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Environmental Effects on Recruitment of Short-finned Squid (Illex illecebrosus)

by

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Abstract

Effects of environmental variables on abundance of short-finned squid (Illex illecebrosus) in Canadian Atlantic waters 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 to be used in the modelling exercise. 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 a water temperature index and a Gulf Stream index. One model utilized the catch based index, whereas the other used a fishery-independent survey index as the dependent variables. All analyses considered generally indicate 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 temperature and southward shift in the position of fronts within the Gulf Stream System. Possible causal mechanisms are discussed.

Introduction

The northern short-finned squid (Illex illecebrosus) is distributed from central Florida to Newfoundland and Labrador (Squires 1957, Dawe and Warren 1993). It supports summer-fall 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, presumably in close proximity to the Gulf Stream (Trites 1983). Spawning occurs throughout most of the year, with several seasonal peaks, the major peak being in winter (Lange and Sissenwine 1983). Young stages are advected northeastward by the Gulf Stream (Trites 1983). Larvae, 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 (Fedulov and Froerman 1980, Dawe et al. 1982, Dawe and Beck 1985a, 1985b, Rowell and Trites 1985, Rowell et al. 1985, Hatanaka et al. 1985). Larger juveniles off Newfoundland are concentrated at the Shelf-Slope Front in spring (Fig. 2). Squid catches from directed squid surveys in May-June on the southwest slope of the Grand Bank were generally associated with incursion of the Shelf-Slope Front and bottom temperatures of 5°C or greater (Dawe and Warren 1993). Similarly, squid occurrence in Newfoundland coastal waters is associated with local water temperature exceeding 5°C, in water depths generally less than 30 m (Beck et al. 1994). Squid distribution on the Nova Scotian Shelf is associated with bottom temperatures greater than 6°C (Rowell et al. 1985).

It may be expected that yearclass strength would be greatly affected by environmental variation for an annual species which is so closely related to oceanographic features. This may be especially true at Newfoundland, the approximate northern limit of the species range of distribution (Dawe and Warren 1993, Mann and Drinkwater 1994, Coelho et al. 1994).

In this paper we review annual trends in squid catch and abundance in the Canadian Atlantic squid fishery areas, Nova Scotia (NAFO Subarea 4) and Newfoundland (NAFO Subarea 3) and for the entire Northwest Atlantic population. We attempt to relate annual variation in abundance to indices of broad-scale meteorological and oceanographic variation.

Methods

We use commercial catch by Canadian fishery area as an index of abundance of the single yearclass squid population. Estimates of yearly catch date back to 1920 for Subarea 4 and to 1911 for Subarea 3 (Mercer 1973, Dawe 1981). However, catches have been greatly affected by market-related changes in fishing effort (Fig. 3). 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, 1925-52, 1953-69, and 1970-97 (Fig. 4). Market conditions were relatively constant and catch fluctuations similar within each time period at Newfoundland (Fig. 3). A subjective ranking of Newfoundland inshore abundance generally agrees with trends in catch. The catch indices were significantly positively correlated between Subareas 3 and 4 ($r_s = 0.6914$, $p = 0.001$). Therefore the two area-specific indices were averaged to produce a catch-based squid abundance index for Canadian Atlantic waters.

Indices of environmental variation used for correlation with the squid catch index (Table 1) included the large-scale atmospheric circulation pattern as reflected in the North Atlantic Oscillation (NAO), the Newfoundland Shelf ice area (ICE), and bottom (BT) and vertically-averaged temperatures (VT) at Station 27, a hydrographic monitoring site located approximately 10 km east of St. John's, Newfoundland. We include these two ocean 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 continental shelf index used was thickness of the Cold Intermediate Layer (CIL) off Newfoundland. Oceanic indices which reflect variability within the Gulf Stream System were latitudinal displacement of the surface position of the north wall of the Gulf Stream (GSF) and the Shelf-Slope Front (SSF), the boundary between the shelf waters and the adjacent offshore slope waters (Drinkwater et al., 1994). For all comparisons Spearman correlation coefficients were calculated.

The relationship among environmental variables was inferred from the correlation matrix. Environmental variables were chosen for time series analysis based on the relative strength of their individual correlations with the squid catch index.

Time series analysis involved multiple linear regression with the squid index as the dependent variable and year as well as selected environmental indices as regressors. Multiple linear regression included a first order autoregressive parameter to account for autocorrelation. The analysis began with a full model and progressively eliminated non-significant terms (at the $p = 0.25$ probability level), in a step-wise fashion. Models were fitted by unconditional least squares. This analysis was performed using SAS Basics software (SAS Institute Inc., Cary, North Carolina).

Results and Discussion

The environmental indices were significantly correlated, with few exceptions (Table 1). The strong correlations between the NAO index and the continental shelf indices (ICE, CIL, BT, and VT) reflect the effects of strong northwesterly winds associated with high NAO anomalies. These winter-spring strong winter northwesterlies bring cold Arctic air into the Newfoundland area which promotes ice coverage and reduces melting (Colbourne et al. 1994). These winds also promote downward mixing of cold water (Mann and Drinkwater 1994). A high NAO and strong cyclonic circulation is also related to a northward displacement of the Gulf Stream Front and Shelf Water-Slope Water Front. Taylor et al. (1992) noted that shifts in the Gulf Stream are related to changing weather patterns over the North Atlantic. However, the mechanism is unclear because northwesterly winds oppose northward displacement of the fronts. Taylor (1996) noted that northward displacement is associated with reduced cyclone frequency and that meandering may not be simply related to any single atmospheric variable.

The squid catch index was significantly correlated with all the environmental indices (Table 2). Environmental variables selected for use in time series analysis included an index of atmospheric forcing (NAO), an index of ocean temperature (BT), and an index of Gulf Stream System variability (SSF).

A long time series (1925-97) was available for modelling effects of atmospheric forcing on catch. In this analysis YEAR and NAO were regressed on CATCH. The resultant model:

$$(1)\quad \text{CATCH} = 5.1013 - 0.0025\,(\text{YEAR}) - 0.0056\,(\text{NAO}) + \varepsilon$$

accounted for 34% of the variability in CATCH (Table 3), with the autoregressive term representing the main determinant of catch (Fig. 5). However, NAO was a significant parameter ($p = 0.05$) retained in the model and was negatively correlated with CATCH. YEAR was also negatively correlated with CATCH, reflecting increasing frequency of years of low catch throughout the time series.

For a shorter time series (1973-97) it was possible to include all the selected environmental variable in the modelling exercise. The full model (CATCH = YEAR NAO BT SSF) was reduced to one which included YEAR NAO and SSF as explanatory variables:

$$(2)\ \text{CATCH} = 1.0109 - 0.0099\ (\text{YEAR}) - 0.3056\ (\text{SSF}) - 0.0073\ (\text{NAO}) + \varepsilon$$

This model accounted for 70% of the variability in CATCH (Table 4, Fig. 6). As in the first model, the autoregressive term was the main determinant of catch, but, taking the autoregressive term into account, NAO was a significant contributor ($p = 0.05$). SSF was also retained in the final model ($p = 0.14$), and both NAO and SSF were negatively correlated with CATCH.

It was possible to test this second model using a fishery-independent index of squid abundance as the dependent variable, for the same time period (1973-97). Catch rates (kg/tow) are available for this period 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 and each is well-correlated with catch at Newfoundland and on the Scotian Shelf (Dawe and Hendrickson 1998). We selected the autumn USA survey series for this modelling exercise because it is better correlated with Canadian catches than is the July Scotian Shelf survey series (Dawe and Hendrickson 1998), probably because of the timing of the survey.

As with the previous analyses, we began with the full model (CATCH RATE = YEAR NAO BT SSF) and found that we could eliminate NAO, to arrive at the final model:

$$(3)\ \text{CATCH RATE} = 9.1135 - 0.0751\ (\text{YEAR}) - 3.2561\ (\text{SSF}) + 3.3380\ (\text{BT}) + \varepsilon$$

This model accounted for 47% of the variability in CATCH RATE (Table 5, Fig. 6). As in the catch-based model SSF was important ($p = 0.22$) and negatively correlated with the abundance index. However in this case BT, rather than NAO, was retained in the final model. BT was the most important contributor to the model ($p = 0.07$) and was positively correlated with CATCH RATE. In this model, however there was no autocorrelation within the dependent variable and the autoregressive term was not an important contributor to the model. This implies that the first order autocorrelation in the CATCH series is most likely due to fishery trends rather than dependence on the previous generation.

Comparison among the three models suggests that squid abundance in Canadian waters, and total Northwest Atlantic population size are directly related to a favourable oceanographic regime associated with a weak NAO, high bottom temperature at Station 27, and southward shift of frontal positions within the Gulf Stream System. The causative mechanisms are unclear, as is often the case with such heuristic models. However, based on the close association of young stages of squid with Gulf Stream dynamics, especially in winter, we hypothesize that Gulf Stream System variability affects survival and dispersal of young stages.

Our results indicate that squid abundance is, at least in part, related to a southward shift of fronts within the Gulf Stream system, but the mechanism is unclear. A southward displacement of the stream is associated with a decrease in the geostrophic transport of the Gulf Stream (r=0.86, p=0.05; Drinkwater and Myers, unpublished). (Note that this relationship is opposite to the one suggested originally by Drinkwater and Myers (1993). Based on geostrophic adjustment, they argued that an increase in the speed of the Gulf Stream should result in steeper isopycnals, leading to a southward displacement of the surface position of the north wall of the Stream. This hypothesis is not supported by the recent data, however.) The slower Stream and associated weaker front may allow more squid to "escape" from the Stream into the slope waters and from there, subsequently onto the shelf. On the other hand, the southward displacement of the Stream may have an indirect rather than direct effect upon squid. Its influence may be associated with extensive meandering that effectively increases the length of the Gulf Stream Front. There is a tendency for larger meanders to develop when the Stream is further southward. Warm Core Eddies (WCE's) are frequently formed by 'pinching-off' of Gulf Stream meanders (Trites 1983). Large quantities of larvae and juveniles are entrained in the periphery of WCE's (Dawe et al. 1982, Dawe and Beck 1985b). Thus, anticyclonic WCE's represent 'concentrated packages' of young squid, which may move to the southwest in Slope Water as far 'upstream' as Cape Hatteras before they dissipate or are resorbed by the Gulf Stream (Trites 1983). Larger number of eddies generally result in the Shelf/Slope front being pushed northward (Myers and Drinkwater, 1989) Given the negative relationship between the SSF and squid abundance, it would appear that any impact eddies have on squid would be negative.

One interpretation of the positive impact of a southward displacement of the SSF and the Gulf Stream is increased efficiency of advection of young stages through the Slope Waters onto the Shelf. However, we favour an indirect effect because juveniles are relatively large active migrators when they move onto the shelf in spring. Also, yearly differences in the distribution and size of juveniles during winter (Dawe and Beck 1985b, Fedulov and Froerman 1980, Fedulov et al. 1984) suggest that yearclass strength is established early in the life cycle and is somehow related to annual variation in the timing of peak spawning. Interestingly, a similar relationship was found between southward displacement of the Gulf Stream and increased recruitment of eels (Anguilla sp.), which spawn in the Sargasso Sea and rely upon the Gulf Stream for advection of young stages up to and eventually onto the North American continental shelves (Castonguay et al. 1994). Southward displacement of the Stream is also directly related to zooplankton production in the NE Atlantic (Taylor and Stephens 1980, Taylor et al. 1992, Taylor 1995).

Relationships described here for northern fishery areas probably reflect effects on the entire single stock population, since abundance trends are significantly positively correlated among all three fishery areas (Dawe and Hendrickson, 1998).

These environmental relationships are supportive of a general life history strategy proposed for short-finned squid by Coelho et al. (1994). A relatively stable resource exists in the southern-most fishery area in USA waters. Total population size or yearclass 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 yearclasses also favour population expansion through expedient advection of young stages and a suitable oceanographic regime in the northern-most area. This assures sufficiently rapid growth and maturation to support the long spawning migration and so complete the life cycle.

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Table 1. Correlation matrix for environmental indices, including Spearman's r_s, probability value and number of years. P values in bold are significant at the 0.05 probability level.

Index	NAO	ICE	CIL	BT	VT	GSF
ICE	0.5238 **0.0035** 29					
CIL	0.3930 **0.0048** 50	0.5397 **0.0025** 29				
BT	-0.5118 **0.0002** 48	-0.8813 **0.0001** 29	-0.4326 **0.0021** 48			
VT	-0.4299 **0.0023** 48	-0.7813 **0.0001** 29	-0.3067 **0.0340** 48	0.7990 **0.0001** 48		
GSF	0.5374 **0.0015** 32	0.7006 **0.0001** 29	0.2355 0.1943 32	-0.60591 **0.0002** 32	-0.5371 **0.0015** 32	
SSF	0.1870 0.3707 25	0.6419 **0.0005** 25	0.3055 0.1374 25	-0.5812 **0.0023** 25	-0.4655 **0.0190** 25	0.5883 **0.0020** 25

NAO- North Atlantic Oscillation annual anomaly (1920-97)
ICE - Newfoundland shelf ice area; km^2 x 10^3 (1969-97)
CIL - Thickness of the Cold Intermediate Layer, m (1948-97)
BT - Station 27 annual mean Bottom Temperature, °C (1950-97)
VT - Station 27 annual mean Vertically Integrated Temperature, 0-176 m (1950-97)
GSF - Latitudinal displacement of the Gulf Stream Front (55°W-75°W), annual anomaly (1973-97)
SSF - Latitudinal displacement of the Shelf Water-Slope Water Front (55°W-75°W), annual anomaly (1973-97)

Table 2. Correlations of catch index with environmental indices. Each cell includes Spearman's correlation coefficient, probability value, and number of years.

Index	NAO	ICE	CIL	BT	VT	GSF	SSF
Catch index	-0.03095 0.0077 73	-0.4012 0.0310 29	-0.3961 0.0044 50	0.4673 0.0008 48	0.3596 0.0120 48	-0.4069 0.0435 25	-0.6317 0.007 25

Table 3. Output from multiple regression analysis with CATCH as dependent variable and YEAR NAO as regressors.

```
                 Unconditional Least Squares Estimates

             SSE              2.837478    DFE                69
             MSE              0.041123    Root MSE     0.202788
             SBC              -12.4788    AIC          -21.6406
             Reg Rsq            0.0728    Total Rsq      0.3414
             Durbin-Watson    2.0759


Variable       DF         B Value   Std Error   t Ratio Approx Prob

Intercept       1        5.101365      4.1108     1.241      0.2188
YEAR            1       -0.002484     0.00210    -1.185      0.2400
NAO             1       -0.005640     0.00284    -1.986      0.0510
A(1)            1       -0.482515      0.1071    -4.506      0.0001


            Autoregressive parameters assumed given.


Variable       DF         B Value   Std Error   t Ratio Approx Prob

Intercept       1        5.101365      4.1105     1.241      0.2188
YEAR            1       -0.002484     0.00210    -1.185      0.2400
NAO             1       -0.005640     0.00280    -2.015      0.0478
```

Table 4. Output from multiple regression analysis with CATCH as dependent variable and YEAR NAO SSF as regressors.

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                   Unconditional Least Squares Estimates

          SSE                 0.436216    DFE               20
          MSE                 0.021811    Root MSE    0.147685
          SBC                 -13.7517    AIC         -19.8461
          Reg Rsq               0.3286    Total Rsq     0.6974
          Durbin-Watson         1.7757

 Variable      DF         B Value    Std Error   t Ratio Approx Prob

 Intercept      1        1.010939       0.7235     1.397      0.1776
 YEAR           1       -0.009922      0.00847    -1.172      0.2550
 SSF            1       -0.305619       0.2075    -1.473      0.1563
 NAO            1       -0.007362      0.00357    -2.060      0.0527
 A(1)           1       -0.585255       0.1914    -3.058      0.0062


              Autoregressive parameters assumed given.

 Variable      DF         B Value    Std Error   t Ratio Approx Prob

 Intercept      1        1.010939       0.7230     1.398      0.1773
 YEAR           1       -0.009922      0.00846    -1.173      0.2546
 SSF            1       -0.305619       0.2002    -1.527      0.1425
 NAO            1       -0.007362      0.00354    -2.079      0.0507
```

Table 5. Output from multiple regression analysis with CATCH RATE (USA autumn survey kg/tow) as dependent variable and YEAR BT SSF as regressors.

```
                 Unconditional Least Squares Estimates

             SSE              72.18819   DFE                 20
             MSE              3.609409   Root MSE      1.899845
             SBC              113.5766   AIC           107.4823
             Reg Rsq            0.5342   Total Rsq       0.4737
             Durbin-Watson      1.9088


 Variable      DF        B Value    Std Error   t Ratio Approx Prob

 Intercept      1       9.088172       4.1942     2.167      0.0425
 YEAR           1      -0.074821       0.0489    -1.529      0.1420
 BT             1       3.333233       1.7601     1.894      0.0728
 SSF            1      -3.284239       2.5558    -1.285      0.2135
 A(1)           1       0.158107       0.2331     0.678      0.5054


               Autoregressive parameters assumed given.

 Variable      DF        B Value    Std Error   t Ratio Approx Prob

 Intercept      1       9.088172       4.1603     2.185      0.0410
 YEAR           1      -0.074821       0.0486    -1.541      0.1390
 BT             1       3.333233       1.7521     1.902      0.0716
 SSF            1      -3.284239       2.5227    -1.302      0.2078
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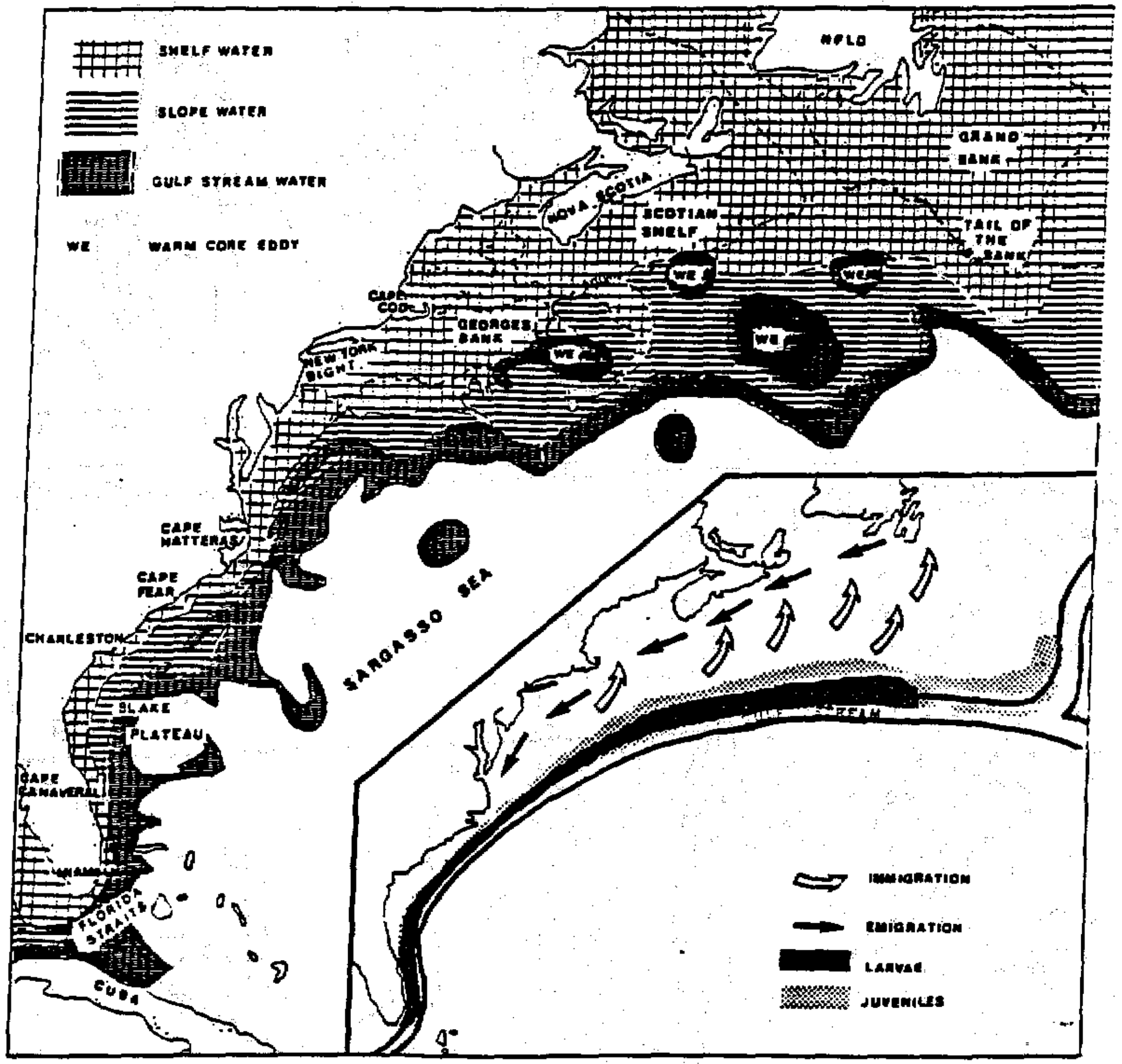

Fig. 1. Schematic representation of the life history of short-finned squid in relation to dynamics of the Gulf Stream System (from Rowell and Trites 1985).

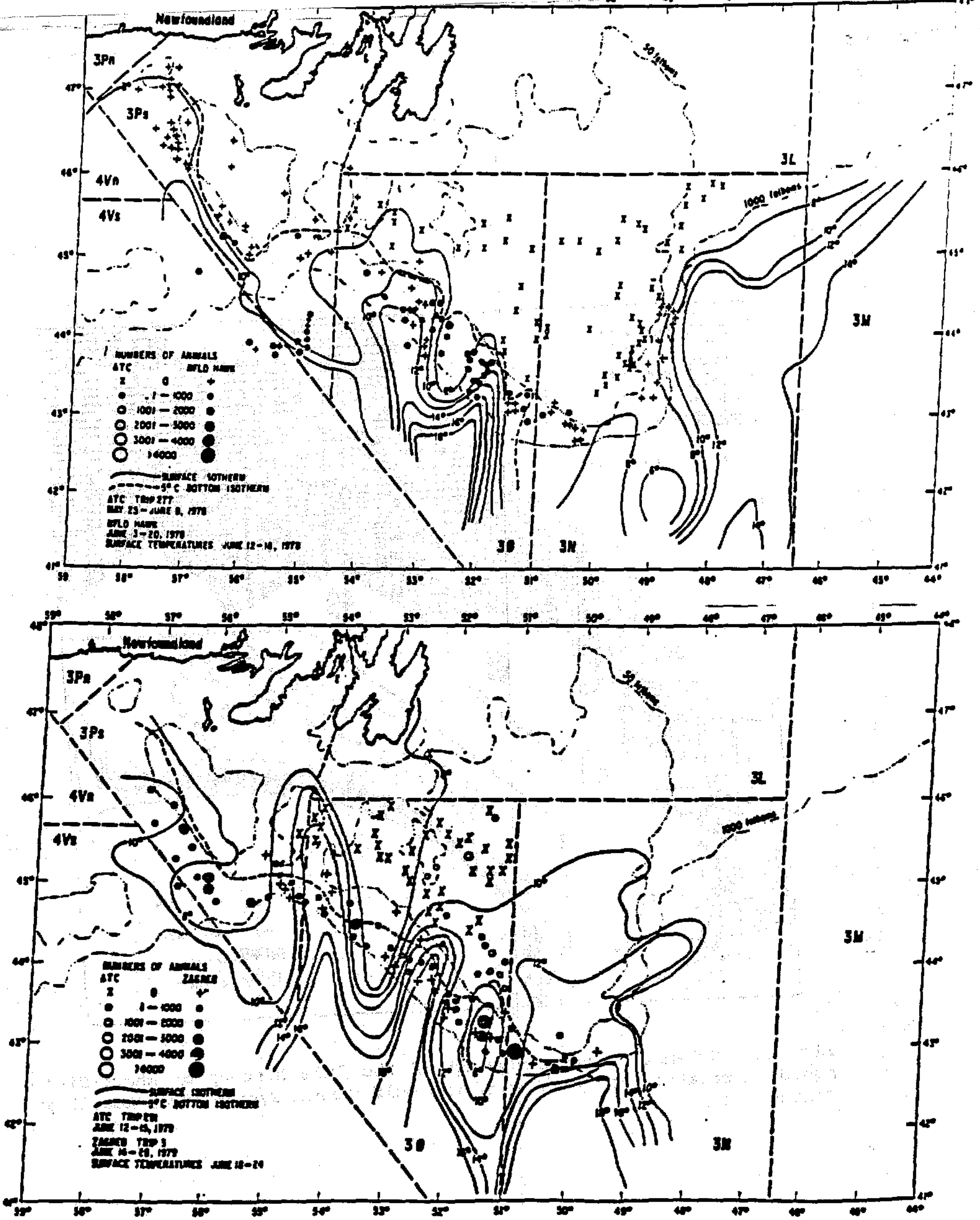

Fig. 2. Squid catches during 1978 and 1979 spring bottom trawl surveys in relation to the surface Shelf-Slope Front (closely spaced isotherms) and the 5°C bottom isotherm.

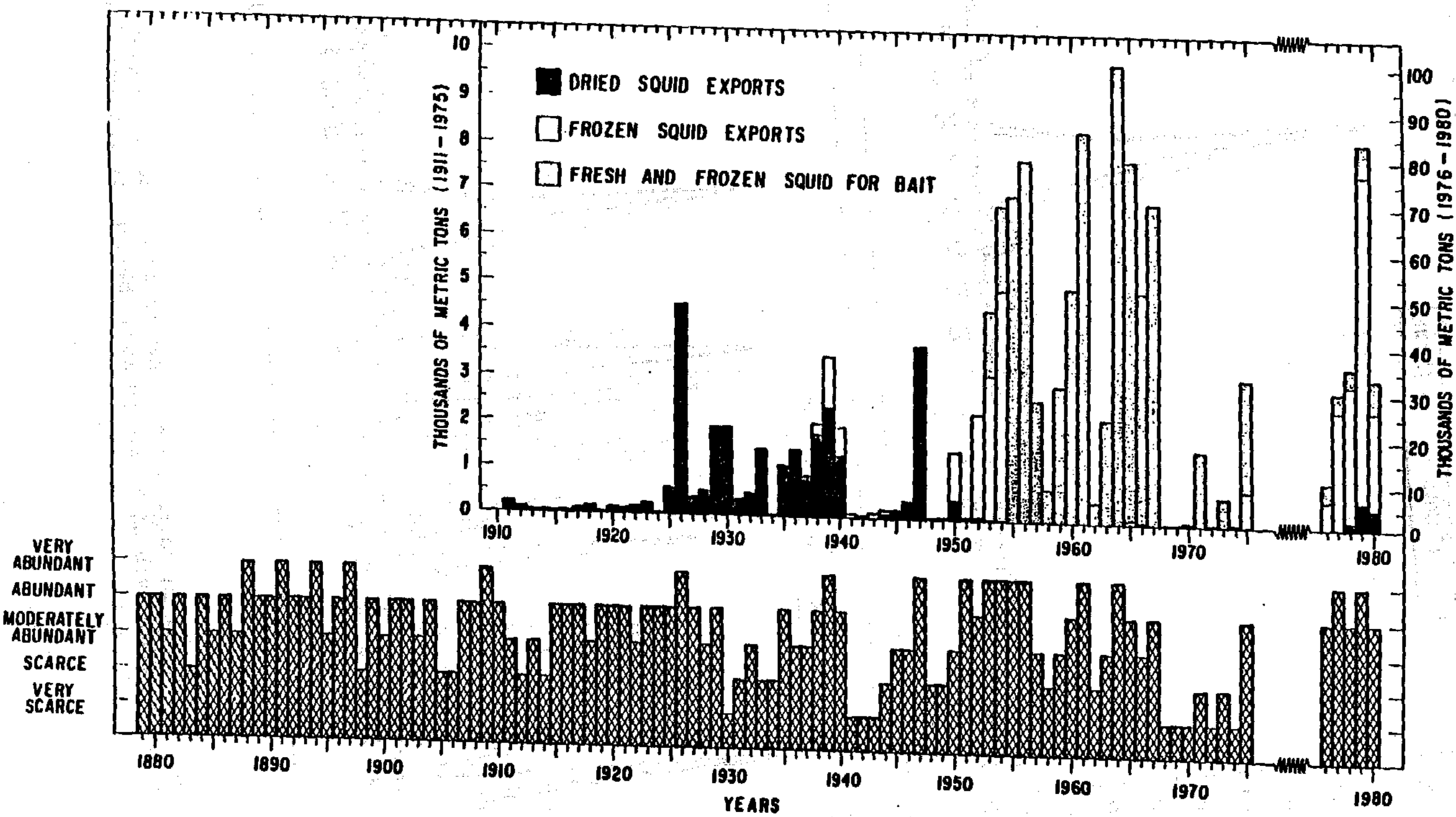

Fig. 3. Breakdown of Subarea 3 catch 1911-1980 by processing category and qualitative estimates of inshore abundance at Newfoundland, 1879-1980 (from Dawe 1981).

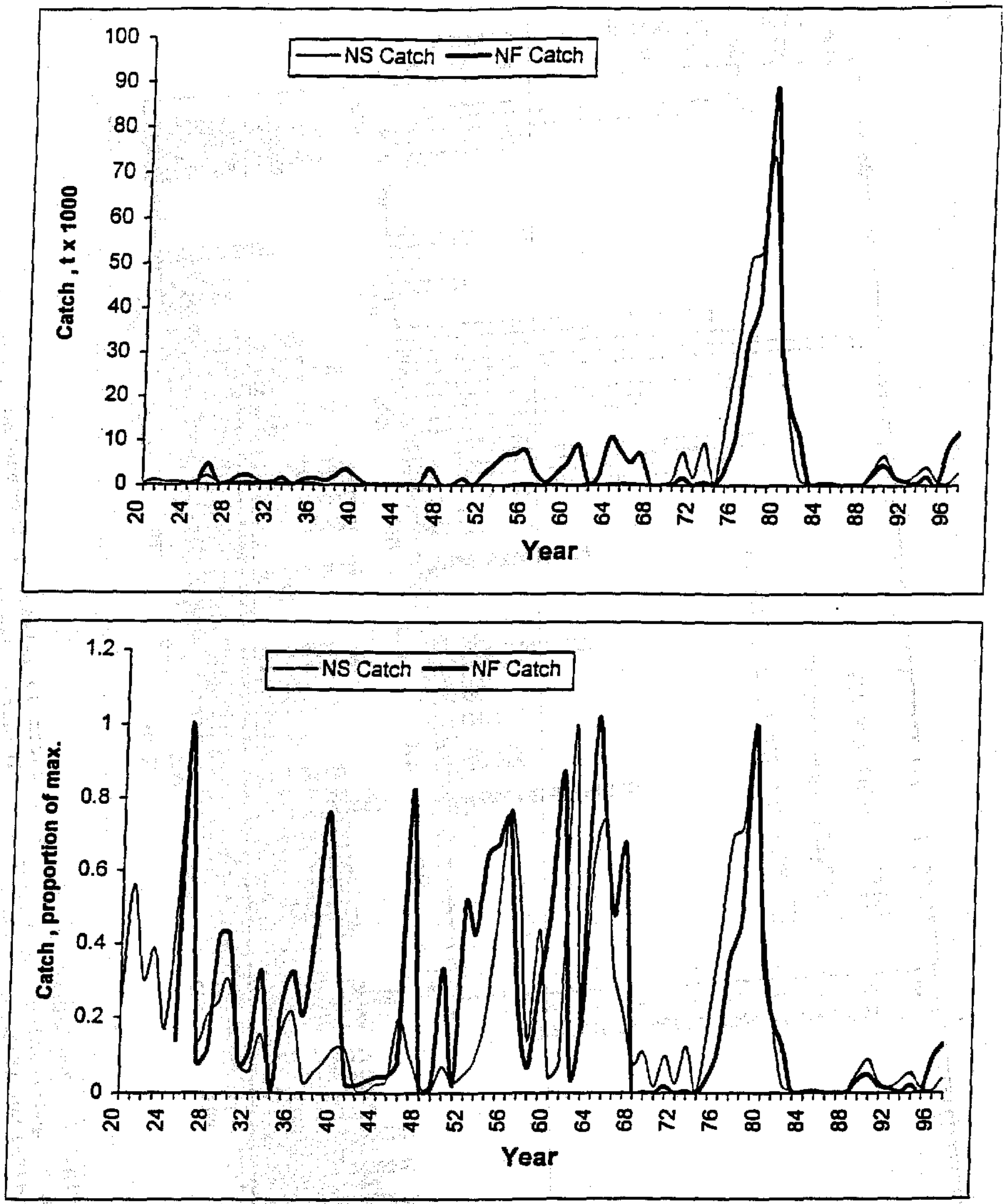

Fig. 4. Annual trends in catch (above) and in catch index; proportion of maximum catch within each of 3 time periods (below), by fishery area.

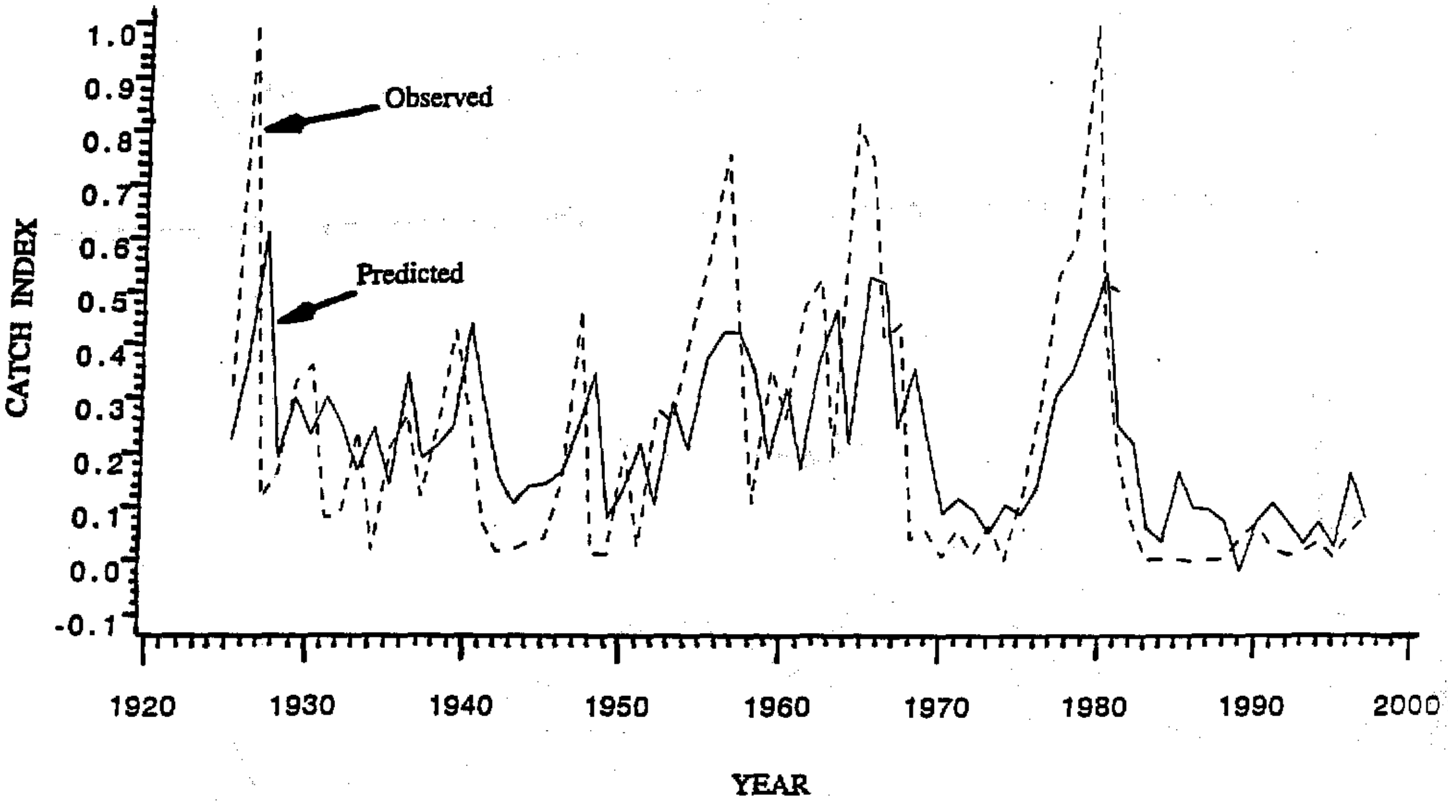

Fig. 5. Comparison of empirical catch index values with those predicted by Model 1: CATCH = 5.1013 - 0.0025 (YEAR) - 0.0056 (NAO) + ε.

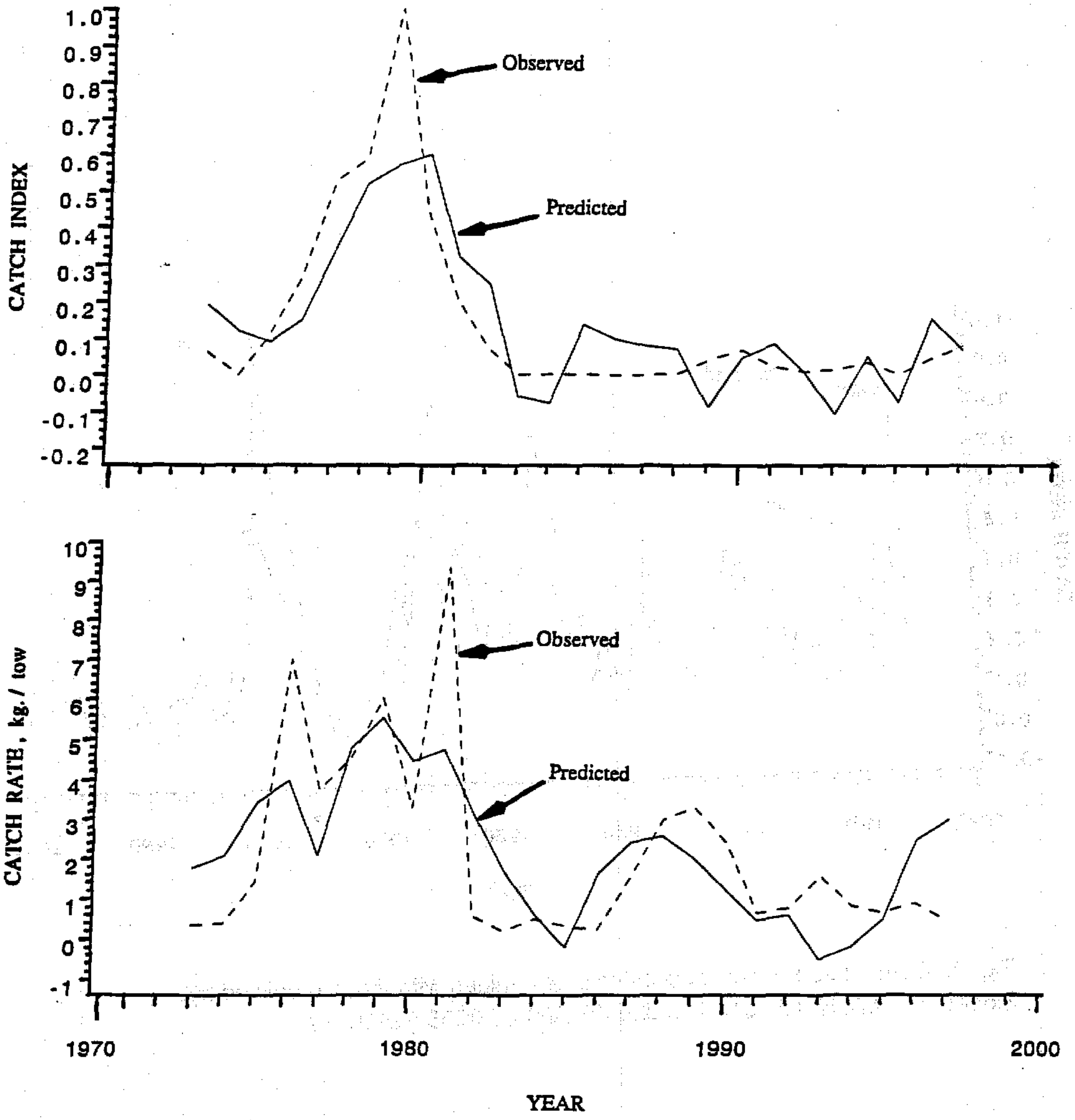

Fig. 6. Comparison of empirical catch index values with those predicted by Model 2: CATCH = 1.0109 - 0.0099 (YEAR) - 0.3056 (SSF) - 0.0073 (NAO) + ε (above) and comparison of empirical USA survey catch rate values with those predicted by Model 3: CATCH RATE = 9.1135 - 0.0751 (YEAR) - 3.2561 (SSF) + 3.3380 (BT) + ε (below).