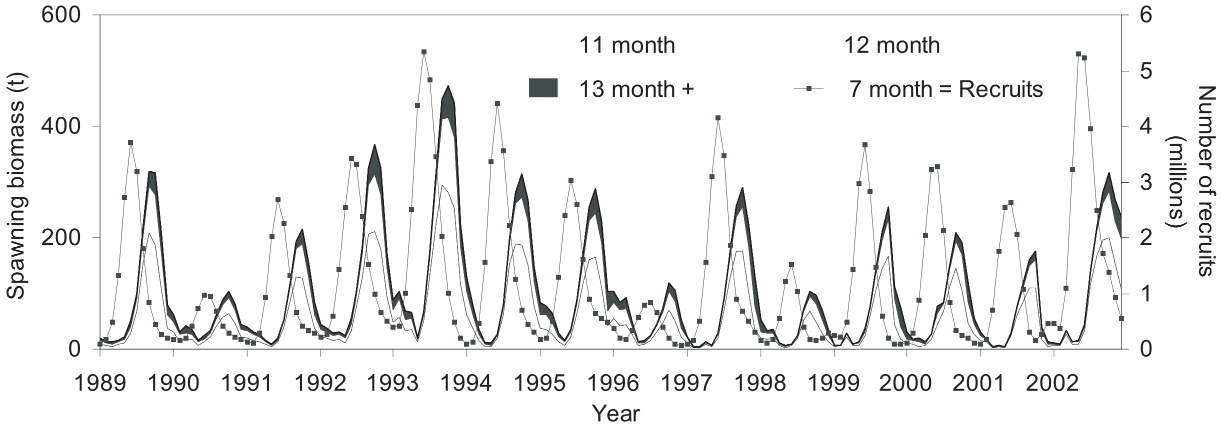

Fig. 4. Estimates of spawning stock biomass and recruits of *Loligo forbesi* from cohort analysis at a monthly scale.

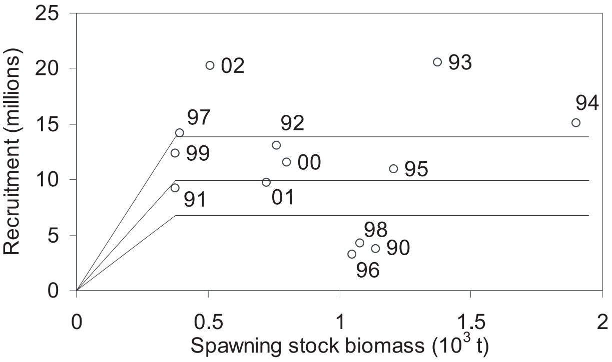

Fig. 5. Stock-recruitment data for the *Loligo forbesi* squid in the English Channel. Points are labeled by the recruitment year. The solid line describes the segmented regression.

is low (1993 and 1994) and a low level of recruitment when temperature is high (1990, 1996 and 1998).

Combined effects of SSB and temperature were therefore incorporated in a simple linear model of recruitment. The analysis of variance showed that the combined model f (SST, SSB) was significant ($p = 0.027$, Table 3). Although the combined model explained 51% of the variation in recruitment instead of 42% in the f (SST) model, the analysis of variance did not point to a significant improvement ($p = 0.22$) resulting from adding the SSB term. However, the combined model indicated that the SSB coefficient, was negative, suggesting the presence of density-dependent processes (Table 3). The fitted curves are depicted in Figure 7, which shows that year-to-year recruitment fluctuations can be better described by the combined model although the year 2002 peak is still poorly predicted.

4 Discussion

In the English Channel, fluctuations in recruitment of *Loligo forbesi* may not be related to fishing pressure on adults (Royer et al. 2002). Sufficient numbers of spawners are required to lay enough eggs to produce average recruitment. However, loliginid squid are annual and semelparous species, generations do not overlap and stock size is likely to have a limited influence on recruitment strength, because the animals die soon after spawning (Caddy 1983). The environment that early life stages experience may therefore be the major factor that influences recruitment. The present study provides no evidence of a stock-recruitment relationship, but demonstrates a significant and indirect effect of environmental conditions (namely SST) on recruitment strength. The timing of environmental conditions that have a significant effect on recruitment suggests that hatchlings and early life stages are sensitive.

Stock-recruitment relationships are based on the idea that parental stock biomass can be used as a proxy for egg production, as suggested by Hilborn and Walters (1992). Most analyses consider SSB as a predictor for recruitment variability, because it is easily measured from stock assessment methods. The present study shows non-significant relationships (Ricker, Beverton-Holt, Shepherd, Saila-Lorda) for the English Channel stock of *Loligo forbesi*, and the poor correlation seen in other studies (Mohamed and Rao 1997) also leads us to believe that SSB alone is not a good predictor of recruitment strength in the case of cephalopods. Further, the results from the segmented regression do not point to a level of SSB below which recruitment could be impaired. However, there are no data for SSB < 377 tonnes. Egg production can be influenced by the reproductive condition of the spawners, as for instance in Northeast Arctic cod (Marshall et al. 1998) and capelin in the Barents Sea (Tereshchenko 2002). Egg production seems to be a more sensitive variable than adult biomass, because of interannual fluctuations in fecundity. Annual fecundity has been shown to vary with length in *Loligo vulgaris* (Coelho et al. 1994), and depends on environmental conditions and food-availability in the dumpling squid *Euprymna tasmanica* (Steer et al. 2004). The high degree of plasticity in growth and fecundity probably affects the magnitude of recruitment in cephalopods.

Survival of the larval stage is probably the main source of variability in recruitment (Rothshild and Fogarty 1989), being a better predictor than egg production or SSB in cod (Helle et al. 2000). In cephalopods, larval abundance of *Todarodes pacificus* is positively correlated with subsequent recruitment success (Okutani and Watanabe 1983) and with annual abundance indices (Sakurai et al. 2000), suggesting that if density-dependent processes operate they would do so after

Table 2. Equations, models parameters and goodness of fit for stock-recruitment relationships for *Loligo forbesi* in the English Channel. Y: number of recruits (in millions), S: spawning stock biomass (in 10^3 tonnes).

Methods	Equations	α	β	γ	R^2
Ricker non linear	$Y = \alpha \text{ S} \exp(\beta \text{ S})$	46.7	1.4		0.098
Beverton & Holt non linear	$Y = \alpha \text{ SSB} / (\beta + \text{S})$	11.2	1.10^{-6}		<0.001
Saila & Lorda non linear	$Y = \alpha \text{ S}^{\gamma} \exp(-\beta \text{ S})$	93.2	2	1.9	0.289
Shepherd non linear	$Y = \alpha \text{ S} / (1 + (\text{S} / \beta)^{\gamma})$	51.2	0.5	1.9	0.111
Segmented regression	$0 < \text{S} < \gamma, Y = \alpha \text{ S}$	26.2		0.377	
	$\gamma < \text{S}, Y = \beta$		9.87	0.377	

Table 3. Simple and multiple regression coefficients and statistics for environmental/stock-recruitment relationships for *Loligo forbesi* in the English Channel. Y: number of recruits (in millions) NAO: North Atlantic Oscillation index, SST: sea surface temperature (in °C), SSB: spawning stock biomass (in 10^3 tonnes).

Model	R^2	Model p-value	Constant	p-value	SST / NAO	p-value	SSB	p-value
Y = f (NAO)	0.17	---	11.8	***	2.9	---		
Y = f (SST)	0.42	*	112	**	–7.1	**		
Y = f (SST, SSB)	0.51	*	136.8	**	–8.6	**	–3.8	---

*** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, --- not significant.

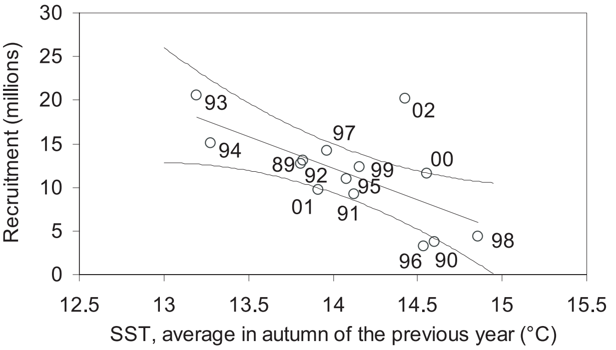

Fig. 6. Relationship between the number of recruits and SST in autumn of the previous year. Points are described by the year the recruitment. The linear model includes 95% confidence intervals.

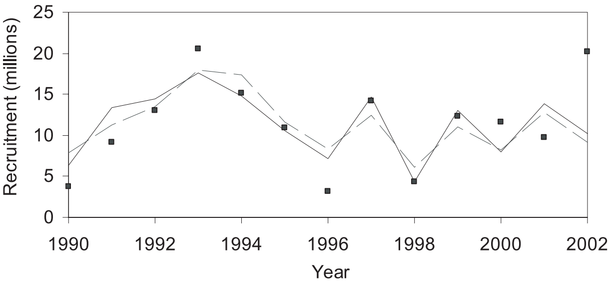

Fig. 7. Predicted recruitment from sea surface temperature and spawning stock biomass for *Loligo forbesi* stocks in the English Channel (n = 13, ■: observed data, solid line: predicted recruitment from SST and SSB, dashed line: predicted recruitment from SST).

the larval stage. Density-dependence mechanisms normally operate after hatching, but they may be obscured in *Loligo forbesi* by environmental processes. The early life stages of cephalopods are the ones more affected by environmental factors (Forsythe 1993), which hence need to be incorporated into stock-recruitment relationships.

Recruitment variability of *Loligo forbesi* English Channel stocks is significantly correlated with the sea surface temperature while the NAO index has no apparent influence on recruitment dynamics. Since temperature and NAO are usually strongly correlated (Hurrel et al. 1995), this result was unexpected. Sims et al. (2001) demonstrated that *Loligo forbesi* movement is temperature-dependent, and appears to be governed by climatic changes associated with the NAO. Recruitment timing may be expected to vary as a result of global warming, as suggested for *Illex illecebrosus* (Dawe et al. 2000) and *Loligo forbesi* stocks in Scottish waters (Zuur and Pierce 2004). However, most studies use the NAO index during wintertime due to its greater intensity compared to the other seasons. The autumn time was employed here to be consistent with the assumption of a potential effect of climatic variable on early life stages.

The effect of temperature on recruitment variability of *Loligo forbesi* in the English Channel stocks is similar to that seen for *Loligo gahi* in the Falkland Islands (Agnew et al. 2000). High recruitment appears to be associated with low temperature – in the autumn of the previous year in this study. Abundance variability between fishing seasons is generally attributed to environmental conditions, again often represented by temperature (Pierce et al. 1998; Waluda et al. 1999; Dawe et al. 2000). It is generally agreed that temperature influences recruitment when it affects early life stages (Rodhouse et al. 1992; Dawe and Warren 1993; Bakun and Csirke 1998; Waluda et al. 1999). A slight increase in temperature can directly accelerate growth rates during the paralarval and juvenile phase (Hatfield 2000; Forsythe et al. 2001; Hatfield et al. 2001).

In our combined model of recruitment, the effect of temperature is strongly significant, and negatively correlated with recruitment. Although SSB is not a significant additional parameter, it displays a weak negative relationship with recruitment in the combined model. At high temperatures, one might expect competition for food or oxygen to be more limiting than at low temperatures, and one might also expect this to be exacerbated at times of high larval abundance following years of high SSB. However, this is not a strong effect. In conclusion, as for several other species of squid (*Illex argentinus*: Waluda et al. 1999; *Illex illecebrosus*: Dawe et al. 2000; *Loligo gahi*: Agnew et al. 2000, 2002), *L. forbesi* recruitment is mostly dependent upon environmental conditions such as temperature.

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