Environmental effects on recruitment of short-finned squid (*Illex illecebrosus*)

E. G. Dawe, E. B. Colbourne, and K. F. Drinkwater

Effects of variation in the ocean environment on abundance of northern short-finned squid (*Illex illecebrosus*) in the northwest Atlantic Ocean were investigated using a multiple regression model. A catch-based abundance index from two Canadian fishery areas was used as the dependent variable in time series analysis. Simple correlation analysis was used to select environmental indices. A model based on a 73-year time series of catch and meteorological data suggested that atmospheric forcing was related to squid abundance. Two other models were explored using a shorter (25-year) time series, which included an ocean temperature index and a Gulf Stream position index. One model utilized the catch-based index, whereas the other used a fishery-independent survey index as the dependent variable. All analyses indicated that squid abundance was positively related to a favourable oceanographic regime associated with a negative North Atlantic Oscillation (NAO) index (weak winter northwesterly winds), high water temperatures off Newfoundland and a southward shift in the position of the Gulf Stream and the boundary between the shelf waters and the offshore slope waters. In addition, increased meandering of the Gulf Stream appears to promote increased abundance, probably through enhanced shoreward transport of squid. Environmental relationships with squid indices are believed to reflect effects of broad-scale winter atmospheric circulation patterns on Gulf Stream dynamics, which largely regulate year-class strength of the dominant winter-spawning group early in life.

E. G. Dawe (corresponding author), and E. B. Colbourne: Science Branch, Department of Fisheries and Oceans, PO Box 5667, St John's, Newfoundland, Canada, A1C 5X1 (tel.: +1 709 772 2076; fax: +1 709 772 4105; e-mail: dawe@athena.nwafc.nf.ca); K. F. Drinkwater: Bedford Institute of Oceanography, PO Box 1006, Dartmouth, Nova Scotia, Canada, B2Y 4A2.

Introduction

The northern short-finned squid (*Illex illecebrosus*, LeSueur) is distributed from central Florida to Newfoundland and Labrador (Squires, 1957; Dawe and Warren, 1993). It supports summer–autumn fisheries on the eastern USA Shelf, the Nova Scotia Shelf and in Newfoundland coastal waters.

This species spawns south of Cape Hatteras to central Florida, in proximity to the Gulf Stream (Trites, 1983). Spawning occurs throughout most of the year, with several seasonal peaks, the major one usually being in winter (Lange and Sissenwine, 1983). Young stages are advected northeastward by the Gulf Stream (Trites,

1983). Paralarvae, and probably egg masses, are transported within the fast-flowing landward portion of the Gulf Stream (Fig. 1; Rowell and Trites, 1985; Hatanaka *et al.*, 1985) whereas small juveniles of about 1–3 cm mantle length (ML) are concentrated in the Gulf Stream Front (GSF; Dawe and Beck, 1985a, 1985b; Rowell and Trites, 1985; Rowell *et al.*, 1985a; Hatanaka *et al.*, 1985). Larger pelagic juveniles are concentrated during spring at the boundary between the shelf and offshore waters, called the Shelf-Slope Front (SSF), off the Canadian Continental Shelf (Dawe and Beck, 1985b). Bottom trawl catches from directed squid surveys in May–June on the southwest slope of the Grand Bank were generally associated with on-bank incursions of the SSF
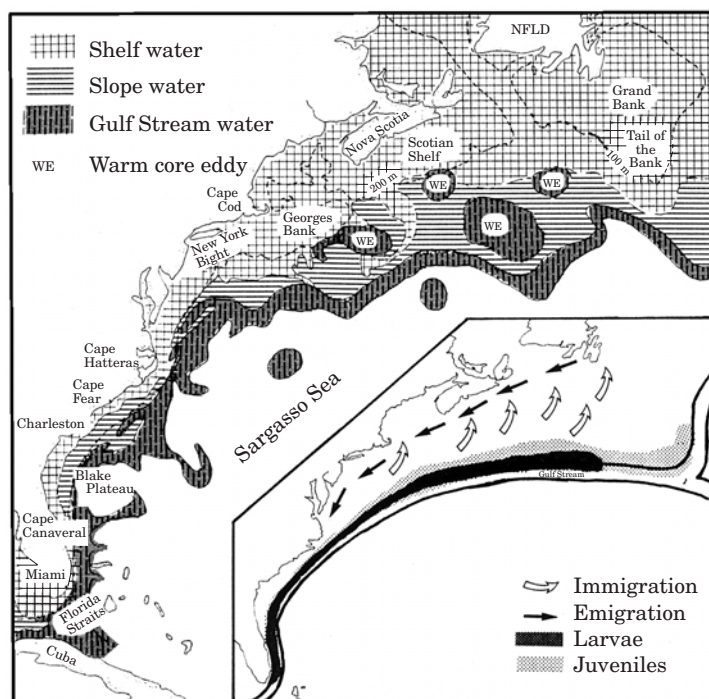
Figure 1. Schematic representation of the life history of short-finned squid in relation to features of the Gulf Stream System (from Rowell and Trites, 1985).

(Fig. 2) and bottom temperatures of 5°C or greater (Dawe and Warren, 1993). Similarly, squid occurrence in Newfoundland coastal waters during summer–autumn is associated with local water temperature exceeding 5°C, in water depths generally less than 30 m (Hurley, 1980). Squid distribution on the Nova Scotian Shelf is associated with bottom temperatures greater than 6°C (Rowell *et al*., 1985b).

It may be expected that environmental variation would affect year-class strength for a species whose annual life cycle is so closely related to oceanographic features, especially at Newfoundland where this species is near the northern limit of its distributional range (Mann and Drinkwater, 1994; Coelho *et al*., 1994). An initial investigation of environmental effects on short-finned squid recruitment (Dawe and Warren, 1993) utilized simple correlation analysis between an abundance index and three environmental indices. The limitations of that study included a qualitative squid index based on a subjective five-level scale of inshore abundance at Newfoundland. Also, a crude index of Gulf Stream variability was used based upon January sea surface temperature (SST) at nine fixed oceanic stations sampled by ships of opportunity. The other two indices, spring bottom temperatures at a standard hydrographic site near St John's, Newfoundland (Station 27, Fig. 2), and the annual number of icebergs drifting south of latitude 48°N, were linked to the Labrador Current. It

was stressed that because of the limitations of both the data and the analysis, the objective was simply to "discern any evidence of potentially meaningful structure within the data on which to base hypotheses". Based on this correlation analysis, the proposed working hypothesis was that broad-scale mechanisms regulate recruitment throughout the Northwest Atlantic and that these mechanisms, while unclear, appeared to be related to the variability in the Labrador Current and the Gulf Stream. It was further hypothesized that warm events associated with a more northward Gulf Stream resulted in increased recruitment, whereas cold events associated with an increased influence of the Labrador Current resulted in decreased recruitment.

We address these hypotheses using a more structured approach and formal analysis. This has been made possible through the development of an improved squid abundance index, increased availability of multiple meteorological and oceanographic indices, and extension of the time series of available data.

Methods

We use commercial catch by Canadian fishery areas as an index of abundance of the single-year class squid population. Estimates of yearly catch date back to 1920 for the Scotian Shelf (NAFO Subarea 4) and to 1911 for
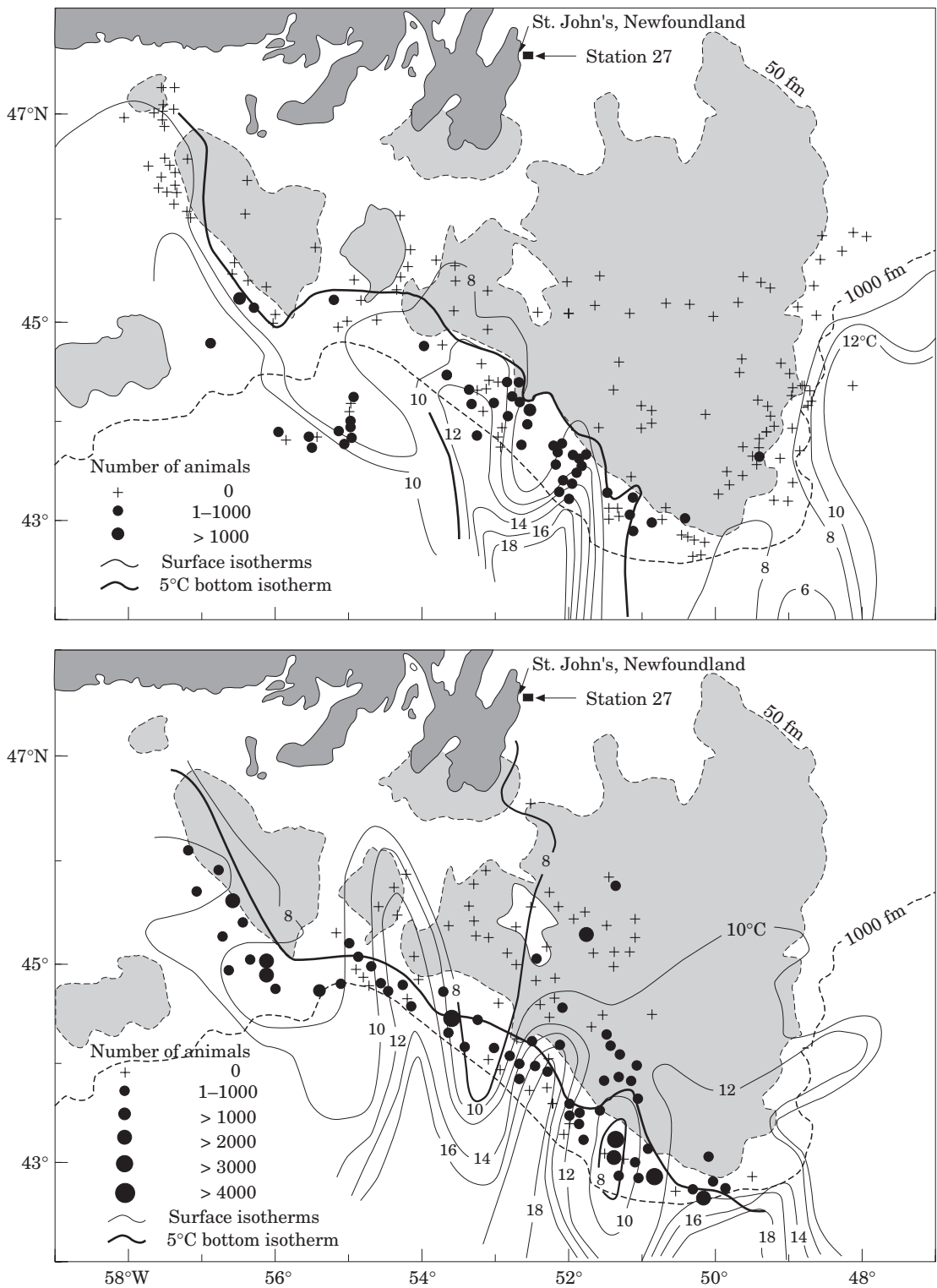
Figure 2. Squid catches during 1978 (above) and 1979 (below) spring bottom trawl surveys in relation to the surface Shelf-Slope Front (closely spaced isotherms) and the 5°C bottom isotherm.
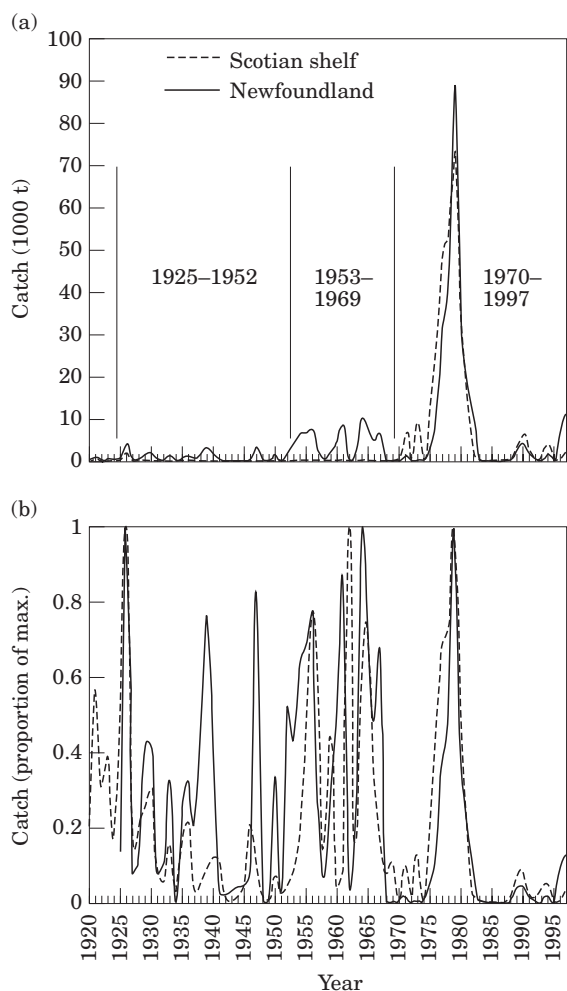
(a)

(b)

Figure 3. Annual trends in (a) catch and in (b) catch index (proportion of maximum catch within each of three time periods), by fishery area.

Newfoundland (NAFO Subarea 3; Mercer, 1973; Dawe, 1981; Dawe and Warren, 1993). Catches have been greatly affected by market-related changes in fishing effort (Dawe, 1981). We adjusted for periodic changes in fishing effort by expressing catch as a proportion of the maximum within each of three relatively distinct time periods. Dawe (1981) showed that periodic shifts in catch level among the time periods 1925–1952, 1953–1969, and 1970–1997 (Fig. 3a) matched closely changes in the market place. However, market conditions were relatively constant within each of the time periods. The catch indices for Nova Scotia and Newfoundland were significantly positively correlated (Fig. 3b; Spearman rank correlation coefficient $r_s = 0.69$, $p = 0.001$) and thus the two area-specific indices were averaged to produce one catch-based squid abundance index for Canadian Atlantic waters. The assumption that catch trends reflect

actual trends in squid abundance at Newfoundland is supported by trends in the prevalence of squid within the diet of northern gannets (*Sulsa bassana*) since 1977 (Montevecchi and Myers, 1995, 1997).

A concern with this approach is that maximum recruitment levels may not actually be comparable among the three time periods. We believe our approach is justified because the catch index agrees closely with an independent scale based on subjective ranking of Newfoundland inshore squid abundance (Dawe, 1981). However, because of the possibility of differences among time periods we also utilize a statistical technique (meta-analysis) for investigating relationships between squid abundance and the environment within each of the three time periods separately and then pool the results of these independent analyses.

Environmental indices used for correlation with the squid catch index (Table 1) include the North Atlantic Oscillation (NAO) index that reflects the large-scale atmospheric circulation pattern, the area of sea ice on the Newfoundland Shelf south of 55°N (ICE), and bottom (BT) and vertically-averaged (0–175 m) temperatures (VT) at Station 27 (Fig. 2). The NAO index is based upon the wintertime (average of December, January, and February) pressure difference in mb between the Azores and Iceland. A high index indicates an intense Icelandic Low and generally cold conditions in the Labrador Sea, including the coastal waters off Newfoundland. We include the two Station 27 temperature indices because the short-finned squid is a diel migrator, being near bottom during daylight and dispersed in the water column at night. Another temperature-related index from the Newfoundland shelf used was the area of the Cold Intermediate Layer (CIL). The CIL is the cross-sectional area of <0°C water overlying the continental shelf along a transect which extends northeast across the Labrador Current from Cape Bonavista, about 120 km northwest of St John's (Fig. 2).

Off-shelf ocean indices included latitudinal displacements of the surface position of both the SSF and the north wall of the Gulf Stream, hereafter referred to as the Gulf Stream Front (GSF). Monthly means of the latitudinal position of the SSF and the GSF at each degree of longitude from 50°W to 75°W between 1973–1992 were estimated from satellite imagery by Drinkwater *et al.* (1994) and updated to 1997. Annual indices were defined as the annual mean displacements of the fronts averaged over all available longitudes. We also included the mean latitudinal distance between the SSF and the GSF and an index of the high-frequency (short-period) variability of the Gulf Stream. The latter was defined as the standard deviation of the monthly means of the latitudinal displacements within the calendar year after removal of the seasonal and low-frequency components of the variability and reflects the

Table 1. Correlation matrix for environmental indices, represented by Spearman's correlation coefficient (r_s), probability value (p; values in bold are significant at 0.05) and number of years (n).

Index		NAO	ICE	CIL	BT	VT	GSF	SSF	SSF–GSF
ICE	r_s	0.52							
	p	**0.004**							
	n	29							
CIL	r_s	0.39	0.54						
	p	**0.005**	**0.003**						
	n	50	29						
BT	r_s	− 0.51	− 0.88	− 0.43					
	p	**0.0002**	**0.0001**	**0.002**					
	n	48	29	48					
VT	r_s	− 0.43	− 0.78	− 0.31	0.80				
	p	**0.002**	**0.0001**	**0.03**	**0.0001**				
	n	48	29	48	48				
GSF	r_s	0.54	0.70	0.24	− 0.61	− 0.54			
	p	**0.002**	**0.0001**	0.19	**0.0002**	**0.002**			
	n	32	29	32	32	32			
SSF	r_s	0.19	0.64	0.31	− 0.58	− 0.47	0.57		
	p	0.37	**0.0005**	0.14	**0.002**	**0.02**	**0.002**		
	n	25	25	25	25	25	25		
SSF–GSF	r_s	− 0.31	− 0.06	0.07	0.12	0.10	− 0.50	0.37	
	p	0.13	0.76	0.75	0.56	0.63	**0.01**	0.07	
	n	25	25	25	25	25	**25**	25	
GS HF	r_s	− 0.11	− 0.60	− 0.29	0.65	0.62	− 0.62	− 0.51	0.14
	p	0.68	**0.01**	0.26	**0.005**	**0.009**	**0.008**	**0.04**	0.58
	n	17	17	17	17	**17**	**17**	**17**	17

NAO, North Atlantic Oscillation annual anomaly (December through February), 1920–1997; ICE, Newfoundland shelf ice area ($km^2 \times 10^3$), 1969–1997; CIL, Cold Intermediate Layer thickness (m), 1948–1997; BT and VT, Station 27 annual mean bottom and vertically integrated (0–176 m) temperature (°C), respectively, 1950–1997; GSF and SSF, Annual anomaly in latitudinal displacement of the Gulf Stream Front and Shelf-Slope Front (55°W–75°W), respectively, 1973–1997; SSF–GSF, Annual anomaly in distance between the GSF and SSF, 1973–1997; GS HF, s.d. of monthly means within the calendar year of the Gulf Stream positions after removing seasonal and low-frequency signals.

intensity of the meandering of the Stream. The higher the index, the more intense the meandering. The seasonal signal was taken as the historical long-term mean for each month. The low-frequency component was obtained by filtering the time series of monthly anomalies of frontal displacements (after removing the long-term monthly means). A Cartwright filter was used with 25 weights and 50% power reduction at a period of 15 months, which removes most of the fluctuations with periods of 1 year or less. Because of the filtering and missing data (9 months in 1996), the time series for the high-frequency fluctuations was restricted to 1978–1994. For all comparisons, Spearman correlation coefficients were calculated based upon the ranking of the various time series. Environmental variables were chosen for further time series analysis based on the relative strength of their individual correlations with the squid catch index.

The relationship between the squid catch index and those environmental indices selected as input variables for analysis of the full time-series was further investigated using meta analysis (Hedges and Olkin,

1985; Myers, 1997). In this application, correlation analysis was performed for each of the three time intervals described above and these analyses were considered to represent independent "studies". Individual probability values were then pooled using the inverse Chi-square method, as described by Hedges and Olkin (1985).

Time-series analysis was applied, using the catch index as the dependent variable. Model development involved initially testing for the existence of autocorrelation at successive lags and identifying an appropriate process to account for autocorrelation. We found significant autocorrelation only at a lag of one year such that inclusion of a first order autoregressive term was adequate. Multiple linear regression, which included a first order autoregressive term, was then run with the squid catch index as the dependent variable and year, as well as selected environmental indices, as the independent variables. The general form of the initial full model can be expressed as:

$$C_t = a + b_1 X_{1t} + b_2 X_{2t} + . . . + c Y_t + v_t,$$

Table 2. Correlations of catch index with environmental indices (see Table 1), represented by Spearman's correlation coefficient (r_s), probability value (p; values in bold are significant at 0.05), and number of years (n).

	NAO	ICE	CIL	BT	VT	GSF	SSF	SSF–GSF	GS HF
r_s	− 0.31	− 0.40	− 0.40	0.47	0.36	− 0.41	− 0.63	− 0.17	0.62
p	**0.008**	**0.03**	**0.004**	**0.001**	**0.01**	**0.04**	**0.007**	0.41	**0.008**
n	73	29	50	48	48	25	25	25	17

where C_t is the catch index at time t, a is the model intercept, X_i is an input variable (environmental index) and b is its associated regression coefficient, Y is Year and c is its regression coefficient, and v is the structural error term, defined as:

$$v_t = \varepsilon_t - qv_{t-1},$$

where q is the autocorrelation function or autoregressive parameter and ε_t is a random error term. The analysis began with the full model and progressively eliminated non-significant terms (at the p=0.15 probability level), in a step-wise fashion. This analysis was performed using SAS Basics software (SAS Institute Inc., Cary, North Carolina).

As a means to validating the results based upon the catch-based index, the same approach was applied using a fishery-independent squid index. Catch rates (kg/tow) were available for 1973–1997 from bottom trawl surveys carried out in July on the Nova Scotian Shelf and during autumn on the Northeast USA Shelf (NAFO, 1998; Dawe and Hendrickson, 1998). These survey catch rates are closely correlated to each other and with catch at Newfoundland and on the Scotian Shelf (Dawe and Warren, 1993; Dawe and Hendrickson, 1998). We selected the autumn USA survey series for this exercise because it is better correlated with Canadian catches than is the July Scotian Shelf survey series (Dawe and Warren, 1993; Dawe and Hendrickson, 1998), probably because of the timing of the survey.

Results

The environmental indices were generally significantly correlated with each other with a few exceptions (Table 1). There were high levels of correlations among all of the continental shelf indices within the Labrador/ Newfoundland area (ICE, CIL, BT, and VT) and between these and the NAO index; results consistent with previous studies (Colbourne *et al.*, 1994; Drinkwater, 1996).

All of the Gulf Stream and shelf/slope indices were also correlated among themselves, with the notable exception of the distance between the two fronts. The GSF and SSF were positively correlated and both were

negatively correlated with the hi-frequency variability in the Gulf Stream. The latter indicates more meandering when the Stream (and the SSF) is located further to the south. Of these oceanic indices, only the GSF was significantly correlated with the NAO, with northward displacement of the Gulf Stream Front associated with high NAO, as was also found by Taylor (1996). The position of the GSF and the SSF were positively correlated with the ice area and negatively correlated with temperatures at Station 27 (BT and VT) implying that a northern displacement of the GSF and the SSF occurred simultaneously with cold conditions (lower temperatures and more ice).

The squid catch index was significantly correlated with all the environmental indices except the distance between the GSF and the SSF (Table 2). Environmental variables selected for use in time series analysis (Fig. 4) included one index representative of each of the large-scale atmospheric forcing (NAO), the Newfoundland/ Labrador condition (BT), and variability in the Gulf Stream/shelf-slope region (SSF). The NAO was the only large-scale atmospheric index and contained the longest time series. The BT and SSF indices were selected because their correlations with catch were the highest. The results of meta-analysis supported those obtained from the general correlation analysis, although the correlations were weaker. They indicated that the catch index was significantly positively correlated with BT (P=15.11, p<0.025) and negatively, although not significantly, correlated with NAO (P=9.04, p>0.05). SSF data were available only for the most recent time interval and hence could not be used in the meta-analysis.

A long time series (1925–1997) was available for modelling the effects of atmospheric forcing on catch. Initially, Year, NAO and the autoregressive term were regressed on the catch index. When Year was eliminated (Table 3), the model accounted for 32% of the variability in the catch index with the autoregressive parameter representing the main determinant of catch (Fig. 5). However, NAO, which was negatively correlated with the catch index, was a significant parameter (p=0.04).

It was possible to include all three selected environmental variables in the modelling exercise using the years 1973–1997. The full model, which included Year,
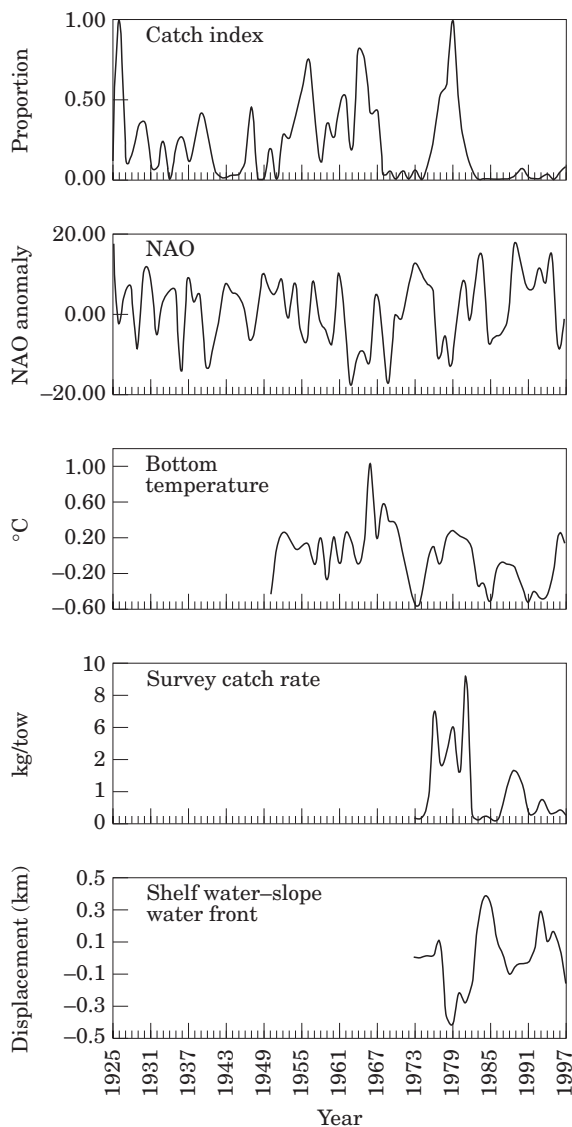
Figure 4. Annual trends in squid abundance indices and in the environmental indices used as input variables in time series analysis.

Table 3. Description statistics and parameter estimates for the catch model $C_t = a + b\ (NAO_t) + v_t$.

	Estimate	t	p
Sum of square error	2.910		
Mean square error	0.042		
df Error	70		
r^2	0.32		
Parameter	Estimate	t	p
Autoregressive (q)	− 0.439	− 4.08	—
Intercept (a)	0.230	5.44	0.0001
NAO (b)	− 0.006	− 2.09	0.04

full model, but NAO and SSF were found not to significantly contribute to the variance and hence were eliminated. The resultant model accounted for 43% of the variability in catch rate (Table 5; Fig. 6b). BT was the most important contributor to the model (p=0.002) and was positively correlated with catch rate. There was no significant autocorrelation of the dependent variable and hence the autoregressive term was not an important contributor.

Fewer years were available for stepwise regression that included the high-frequency variability (1979–1994). For this analysis, the squid catch index was the dependent variable and independent environmental variables were the NAO, GSF, SSF, the distance between the Gulf Stream and the SSF, and the high-frequency variability of the Gulf Stream. The only significant environmental variables remaining were the high-frequency Gulf Stream fluctuations and the NAO. More high-frequency fluctuations (meandering) and a low NAO index were conducive to increased squid abundance. This model accounted for 62% of the variability in the catch index.

Discussion

Generally there was strong correlation among the environmental indices investigated. Many of the linkages are believed to occur through atmospheric forcing of the oceanographic regime. High NAO anomalies indicate an intensification of the subpolar (Icelandic) atmospheric low, which generates strong northwesterly winds in winter and carries cold Arctic air south over the Labrador Sea and Newfoundland. This promotes extensive sea-ice coverage on the Labrador and Newfoundland shelves in winter, delays ice melting in spring and cools the water column (Table 1; see also Colbourne et al., 1994; Mann and Drinkwater, 1994; Drinkwater, 1996; Prinsenberg et al., 1997). High NAO anomalies are also associated with a northward displacement of the Gulf Stream as noted by Taylor (1996) and Drinkwater et al. (1999), and with higher baroclinic transports (WCRP, 1998). The latter may be due to a higher wind stress curl over the sub-tropical Atlantic (intensification of the Azores High). Changes in the position of the
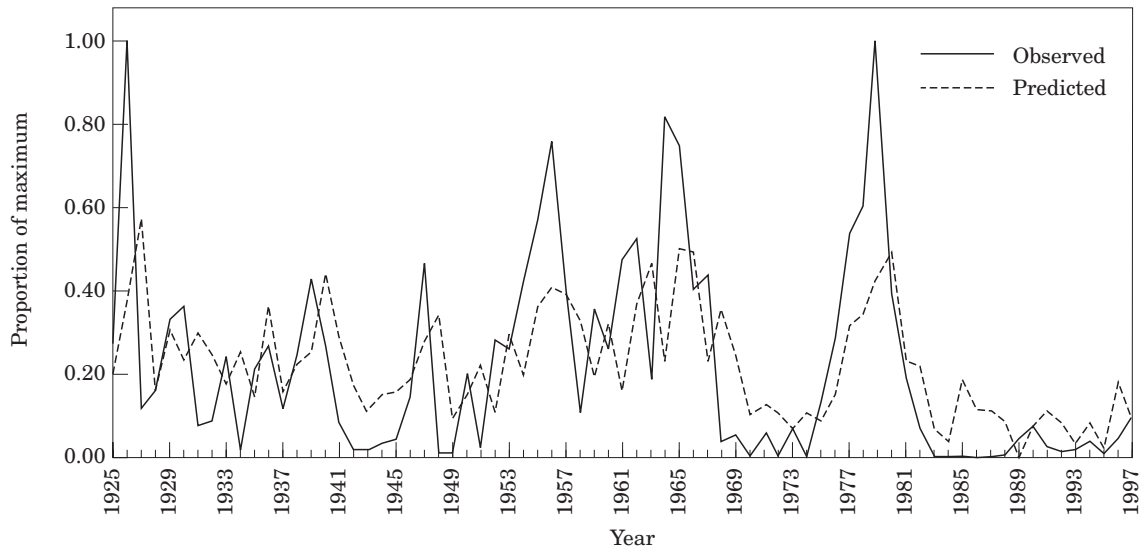
NAO, BT and SSF as input variables, was reduced to one that included only Year, NAO and SSF as significant explanatory variables. This model accounted for 69% of the variability in catch (Table 4; Fig. 6a). As in the model based on the longer time series, the autoregressive parameter was the main determinant of catch. Both NAO and SSF were negatively correlated with catch. The significant negative effect of Year in this model was due to a decrease in the catch throughout the time series.

This second model was also tested using the survey catch rate as the dependent variable, for the same time period. As with the previous analyses, we began with the

Figure 5. Comparison of empirical catch index values with those predicted by the model: $C_t = a + b\,(NAO_t) + v_t$.

Table 4. Description statistics and parameter estimates for the catch model $C_t = a + cY_t + b_1\,(NAO_t) + b_2(SSF_t) + v_t$.

Sum of square error	0.450		
Mean square error	0.023		
df Error	20		
r^2	0.69		
Parameter	Estimate	t	p
Autoregressive (q)	− 0.403	− 1.97	—
Intercept (a)	1.047	1.88	0.08
Year (c)	− 0.010	− 1.57	0.13
NAO (b_1)	− 0.082	− 2.21	0.04
SSF (b_2)	− 0.391	− 1.97	0.06

Gulf Stream and shelf-slope fronts are also positively correlated; i.e. they tend to move north or south together. The high-frequency (short-period) variability, indicative of meandering, tends to be greatest when the Gulf Stream is further to the south, although the cause is uncertain.

Higher squid abundance in Canadian waters, as well as for the total Northwest Atlantic, occurs in years of weak atmospheric circulation (low NAO index), warm conditions in the Newfoundland area (higher temperatures and less ice), a southward movement of the oceanic fronts (the Gulf Stream and shelf-slope boundary) and more meandering of the Gulf Stream. Our results of warmer conditions promoting higher squid abundance confirms earlier findings (Dawe and Warren, 1993), although we had hypothesized, based on that study, that warm conditions and high squid abundance were related to northward rather than southward displacement of the Gulf Stream. The causative mechanisms between environmental indices and squid are unclear, however,

as is often the case with such heuristic models (Fogarty, 1989). The strong linkages between the environmental indices contribute to the difficulty in sorting out the mechanisms but certain hypotheses can be advanced.

Such hypotheses must not only be consistent with the environmental relationships described, but must also be able to account for observed patterns of population abundance and distribution. Annual abundance and recruitment trends are similar among all fishery areas off North America, but variability increases with distance downstream of the spawning area (Dawe and Warren, 1993). The greater stability for the most southern fishery area off the USA may reflect availability of multiple population components (i.e. spawning groups) while increased recruitment variability in the areas further to the northeast may be because of dependence on the highly-variable winter-spawning group. In years when total population abundance is high, recruitment tends to be highest in the most northeastern areas.

This pattern suggests that some mechanism concurrently regulates both total population abundance and the portion of the population that recruits to fishery areas near the northeastern limit of their distribution. Annual variability in abundance and recruitment in fishery areas so remote from the spawning area may be related to variability in efficiency of downstream advection, variability in annual survival in such marginal habitat, or both. On this basis, two possible mechanisms are hypothesized, which are not necessarily mutually exclusive.

One hypothesis is that latitudinal displacement of fronts is related to variation in efficiency of downstream dispersal. This dispersal not only includes the along-Stream transport, but the movement of the squid across
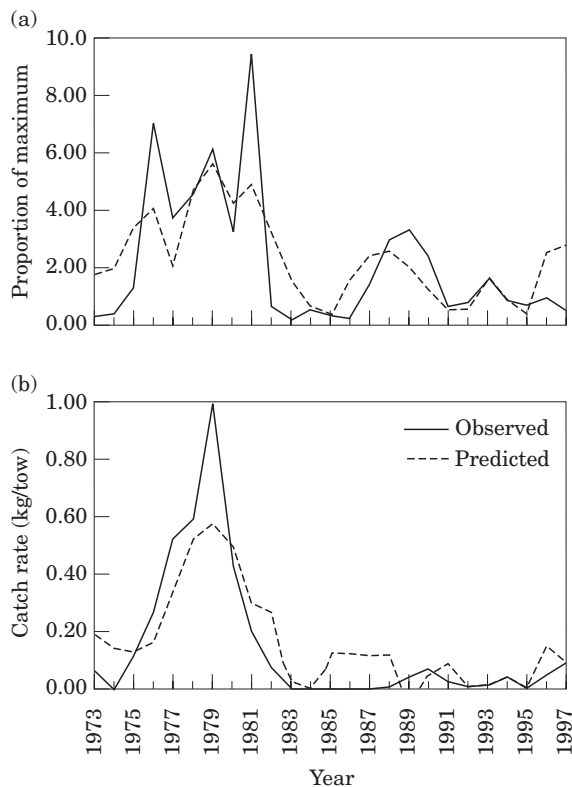
(a)

(b)

Figure 6. Comparison (a) of empirical catch indices with those predicted by the model: $C_t = a + cY_t + b_1 (NAO_t) + b_2 (SSF_t) + v_t$ and (b) of empirical USA survey catch rates with those predicted by the model: $CR_t = a + cY_t + b (BT_t) + v_t$.

Table 5. Descriptive statistics and parameter estimates for the catch rate model $CR_t = a + cY_t + b (BT_t) + v_t$.

Sum of square error	77.862		
Mean square error	3.708		
df Error	21		
r^2	0.43		
Parameter	Estimate	t	p
Autoregressive (q)	0.073	0.34	—
Intercept (a)	10.786	2.51	0.02
Year (c)	−0.093	−1.83	0.08
BT (b)	4.838	3.55	0.002

the slope water region to the SSF and their feeding grounds near the continental shelf. This hypothesis is consistent with the idea that favourable transport conditions promote recruitment success (Bakun and Csirke, 1998). Such conditions could affect paralarvae as well as small juveniles, which probably do not become active migrators until they achieve about 3 cm mantle length (Dawe and Beck, 1985b).

Our statistical results indicate high levels of squid abundance in years when the GSF and SSF were displaced south. These were also years of increased

meandering and reduced transport of the Stream. Southward displacement of the fronts would not be expected to enhance downstream advection, however, because a decreased volume transport implies reduced speed and meandering results in increased effective Stream length.

Why then should a Gulf Stream that is displaced away from the shelf, slow, and meandering extensively, be advantageous to squid? One possibility is that it relates to meander-induced upwelling at the GSF. Upwelling and subsequent biological enrichment occurs on the divergent side (anticyclonic curvature) of a meander (Arnone et al., 1990). This may provide increased food supply for paralarvae at the GSF, increasing their chances of survival (Bakun and Csirke, 1998). The more meandering, the more upwelling and the higher the probability of survival. An increased survival rate would allow more squid to reach the northeastern region of their range. A second possibility is that diffusion processes related to the meander activity may eject juveniles from the GSF towards the SSF (Bakun and Csirke, 1998). Thus, years during which there was more meandering (with subsequent increased transport of squid towards the shelf) would be years of high abundance. The importance to squid of the high-frequency variability (meandering) in the Gulf Stream was further indicated by the results of step wise regression analysis, although we recognize that these are based upon only a few years.

The increased meandering may at first thought be expected to increase the number of warm-core eddies (WCEs). These anticyclonic eddies are frequently formed by the "pinching-off" of Gulf Stream meanders (Trites, 1983) and large quantities of larvae and juveniles are entrained in their periphery (Dawe and Beck, 1985b). Thus, WCEs represent "concentrated packages" of young squid. However, contrary to expectations, more WCEs have been found to be associated with a northward, rather than a southward, displacement of the fronts (Myers and Drinkwater, 1989). Since squid are more abundant when the fronts are further south, this suggests that WCEs are inhibitory. This is consistent with our dispersion hypothesis and the idea of Bakun and Csirke (1998) that WCEs limit downstream dispersal of squid. The argument is that once an eddy separates from the Stream, it tends to move southwestward through the slope water, carrying squid with it. These eddies continue until they dissipate or are reabsorbed by the Stream, some travelling as far "upstream" as Cape Hatteras before being reabsorbed (Trites, 1983). Eddies can thereby transport squid upstream and certainly inhibit transport of squid to the northeast.

It is possible that a retention mechanism may also exist nearer the spawning area, upstream of Cape Hatteras. Data from winter surveys limited to years of low abundance (1983–1985), showed that paralarvae

and juveniles caught upstream of Cape Hatteras ranged broadly in size (Rowell and Trites, 1986; Rowell *et al.*, 1985a). During one survey, mean size even increased to the southwest. It was suggested that, despite the potential for rapid downstream transport, some mechanism might exist for retaining and eventually mixing successive broods (Rowell *et al.*, 1985a). Such mechanisms may be more operative during periods of low abundance.

The second hypothesized mechanism is that warm conditions in Canadian waters directly or indirectly promote rapid growth and high survival, particularly in the vicinity of the SSF. Growth rate is a function of size, food ration, and conversion efficiency, the latter being temperature-related (O'Dor *et al.*, 1980; Forsythe and van Heukelem, 1987; Forsythe, 1993). Perez and O'Dor (1998) suggest that the Gulf Stream Front is a suitable habitat for paralarvae, but that life in the Stream eventually becomes too costly for juvenile squid because of food limitation and the energetical expenses due to the high temperatures. They further note that juvenile growth improves shoreward as the squid abandon the Gulf Stream and approach the SSF off the Canadian east coast. This is thought to reflect increased conversion efficiency at lower temperatures together with increased food availability within the slope waters and at the SSF in particular. The importance of food at the shelf/slope front could explain the negative correlation observed between squid and the SSF observed. A possible scenario is that in years when the SSF is displaced south, the squid are able to reach it and its associated high food concentrations relatively early, with resulting increased survival. If reaching their food supply early was advantageous, then the factor controlling abundance might be expected to be the distance squid have to travel from when they leave the Stream until they reach the SSF. Correlations of the distance between the SSF and GSF with squid, however, were low and not significant.

The role of WCEs, under this second hypothesis could be quite different from that suggested under the dispersion hypothesis. Smith (1978) and Trites (1981) have shown that eddies close to the shelf tend to entrain significant amounts of shelf waters offshore into the slope water region. Offshore transport, away from the SSF and high food concentrations, of fish larvae spawned on the shelf and shelf edge by WCEs has also been observed (Drinkwater *et al.*, 2000). Years with low number of eddies would thus be advantageous for squid.

Neither of the two hypotheses we advanced address the possibility that year-class strength may be established early, at the paralarval stage. This is suggested by the similarity in recruitment trends among fishery areas. Also, winter surveys downstream of Cape Hatteras suggest that year-class strength is established during the passive paralarval-early juvenile stage, although this is uncertain due to changes in sampling methodology

(Dawe and Beck, 1985b). Establishment of recruitment levels early in the life cycle would also be consistent with studies by Sakurai *et al.* (2000) on the Japanese common squid (*Todarodes pacificus*), another ommastrephid squid with a life cycle remarkably similar to that of short-finned squid, which inhabits the Kuroshio Current, a Western Boundary Current like the Gulf Stream. They found that year-class strength of *T. pacificus* was established at the paralarval stage and was related to oceanographic variability within the spawning area.

We still consider it likely that the main elements of both hypothesized mechanisms have roles in year-class strength regulation. Furthermore, the relationships between the variability in the Gulf Stream and the shelf-slope front with inshore Newfoundland temperature fluctuations imply that environmental variability affects all life history stages, including large recruited maturing squid. If this were not the case then, logically, a "bottleneck" would exist at some stage that limits recruitment in all years. Conceivably, there is a limited carrying capacity for squid and the southern region approaches its relatively stable limit each year. The carrying capacity near the northeastern limit of distribution may be much more variable with higher capacity in warm years.

These scenarios, and the broad-scale interrelationships that support them, are consistent with a general life history strategy proposed for short-finned squid (O'Dor and Coelho, 1993; Coelho *et al.*, 1994), and elaborated upon for squid generally (O'Dor, 1998a, 1998b). This strategy was based on recognition that temperate squid species, with annual life cycles, cannot maintain genetic diversity and recruitment stability through the co-existence of multiple year classes, as fishes do. The proposed strategy is that squids achieve stability by broadly distributing reproductive effort in time (seasonally) and space. In the case of broadly-distributed species in large current systems, including *I. illecebrosus* and *T. pacificus*, several spawning groups provide some annual stability in areas near the spawning ground. Total population size or year-class strength is affected predominantly by the winter spawning group, the progeny of which are advected to northern waters in synchrony with the spring productivity peak. This strategy is highly adaptive in that environmental conditions which promote strong year classes also favour population expansion through expedient advection of young stages and a suitable oceanographic regime in the northern-most area. Individuals of the broadly-distributed winter-spawning group are strongly selected for large body size because near maximum growth and delayed maturation may be necessary to survive the lengthy spawning migration and complete the life cycle. In direct support of this strategy, it appears that squid body size at Newfoundland is positively related to

recruitment, indicating early peak spawning or rapid growth rate in warm years of high abundance (Dawe *et al.*, 1999).

Finally, the basic causal mechanism affecting the oceanographic regime throughout the range of distribution of short-finned squid is probably broad-scale atmospheric forcing, reflected in the NAO index. This is supported by our statistical analysis in terms of the effect of the NAO on both squid and on the other important environmental indices. Atmospheric forcing may also regulate paralarval production and survival in tropical waters through its effect on the intensity and location of the Gulf Stream. At the northern limit of the squid distribution, atmospheric forcing associated with changes in the NAO index also regulates the physical oceanographic regime and probably, in turn, biological productivity.

Acknowledgements

References

Arnone, R. A., Newo, R. W., Jech, J. M., and De Palma, I. 1990. Acoustic imaging of biological and physical processes within Gulf Stream meanders. EOS Transactions, American Geophysical Union, 71: 982.

Bakun, A., and Csirke, J. 1998. Environmental processes potentially involved in recruitment variability of *Illex* squids. *In* Squid Recruitment Dynamics, pp. 105–124. Ed. by P. G. Rodhouse, E. G. Dawe, and R. K. O'Dor. Food and Agriculture Organization of the United Nations Fisheries Technical Paper. No. 376. FAO, Rome. xii+273 pp.

Coelho, M. L., Stobberup, K. A., O'Dor, R. K., and Dawe, E. G. 1994. Life history strategies of the squid, *Illex illecebrosus*, in the Northwest Atlantic. Aquatic Living Resources, 7: 233–246.

Colbourne, E., Narayanan, S., and Prinsenberg, S. 1994. Climatic changes and environmental conditions in the Northwest Atlantic, 1970–93. ICES Journal of Marine Science, Marine Science Symposia, 198: 311–322.

Dawe, E. G. 1981. Development of the Newfoundland squid (*Illex illecebrosus*) fishery and management of the resource. Journal of Shellfish Research, 1: 137–142.

Dawe, E. G., and Beck, P. C. 1985a. Distribution and size of short-finned squid (*Illex illecebrosus*) larvae in the Northwest Atlantic from winter surveys in 1969, 1981, and 1982. Journal of Northwest Atlantic Fishery Science, 6: 43–55.

Dawe, E. G., and Beck, P. C. 1985b. Distribution of size of juvenile short-finned squid (*Illex illecebrosus*) (Mollusca: Cephalopoda) south of Newfoundland during winter. Vie et Milieu, 35: 139–147.

Dawe, E. G., Beck, P. B., and Drew, J. 1999. The fishery for short-finned squid (*Illex illecebrosus*) in NAFO Subareas 3 and 4 in 1998. Northwest Atlantic Fisheries Organization

Scientific Council Research Document 99/50, Ser. No. N4109, 13 pp.

Dawe, E. G., and Hendrickson, L. C. 1998. A review of the biology, population dynamics, and exploitation of short-finned squid in the Northwest Atlantic Ocean, in relation to assessment and management of the resource. Northwest Atlantic Fisheries Organization Scientific Council Research Document 98/59, Ser. No. N3051, 33 pp.

Dawe, E. G., and Warren, W. G. 1993. Recruitment of short-finned squid in the Northwest Atlantic Ocean and some environmental relationships. Journal of Cephalopod Biology, 2: 1–21.

Drinkwater, K. F. 1996. Atmospheric and oceanographic variability in the Northwest Atlantic during the 1980s and early 1990s. Journal of Northwest Atlantic Fishery Science, 18: 77–97.

Drinkwater, K. F., Colbourne, E., and Gilbert, D. 1999. Overview of environmental conditions in the Northwest Atlantic in 1997. Northwest Atlantic Fisheries Organization Scientific Council Studies, 32: 75–121.

Drinkwater, K. F., Lochman, S., Taggart, C., Thompson, K., and Frank, K. 2000. Entrainment of redfish (*Sebastes* sp.) larvae off the Scotian Shelf. ICES Journal of Marine Science, 57: 377–382.

Drinkwater, K. F., Myers, R. A., Pettipas, R. G., and Wright, T. L. 1994. Climatic data for the Northwest Atlantic: The position of the Shelf/slope front and the northern boundary of the Gulf Stream between 50°W and 75°W, 1973–1992. Canadian Data Report of Hydrography and Ocean Sciences 125: iv+103 pp.

Fogarty, M. J. 1989. Forecasting yield and abundance of exploited invertebrates. *In* Marine invertebrate fisheries: their assessment and management, pp. 701–724. Ed. by J. F. Caddy. John Wiley and Sons Inc., Toronto. xvi+752 pp.

Forsythe, J. W. 1993. A working hypothesis on how seasonal temperature change may impact the field growth of young cephalopods. *In* Recent Advances in Cephalopod Fisheries Biology: Contributed Papers to 1991 CIAC International Symposium and Proceedings of the Workshop on Age, Growth and Population Structure, pp. 591–606. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo. xv+752 pp.

Forsythe, J. W., and Van Heukelem, W. F. 1987. Growth. *In* Cephalopod life cycles, Vol. II, Comparative reviews, pp. 135–156. Ed. by P. R. Boyle. Academic Press, London. xxi+441 pp.

Hatanaka, H., Lange, A. M. T., and Amaratunga, T. 1985. Geographical and vertical distribution of larval short-finned squid (*Illex illecebrosus*) in the Northwest Atlantic. Northwest Atlantic Fisheries Organization Scientific Council Studies, 9: 93–99.

Hedges, L. V., and Olkin, I. 1985. Statistical methods for Meta-analysis. Academic Press, San Diego. xxi+369 pp.

Hurley, G. V. 1980. Recent developments in the squid, *Illex illecebrosus*, fishery of Newfoundland, Canada. Marine Fisheries Review, 42: 15–22.

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. Food and Agriculture Organization of the United Nations Fisheries Technical Paper 31: ix+452 pp.

Mann, K. H., and Drinkwater, K. F. 1994. Environmental influences on fish and shellfish production in the Northwest Atlantic. Environmental Reviews, 2: 16–32.

Mercer, M. C. 1973. Nominal catch of squid in Canadian Atlantic waters (Subareas 2–4) 1920–68. International

Commission for Northwest Atlantic Fisheries Research Document 73/73, 10 pp.

Montevecchi, W. R., and Myers, R. A. 1995. Prey harvests of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. Marine Ecology Progress Series, 117: 1–9.

Montevecchi, W. R., and Myers, R. A. 1997. Centurial and decadal oceanographic influences on changes in northern gannet populations and diets in the north-west Atlantic: implications for climate change. ICES Journal of Marine Science, 54: 608–614.

Myers, R. A. 1997. Recruitment variation in fish populations assessed using meta-analysis. *In* Early life history and recruitment in fish populations, pp. 451–467. Ed. by R. C. Chambers, and E. A. Trippel. Chapman and Hall, London.

Myers, R. A., and Drinkwater, K. 1989. The influence of Gulf Stream warm core rings on recruitment of fish in the Northwest Atlantic. Journal of Marine Research, 47: 635–656.

NAFO 1998. Report of the Scientific Council. June 1998 meeting. Northwest Atlantic Fisheries Organization Scientific Council Report 1998: 1–154.

O'Dor, R. K. 1998a. Squid life-history strategies. *In* Squid recruitment dynamics. The genus *Illex* as a model. The commercial *Illex* species. Influences on variability, pp. 233–254. Ed. by P. G. Rodhouse, E. G. Dawe, and R. K. O'Dor. Food and Agriculture Organization of the United Nations Fisheries Technical Paper. No. 376. FAO, Rome. xii+273 pp.

O'Dor, R. K. 1998b. Can understanding squid life-history strategies and recruitment improve management? South African Journal of Marine Science, 20: 193–206.

O'Dor, R. K., and Coelho, M. L. 1993. Big squid, big currents, and big fisheries. *In* Recent advances in cephalopod fisheries biology, pp. 385–396. Ed. by T. Okutani, R. K. O'Dor, and T. Kubodera. Tokai University Press, Tokyo. xv+752 pp.

O'Dor, R. K., and Wells, M. J. 1987. Energy and nutrient flow. *In* Cephalopod life cycles, Vol. II, Comparative Reviews, pp. 109–134. Ed. by P. R. Boyle. Academic Press, London. xxi+441 pp.

Perez, J. A. A., and O'Dor, R. K. 1998. The impact of environmental gradients on the early life inshore migration of the short-finned squid *Illex illecebrosus*, pp. 293–303. Ed. by A. I. L. Payne, M. R. Lipinski, M. R. Clarke, and M. A. C. Roeleveld. South African Journal of Marine Science, 20. 469 pp.

Prinsenberg, S. J., Peterson, I. K., Narayanan, S., and Umoh, J. U. 1997. Interaction between atmosphere, ice cover, and ocean off Labrador and Newfoundland from 1962 to 1992. Canadian Journal of Fisheries and Aquatic Sciences, 54: 30–39.

Rowell, T. W., and Trites, R. W. 1985. Distribution of larval and juvenile *Illex* (Mollusca: Cephalopoda) in the Blake Plateau region (Northwest Atlantic). Vie et Milieu, 35(3/4): 149–161.

Rowell, T. W., Trites, R. W., and Dawe, E. G. 1985a. Larval and juvenile distribution of short-finned squid (*Illex illecebrosus*) in relation to the Gulf Stream frontal zone in the Blake Plateau and Cape Hatteras area. Northwest Atlantic Fisheries Organization Scientific Council Studies, 9: 77–92.

Rowell, T. W., Young, J. H., Poulard, J. C., and Robin, J. P. 1985b. Changes in distribution and biological characteristics of *Illex illecebrosus* on the Scotian Shelf, 1980–83. Northwest Atlantic Fisheries Organization Scientific Council Studies, 9: 11–26.

Sakurai, Y., Kiyofuji, H., Saitoh, S., Goto, T., and Hiyama, Y. 2000. Changes in inferred spawning areas of *Todarodes pacificus* (Cephalopoda: Ommastrephidae) due to changing environmental conditions. ICES Journal of Marine Science, 57: 24–30.

Smith, P. C. 1978. Low-frequency fluxes of momentum, heat, salt, and nutrients at the edge of the Scotian Shelf. Journal of Geophysical Research, 83: 4079–4096.

Squires, H. J. 1957. *Illex illecebrosus* (LeSueur), in the Newfoundland fishing area. Journal of the Fisheries Research Board of Canada, 14: 693–728.

Taylor, A. H. 1996. North-south shifts of the Gulf Stream: Ocean-atmospheric interactions in the North Atlantic. International Journal of Climatology, 16: 559–583.

Trites, R. W. 1981. Application of satellites and remote sensing to studies of surface circulation off the Nova Scotian coast. *In* Oceanography in Space, Vol. 13, Marine Science, pp. 189–194. Ed. by J. F. R. Gower. Plenum Press, New York.

Trites, R. W. 1983. Physical oceanographic features and processes relevant to *Illex illecebrosus* spawning in the western North Atlantic and subsequent larval distribution. Northwest Atlantic Fisheries Organization Scientific Council Studies, 6: 39–55.

WCRP 1998. CLIVAR Initial Implementation Plan. World Climate Research Programme No. 103, p. 356.