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Environmental Regulation of the Relative Abundance of Two Squid Species in the Northwest Atlantic Ocean, *Illex illecebrosus and Loligo pealei*

by

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Abstract

An unusually high abundance of long-finned squid (*Loligo pealeii*) at Newfoundland in 2000 is described. Prevalence of maturing females and mature males within samples, together with the collection of a single viable egg mop, provide the first evidence of spawning of this species at the northern limit of its geographic range of distribution. Trends in size and abundance of short-finned squid (*Illex illecebrosus*) suggest that this northward expansion of the long-finned squid population may be related to relief of competition. Trends in local water temperature at Newfoundland suggest that this phenomenon may also be related to environmental variation. We apply time series analysis, with biological and environmental input variables, to each of long-finned and short-finned squid to address the hypothesis that these two species share, to a large extent, a common niche on the Northeast USA Shelf and that opposing responses to ecosystem variation regulate their relative abundance. The resultant models indicate that north-south shifts in location of the Shelf water-Slope Front (SSF) is closely related to direct oceanographic processes that affect both squid species. While these two species exhibit opposing responses to variation in the oceanographic regime, direct mechanisms that regulate year class strength remain unknown. It is quite possible that mechanisms differ between the two species, with local variables directly affecting long-finned squid and broad-scale factors affecting short-finned squid. The expansion of the long-finned squid population in 2000 was associated with an unusual eastward displacement of an intense NAO that may have resulted in unfavourable oceanic conditions for short-finned squid but favourable environmental conditions for long-finned squid on the continental shelf as far north as southern Newfoundland.

Introduction

Cephalopods represent an important component of most major continental shelf ecosystems. Pelagic squids in these ecosystems may be suitable indicator species of environmental or other ecosystem change because their populations respond very quickly to annual variation in the ecosystem. These species generally have annual life cycles that provide for rapid and easily detected response to ecosystem variation. Many species are broadly distributed spatially and highly migratory, providing for rapid response in terms of distribution patterns, especially near the limits of their ranges of distribution. Highly variable annual population sizes and growth rates imply easily detected responses in terms of abundance, size, growth rate and condition. Large population size and high biomass provide, through economic importance, the tools (commercial catches and survey indices) to monitor and measure annual changes in distribution, abundance, and size, that can be related to other ecosystem changes.

Generally, the cephalopod fauna in most continental shelf ecosystems globally is dominated by commercially exploited pelagic squids of the families Ommastrephidae (short-finned squids) and Loliginidae (long-finned squids). While these squids are commonly sympatric to a large extent, the ommastrephids are typically oceanic and more highly migratory than the typically neritic loliginids. The most well studied of such sympatric loliginids and ommastrephids are *Loligo pealeii* and *Illex illecebrosus* in the northwest Atlantic Ocean. Time series of data from fisheries and surveys are available for both these species for more than 30 years.

The long-finned squid (*Loligo pealeii*) is distributed from the Gulf of Venezuela to Newfoundland (Summers, 1983; Dawe *et al.*, 1990) and seasonal changes in distribution are limited to the continental shelf. The short-finned squid (*Illex illecebrosus*) is distributed from off central Florida to southern Labrador (Dawe *et al.*, 2000) and its life cycle includes an initial oceanic phase before it moves onto the continental shelf. While the northern limits of distribution of both species are similar, the short-finned squid may be commercially fished at its northern limit whereas long-finned squid seldom occur north of Brown's Bank on the Nova Scotian Shelf (Summers, 1983) and the commercial fishery does not extend north of Georges Bank and the Gulf of Maine. Both species coexist in high abundance, and support commercial fisheries, on the USA continental shelf north of Cape Hatteras.

Spatial and seasonal variation in distribution of both species is closely related to oceanographic variation (Trites, 1983; Rowell *et al.*, 1985; Dawe and Warren, 1993; Dawe *et al.*, 2000). Brodziak and Hendrickson (1999) found that the long-finned squid was more strongly associated with spatial variation in environmental factors than was the short-finned squid during autumn on the Northeast USA Shelf. Annual variation in abundance of short-finned squid has also been related to oceanographic variation (Dawe *et al.*, 2000). Dawe and Brodziak (1998) suggested that predatory and competitive interaction between these two species also plays a role in regulation of their annual abundance levels.

In this paper we describe a very unusual expansion of the distribution of long-finned squid in 2000 and we consider possible causative factors. We also hypothesize that these two species share, to a large extent, a common niche on the Northeast USA Shelf and that opposing responses to ecosystem variation regulate their relative abundance. We address this hypothesis by identifying a suite of possible causal biological and environmental variables and we use these as input variables in time series analysis to compare their relative effects on abundance between the two species.

Methods

Observations at Newfoundland in 2000.

A long-finned squid egg mop was collected by SCUBA at Bay Bulls, Newfoundland (Fig. 1), on 15 August 2000. A sample of long-finned squid specimens was acquired by fishing rod with unbaited lure from a beach near Burin, close to the southern extreme of insular Newfoundland (Fig. 1), during 5-6 September 2000. Seasonally comparable data on short-finned squid were available from a near-shore site in Trinity Bay, Nfld. (Fig.1) during the first half of September of 1998 and 2000. Biological sampling for both squid species included determination of sex, mantle length (ML, 0.5 cm) and sexual maturity. The maturity scale of Mercer (1973) was used for short-finned squid whereas that of Macy (1982) was used for long-finned squid. Local inshore monthly temperature data were acquired from thermographs deployed at Arnold's Cove in Placentia Bay (Fig. 1) during 1995-2000. A longer time series (1970-2001) of bottom temperature data was available for southern Newfoundland from April-June annual bottom trawl surveys on the St. Pierre Bank, south of the Burin Penninsula.

Time series analysis.

Time series analysis was performed, for each species, using two different squid abundance indices. First, our catch model used commercial catch (C, t) for the entire Northwest Atlantic Ocean as the dependent variable. Our second model (catch rate model) used catch rate (CR, stratified mean number per tow) from autumn bottom trawl surveys on the Northeast USA Shelf as the dependent variable. Surveys have been conducted annually on the

Northeast USA Shelf, during spring (Feb-Apr), since 1968 and during autumn (Sep-Dec) since 1967. We based our catch rate model dependent variables on the autumn survey series because both species are more abundant and more-broadly distributed within the survey area during autumn than in spring (Fig. 2). The commercial catch (C*, t) or autumn survey catch rate (CR*, stratified mean number per tow) of the other squid species was included as a biological input variable in developing the catch and catch rate models, respectively. Mean body weight (BW, kg) and mean body weight of the other squid species (BW*) were also included as input variables for all models, but were not derived from the autumn survey data, so as to assure their independence from the response variable. This size index, for long-finned squid, was derived from the spring USA survey series, whereas for short-finned squid it was derived from July bottom trawl surveys on the Nova Scotian Shelf, which have been conducted annually since 1970.

Environmental variables selected as input variables in the modelling exercise included mean bottom temperature from the spring survey series on the Northeast USA Shelf (USAbt). Other environmental indices used were more broad-scale, included the North Atlantic Oscillation (NAO) index, that reflects the large-scale atmospheric circulation pattern across the north Atlantic Ocean, and bottom temperature at Station 27 (NFbt), an oceanographic station located 10 nm east of St. John's Nfld. 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. The NAO is expressed here as an annual anomaly relative to the mean for the period 1971-2001. The Station 27 bottom temperature index off Nfld. (NFbt) is the mean temperature at a bottom depth of 176 m, for the first half of each year (Jan-June), and it represents an index of the influence of the cold Labrador Current. An index of the position of the Shelf-Slope Front (SSF) was also included as an off-shelf oceanic index. Monthly means of the latitudinal position of the SSF at each degree of longitude from 50°W to 75°W between 1973-92 were estimated from satellite imagery by Drinkwater *et al*. (1994) and have been updated to 2001. Annual SSF indices were defined as the annual mean displacements (km) of the fronts averaged over all available longitudes.

Time-series analysis was applied, using the catch and catch rate indices as dependent variables for each species. Thus, four models were derived, a catch and a catch rate model for each species. All modelling was based on the 1973-2001 time series, for which reliable data were available for all variables. Model development involved initially testing for the existence of autocorrelation at successive lags and identifying an appropriate process to account for autocorrelation. We found, in some of our models, 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 (AR1), was then run with the squid catch or catch rate index as the dependent variable and year, as well as the selected biological and environmental indices, as the independent variables. The general form of the initial full models can be expressed as

$$C_t = a + b_1X_{1t} + b_2X_{2t} + \ldots + cY_t + v_t$$

and

$$CR_t = a + b_1X_{1t} + b_2X_{2t} + \ldots + cY_t + v_t$$

where C_t and CR_t are the catch and the catch rate index respectively at time t, a is the model intercept, X_i is an input variable (biological or 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

$$v_t = e_t - qv_{t-1}$$

where q is the autocorrelation function or autoregressive parameter and e_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.

Relationships among the environmental indices that were used as model input parameters and the biological indices that were retained in final models were explored using simple correlation analysis. Pearson's correlation coefficients with associated probability levels were compared among all pair-wise comparisons.

Correlations were interpreted as significant based on the conventional 0.05 probability level. All modelling and statistical analysis was performed using SAS Basics software (SAS Institute Inc., Cary, North Carolina).

Results and Discussion

Expansion of long-finned squid distribution in 2000.

A long-finned squid egg mop was collected at Bay Bulls Nfld., on Aug 15 at a depth of about 8 m. It was maintained in the laboratory at ambient inflow temperatures of 14-18°C. All eggs hatched within 24-36 days. Long-finned squid were reported to be abundant throughout August at many coastal communities on the Burin Penninsula of insular Newfoundland (Fig. 1), the southern-most extreme of the Island. During this month long-finned squid were attracted to lights on community wharves at night, when they supported a recreational food fishery using rods with unbaited lures.

A sample of 516 long-finned squid was acquired by fishing rod near Burin (Fig. 1) during Sep 5-6, 2000. This sample (Fig. 3) comprised mostly males (74%). Females were mostly smaller than 20 cm ML and were in an advanced stage of maturation, although none were fully mature. Males were mostly larger than 20 cm ML, and most of these large males were fully mature. The advanced state of maturity of these specimens, together with the collection of a viable egg mop provides the first evidence of spawning as far north as Newfoundland. The 45 specimens collected at Newfoundland in 1986 did not include any mature animals (Dawe *et al.*, 1990).

Long-finned squid females were of comparable size to the first of two modal groups of short-finned squid, collected at about the same time in 2000, whereas male long-finned squid were considerably larger than male short-finned squid (Fig. 3). Comparison of the early-September size composition of short-finned squid between 2000 and 1998 at Newfoundland shows that squid were much smaller in 2000. Although no short-finned squid samples were collected at Newfoundland in 1999, their mean weight on the Scotian Shelf in July had dropped sharply from 1999 to 2000 (Fig. 4), to a record small size seen previously only in 1983. The unusually small size of short-finned squid in Canadian waters in 2000 implies that relief from competition may have contributed to the high abundance of long-finned squid at Newfoundland. Another element of reduced competition is a very low abundance of short-finned squid in 2000 (Fig. 5). Expansion of long-finned squid into Canadian waters in 2000 may have been related to small size and low abundance of short-finned squid together with very high total population abundance of long-finned squid (Fig. 5).

Oceanographic conditions during 2000 may also have contributed to the northward expansion of the long-finned squid population. Local near-shore monthly water temperature at Arnold's Cove Placentia Bay was highest in August of 2000 (14.7 °C, Fig. 6), when long-finned squid were prevalent. August is typically the warmest month, and, while August temperature was not highest in 2000, only 1999 was warmer for earlier months within the past decade (Fig. 6). A longer time series of spring temperature data for offshore areas indicates that the St. Pierre Bank, off the South Coast of Newfoundland, where long finned squid were prevalent in Aug 2000, is warmer than on the Grand Bank off Eastern Newfoundland (Fig. 7). This temperature series also shows that the annual spring bottom temperature on the St. Pierre Bank was warmer in 1999 and 2000 than in any year since 1983.

Squid abundance models.

Our modelling approach is a comparative one, comparing between species for any given model (catch versus catch rate models), and comparing between models for each species. Catch models are broadly representative spatially but are subject to biases associated with annual variation in effort levels, and other fishing practices. In contrast the catch rate models are not subject to such fishery effects, but are spatially more restricted than the catch models, being based upon the Northeast USA Shelf survey area (Fig. 2). Our comparative approach includes seeking common effects between the two types of models.

The fishery-based catch models (Table 1, Fig. 8) provided better fits to the empirical data than did the survey-based catch rate models (Table 2, Fig. 9) for both species. However this difference between model types can be largely attributed to a much higher degree of autocorrelation in the catch series than in the catch rate series. The autoregressive parameter was a significant contributor to the catch model for both species (Table 1) and was by far the most significant model parameter ($p<0.0001$) for short-finned squid. The only environmental variable retained in the catch models was the NAO index, which was common to both species and highly significant (p = 0.01) in both cases. However it had opposing effects between species, being inversely related to catch of short-finned squid but directly related to catch of long-finned squid. This suggests opposing responses to environmental variation between species.

Although the survey-based catch rate models do not explain as much of the total variation in the response variables for either species as do the catch models, they are less strongly affected by trends in fishing practises, as reflected by the relative unimportance of the autoregressive parameter (Table 2, Fig. 9). As in the catch models, the NAO was a significant contributor, and had opposing effects between species (Table 2). However the SSF index was a much more important parameter than the NAO for both species, and it also had opposing effects between species. This implies that the actual causal mechanisms that regulate the relative abundance of these species are more directly related to Gulf Stream System dynamics than to atmospheric forcing.

The catch rate model was virtually unaffected by autocorrelation for short-finned squid, as reflected by the insignificant autoregressive parameter (p = 0.70, Table 2), whereas this parameter was significant for the long-finned squid model (p = 0.06, Table 2). Environmental variables were much more important contributors to the catch rate model for short finned squid than for long-finned squid. The SSF was more highly significant for short-finned squid (p=0.002) than for long-finned squid (p = 0.05), and the short-finned squid model retained an additional environmental variable (USAbt) that was very highly significant (p = 0.0008, Table 2).

It is not surprising that trends in abundance are more closely related to environmental variation for the highly-migratory oceanic species (short-finned squid) than for the more localized neritic species (long-finned squid). However, the negative effect of local bottom temperature (USAbt) on short-finned squid catch rate appears to be in conflict with an overall direct effect of a warm oceanographic regime on short-finned squid abundance (Dawe *et al.*, 2000). This inconsistency may be explained by considering the interrelationships of all environmental variables included in our modelling exercise (Table 3). The two bottom temperature indices (USAbt and NFbt) are inversely related, although not significantly (r = -0.19, p = 0.30) and they have opposing (but not significant) associations of comparable magnitude with the NAO (Table 3). The most significant environmental parameter common to both catch rate models (SSF) is very strongly and inversely correlated with the northern bottom temperature index (NFbt, r = -0.5, p = 0.005, Table 3). Therefore, southward displacement of this ocean front (SSF), which is strongly related to high squid abundance, is also strongly related to high bottom temperature at the northern extreme of short-finned squid distribution.

Our modelling results also showed some consistencies with respect to effects of biological indices. For example, the abundance index and mean size index of the competitor squid species (CR* and BW* respectively) were consistently rejected from all four models, suggesting that direct competition is not a significant determinant of abundance for either species. However mean body weight of the modelled species (BW) was a significant contributor to one of the models for each squid species (Tables 1-2). BW was inversely related to survey catch rate of long-finned squid (t = -2.46, p = 0.02, Table 2), whereas it was directly related to commercial catch of short-finned squid (t = 2.44, p = 0.02, Table 1). The direct relationship between mean body weight and catch of short-finned squid could simply reflect the increase in direct contribution of each squid to catch weight with increasing BW. However it is also believed to reflect variation in the abundance of the winter-spawning group, which generally contributes largest squid to summer-fall fisheries and has historically been the most variable seasonal group, supporting large commercial catches in some years, particularly in Canadian waters (Coelho *et al.*, 1994, Dawe and Beck 1997, Dawe *et al.*, 2000). This is supported by the significant negative correlation between SSF and short-finned-squid BW (r = -0.38, p=0.04, Table 3). This indicates that southward displacement of this ocean front (SSF), which is strongly related to high short-finned squid survey catch rate in numbers/tow, is also related to large mean body weight.

Although there were differences in the environmental indices retained in the models, we conclude that the relative abundance of these two squid species is regulated by opposing responses to annual variation in Gulf Stream System dynamics. Southward displacement of the Shelf water-Slope water Front is related to a warm oceanographic regime at the northern extreme of the distributional range of short-finned squid, as well as high abundance of that species, especially of the largest-bodied, most highly migratory winter-spawning group, that predominates in the northern portion of its distribution. Northward displacement of ocean fronts (i.e. SSF) is related to high abundance of long-finned squid and, perhaps, a warm oceanographic regime on the northeastern USA shelf although the relationship of the southern bottom temperature index with broad-scale variability (i.e. with SSF) is unclear.

Environmental variables that were important in our models must be somehow associated with the direct mechanisms that regulate year class strength. However we recognize that environmental variables are complex and interacting and the direct mechanisms remain unknown. Dawe *et al.*, (2000) provided a review of possible direct mechanisms that could potentially regulate abundance of short-finned squid. It is quite possible that the direct mechanisms differ between our two study species, with local continental shelf variables such as water temperature directly affecting long-finned squid and broad-scale effects such as ocean currents directly affecting the more highly migratory short-finned squid.

Environmental relationships with distribution in 2000.

Unusual events can provide some insight as to direct mechanisms affecting squid abundance. For example, the distribution patterns we observed in 2000 indicate that water temperature is not the variable associated with displacement of ocean fronts (i.e. SSF) that directly affects short-finned squid abundance. The inverse relationship between SSF and our broad-scale Labrador Current temperature index (NFbt) broke down in 2000. Although the SSF remained north of its mean position for the second consecutive year (Fig. 10) the northern temperature index (NFbt) achieved its highest value in the 29-year time series in 2000 (Fig. 10b). Short-finned squid were in very low abundance in 2000, consistent with both the northern displacement of the SSF and the high NAO index (Fig. 10a). The de-coupling of both SSF and NAO from NFbt in 2000 was probably related to an unusual feature of the NAO in 2000. The NAO was intense in 2000 but displaced far to the east of its normal position. The expansion of the long-finned squid population in 2000 was associated with this unusual eastward displacement of the NAO, which may have resulted in unfavourable oceanic conditions for short-finned squid but favourable environmental conditions for long-finned squid on the continental shelf as far north as Newfoundland (Fig. 10b).

Our study suggests that changes in abundance or distribution of annual squid species may provide obvious signals of anomalous meteorological or oceanographic events before they are detected, or that may not be detected, through collection and analysis of the relevant data. Commercially important squid species may represent indicators of anomalous events that would otherwise not be detected, especially in ecosystems where environmental variation is not extensively monitored.

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Table 1. Descriptive statistics and parameter estimates for the Catch models, by species.

Catch models;
Short-finned squid

SSE	11695.1
MSE	467.8
DFE	25
r square	0.74

Variable	DF	B Value	Std Error	t Ratio	p
Intercept	1	6.36	17.33	0.37	0.72
BW	1	259.92	106.43	2.44	0.02
NAO	1	-1.23	0.45	-2.76	0.01
A(1)	1	-0.73	0.14	-5.17	0.0001

Long-finned squid

SSE	445.5
MSE	17.8
DFE	25
r square	0.63

Variable	DF	B Value	Std Error	t Ratio	p
Intercept	1	880.00	362.14	2.43	0.03
YEAR	1	-0.43	0.18	-2.37	0.03
NAO	1	0.27	0.10	2.70	0.01
A(1)	1	-0.53	0.19	-2.79	0.01

Table 2. Descriptive statistics and parameter estimates for the Catch Rate models, by species.

Catch Rate models;
Short-finned squid

SSE	642.86
MSE	27.95
DFE	23
r square	0.59

Variable	DF	B Value	Std Error	t Ratio	p
Intercept	1	711.32	291.76	2.44	0.02
YEAR	1	-0.33	0.14	-2.29	0.03
USAbt	1	-6.61	1.72	-3.84	0.0008
NAO	1	0.29	0.14	2.18	0.04
SSF	1	-21.57	6.08	-3.55	0.002
A(1)	1	-0.08	0.22	-0.38	0.70

Long-finned squid

SSE	566654.78
MSE	23611.00
DFE	24
r square	0.35

Variable	DF	B Value	Std Error	t Ratio	p
Intercept	1	554.51	75.89	7.32	0.0001
BW	1	-6256.00	2547.00	-2.46	0.02
NAO	1	5.09	3.19	1.60	0.12
SSF	1	277.98	135.82	2.05	0.05
A(1)	1	0.39	0.19	2.00	0.06

Table 3. Correlation matrix, including Pearson’s correlation coefficient and associated probability values, for environmental variables included in the initial models and biological variables retained in final models, (p values are italicised and those in bold are significant at the 0.05 probability level). lolBW and illBW represent mean body weight (BW) of *Loligo pealei* and *Illex illecebrosus* respectively.

Index	SSF	NAO	USAbt	NFbt	lolBW	illBW
SSF		0.41 ***0.02***	0.09 *0.63*	-0.50 ***0.005***	0.20 *0.28*	-0.38 ***0.04***
NAO			0.30 *0.12*	-0.28 *0.13*	0.01 *0.92*	-0.08 *0.67*
USAbt				-0.19 *0.30*	0.20 *0.30*	0.04 *0.83*
NFbt					-0.32 *0.09*	0.15 *0.43*
lolBW						0.10 *0.58*

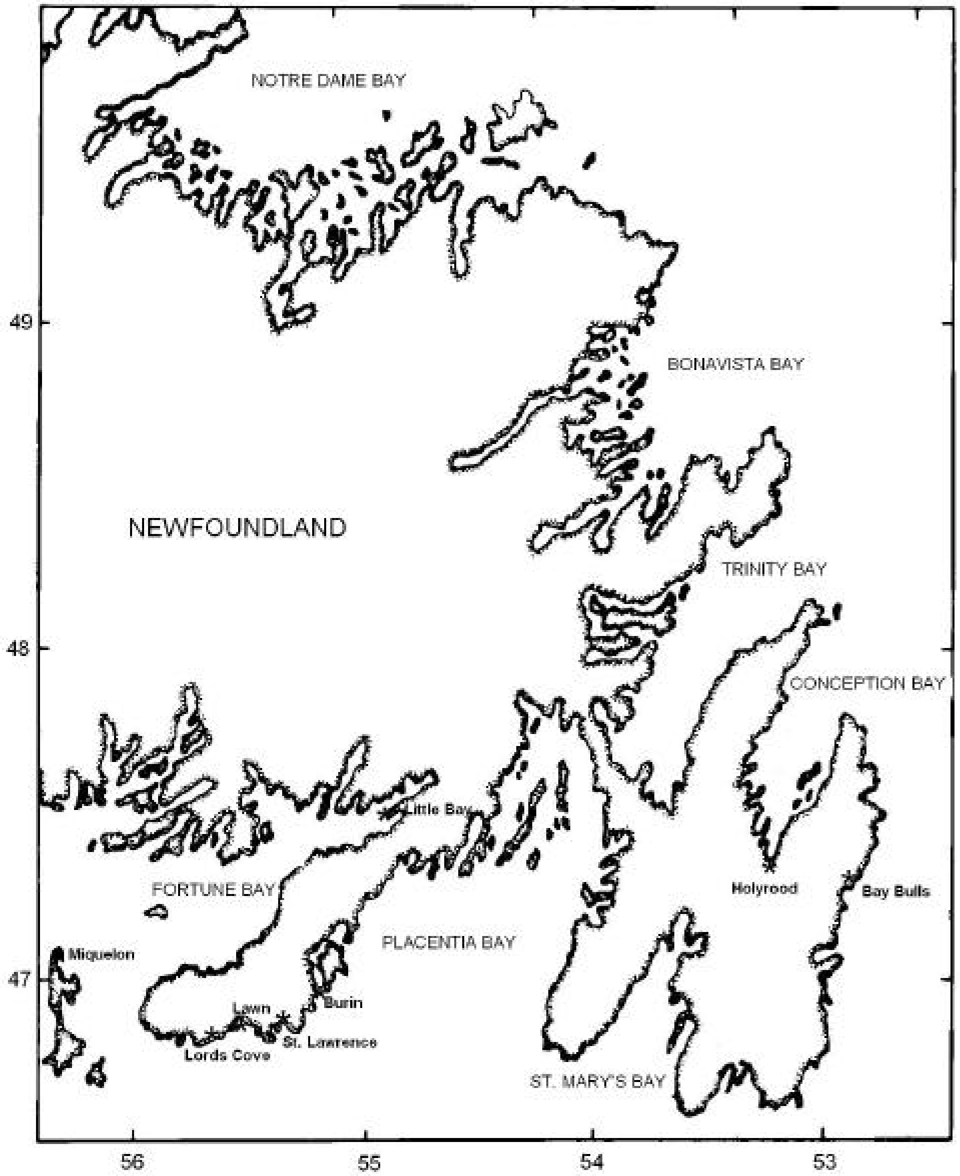
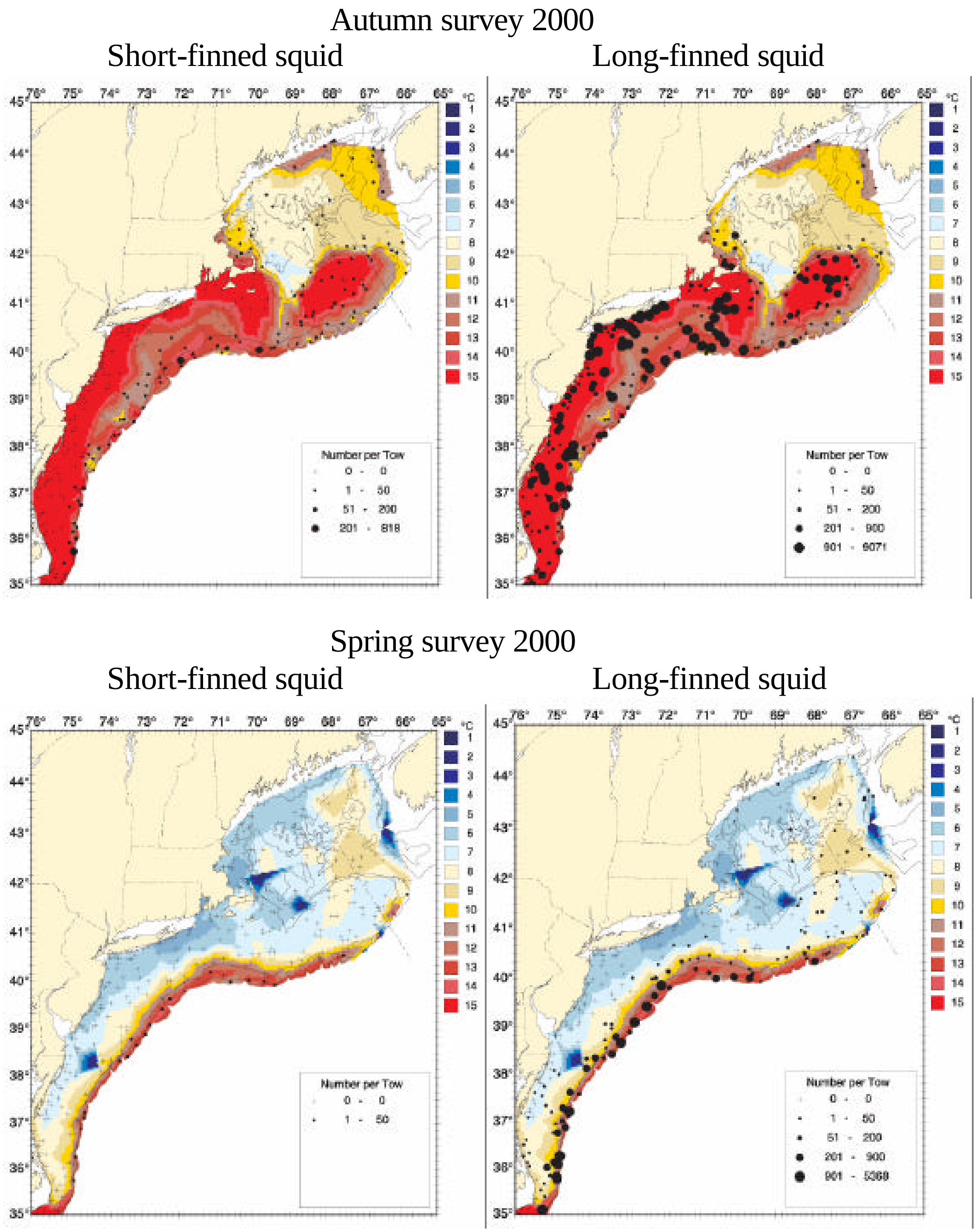


Fig. 1. Map of eastern Newfoundland showing place names referred to in the text.



Autumn survey 2000

Short-finned squid

Long-finned squid

Spring survey 2000

Short-finned squid

Long-finned squid

Fig. 2. Distribution of survey catch rates (no/tow) of short-finned squid (left) and long finned squid (right) in relation to bottom temperature (°C) on the northeastern USA shelf from Northeast Fisheries Science Center surveys in autumn (above) and spring (below) of 2000.

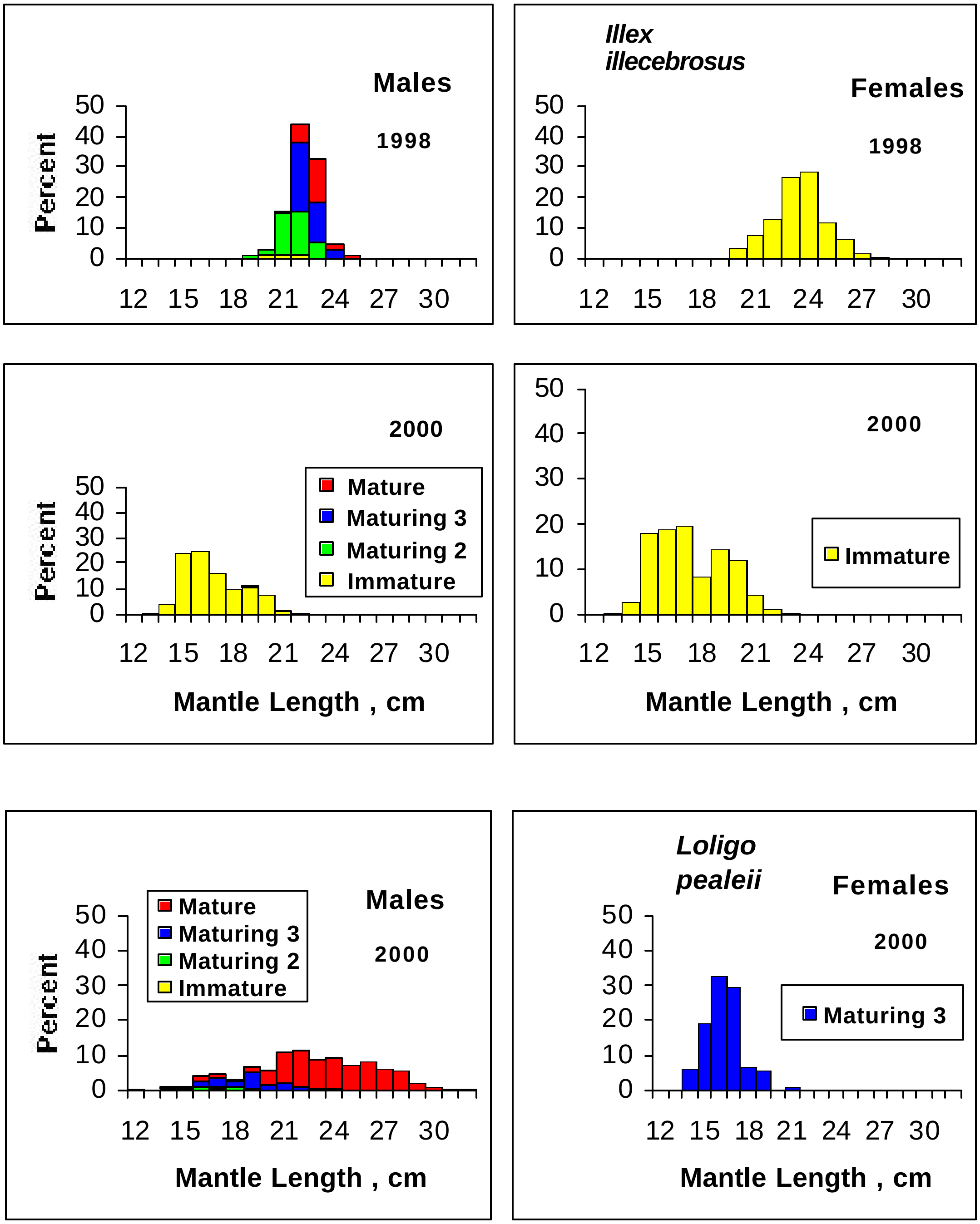


Fig. 3. Length frequency distributions for squid caught inshore at Newfoundland during early September; short-finned squid in 1998 and 2000 (above) and long-finned squid in 2000 (below).

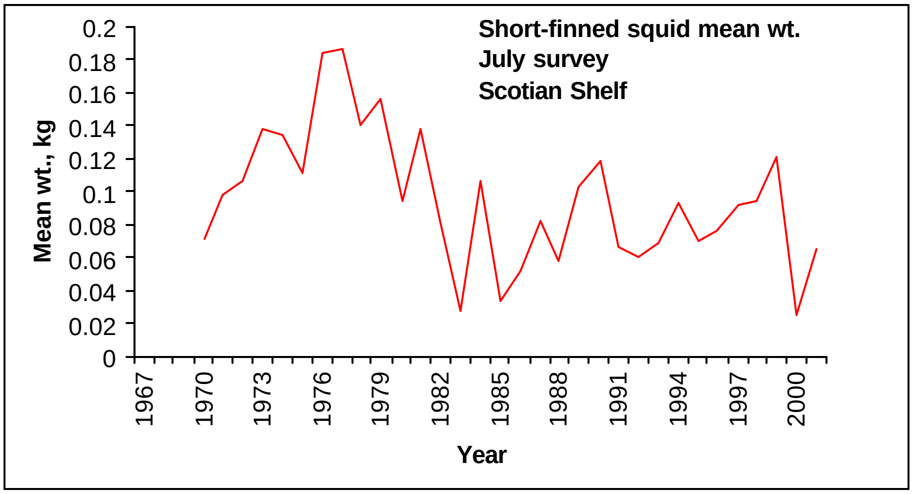


Fig. 4. Mean individual body weight of short-finned squid from annual bottom trawl surveys on the Nova Scotian Shelf during July.

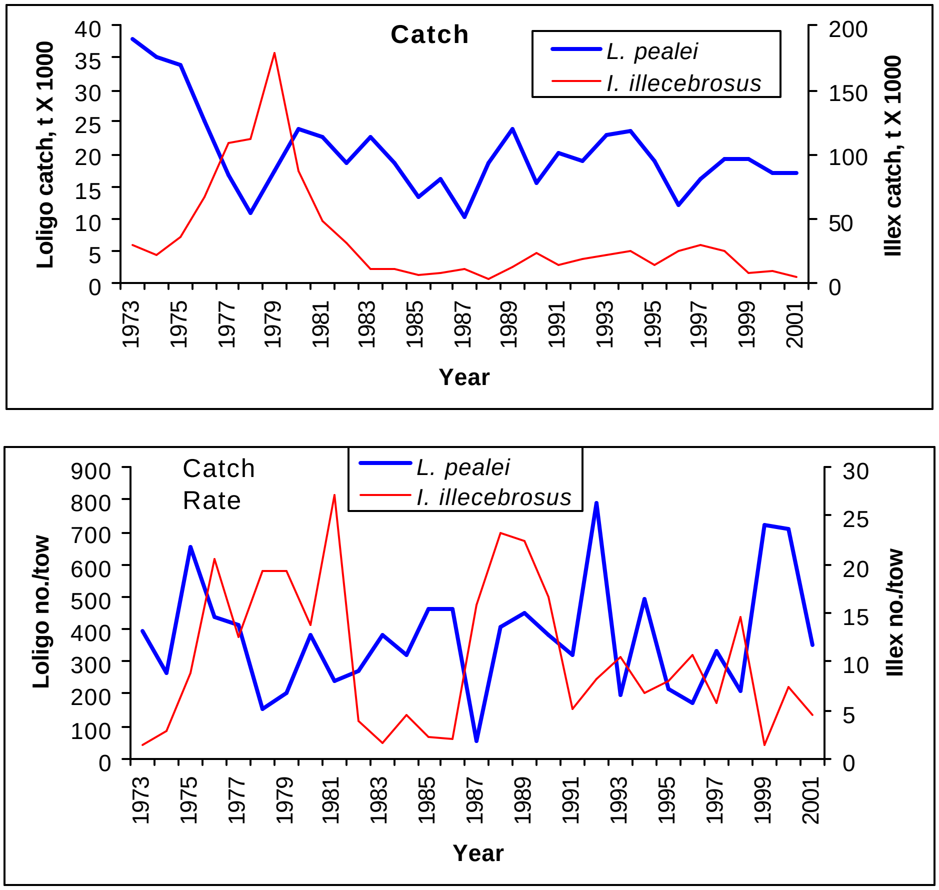


Fig. 5. Annual reported catches, by species, from the entire Northwest Atlantic Ocean (above) and USA autumn survey catch rates, by species (below).

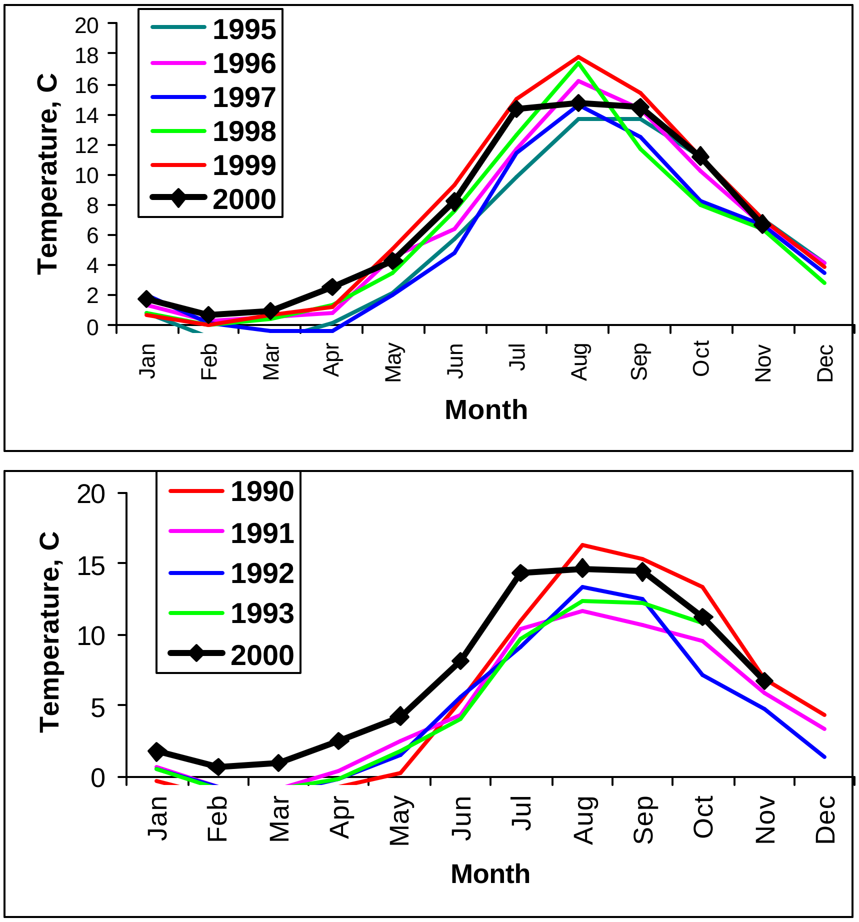


Fig. 6. Monthly trends in bottom tempearture at Arnolds Cove, Placentia Bay during 2000. In comparison with trends during 1990-1993 (above) and during 1995-1999 (below).

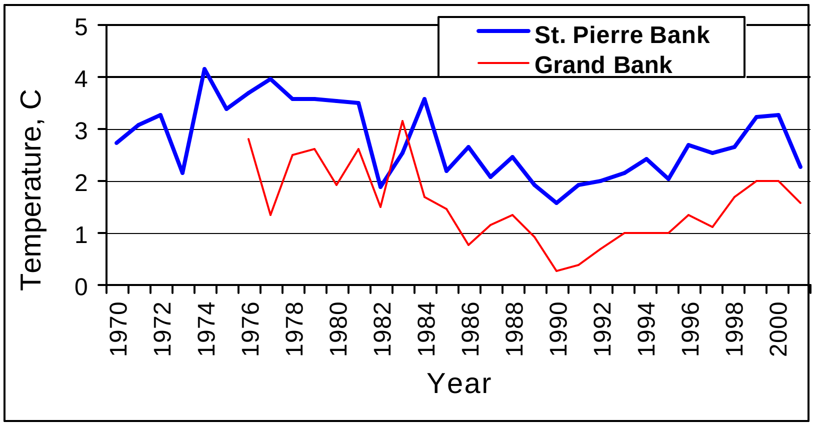


Fig. 7. Annual mean bottom temperature from the St. Pierre Bank and the Grand Bank, 1970-2001.

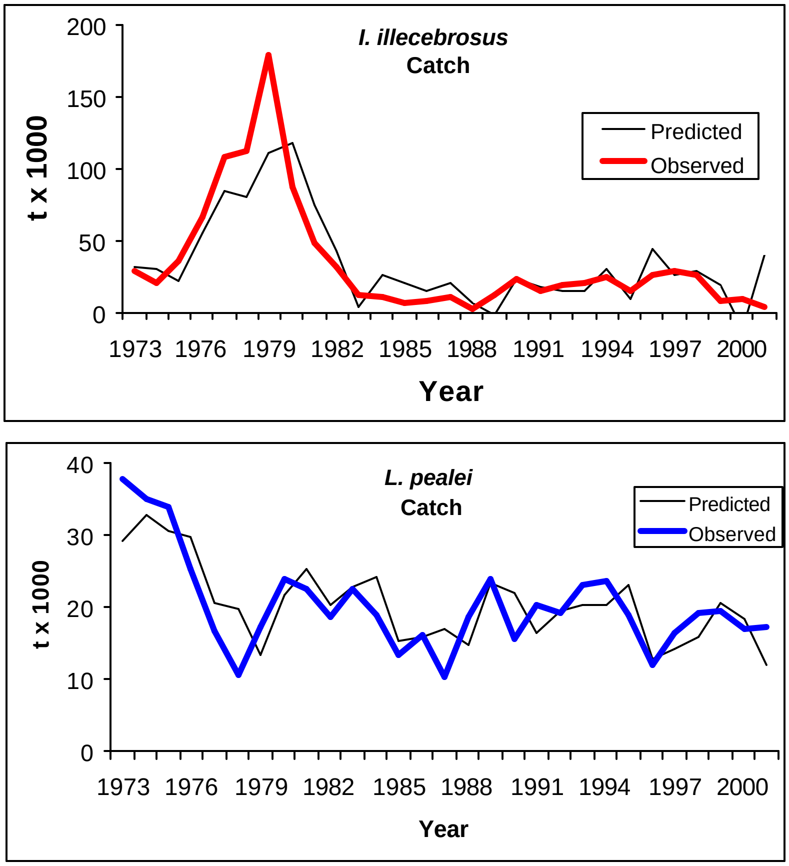


Fig. 8. Comparison of empirical commercial catches with those predicted by the catch models for short-finned squid (above) and for long-finned squid (below).

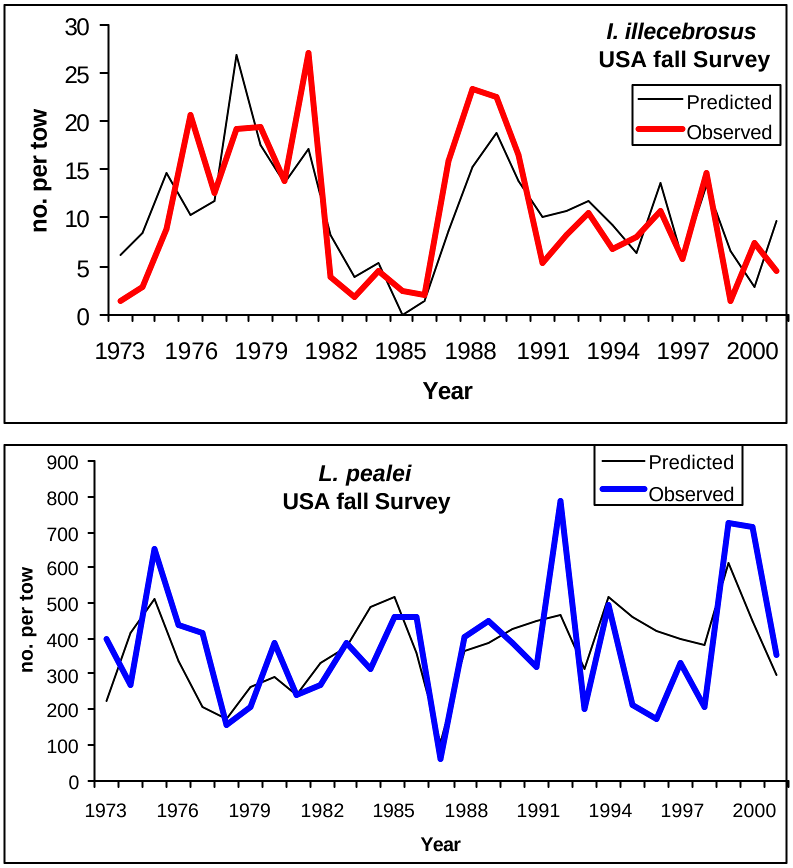


Fig. 9. Comparison of empirical autumn survey catch rates with those predicted by the catch rate models for short-finned squid (above) and for long-finned squid (below).

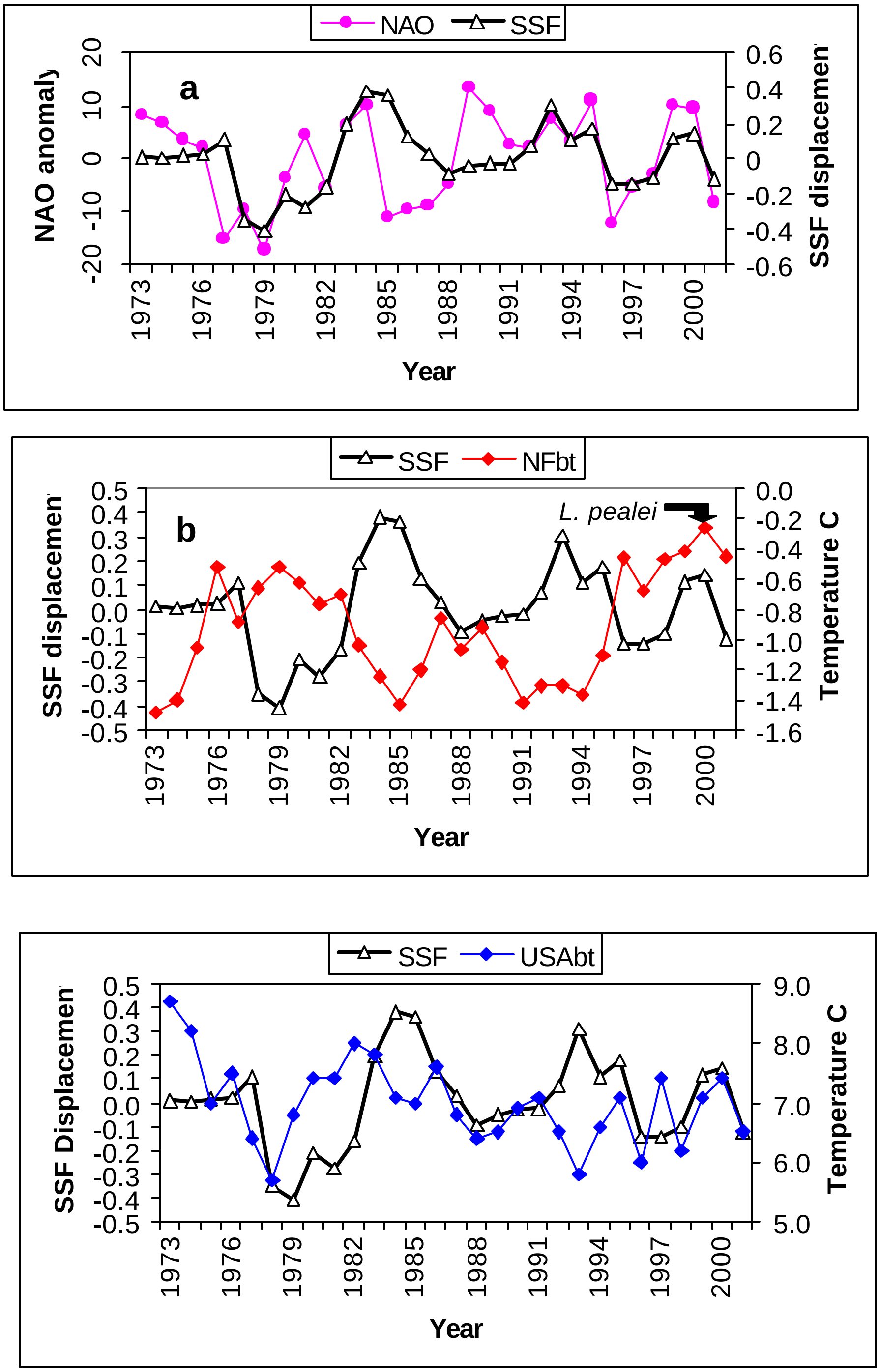


Fig. 10. Relationship north-south displacement (km x 10^2) of the Shelf water-Slope water Front (SSF) with NAO anomaly (a) and with the northern (NFbt) and southern (USAbt) bottom temperature indices (b).