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Annual Variation in the Distribution of Cod (*Gadus morhua*) in the Southern Gulf of St. Lawrence

by

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Abstract

Age-specific distribution of cod in the southern Gulf of St. Lawrence was described with respect to depth, temperature and broad geographic region for the period 1971-1990 using poisson regression models. Effects of all three factors on distribution were highly significant for most ages and years. Extra-poisson variation, which may reflect degree of aggregation, was greater at younger ages and in years of higher abundance. Depth distribution was age dependent, even after accounting for indirect effects of temperature on distribution. Older cod occurred at greater depths. In contrast, temperature distribution was independent of age in most years. Annual variation in the estimated temperature of maximum catch rate was correlated among age groups and with annual variation in bottom temperature in the southern Gulf.

Abundance of cod in the southern Gulf changed dramatically during the 1971-1990 period, from low levels in 1971-1978 to high levels in later years. Cod distribution also changed between these two periods. The age-depth relationship was significantly steeper during the later period of high abundance, and broad regional changes in distribution occurred between the two periods. Cod were concentrated in western regions of the southern Gulf during the earlier period of low abundance. Distribution shifted toward the central and northeastern regions during the later period of high abundance. Possible causes of these changes in distribution are discussed.

COD SYMPOSIUM, SEPTEMBER 1991

Introduction

Abundance of commercially exploited fish species is estimated from catch rates in commercial fisheries and research surveys. These estimates assume that availability to the fishing gear does not change over time. Availability depends on the vertical and horizontal distribution of fish. Changes in fish distribution may contribute significantly to annual variation in estimates of abundance (e.g., Myers, 1988; Smith *et al.*, 1991).

Fish distribution is related to environmental parameters such as depth, temperature, salinity, and bottom type (e.g., Scott, 1982; Mahon *et al.*, 1984; Tremblay and Sinclair, 1985; Perry *et al.*, 1988; Smith, 1990; Smith *et al.*, 1991). Distributions are often age-specific. For example, in the southern Gulf of St. Lawrence during autumn, older Atlantic cod (*Gadus morhua*) tend to occur at greater depths, lower temperatures and higher salinities (Tremblay and Sinclair, 1985). However, relationships between distribution and environmental parameters may show considerable annual variation, and it is difficult to interpret relationships between abundance and single environmental variables due to the strong correlations among environmental variables (Tremblay and Sinclair, 1985).

Smith (1990) described a poisson regression model relating fish abundance to environmental variables (depth, temperature, salinity). In this paper, I use this model to describe annual variability in the age-specific distribution of cod in the southern Gulf of St. Lawrence (NAFO district 4T). The southern Gulf cod stock undergoes an age-dependent annual migration: adult cod migrate between summer spawning and feeding grounds in the southern Gulf and overwintering grounds in the deeper water of the Sidney Bight (NAFO subdistrict 4Vn), whereas juvenile cod remain in the southern Gulf throughout the year (Martin and Jean, 1964; Jean, 1964). I describe the southern Gulf cod distribution during September, the time when cod are believed to have penetrated furthest into the Gulf and be most widely distributed (Clay, 1991).

The southern Gulf cod stock has experienced marked changes in abundance over the last 20 yr. Mean numbers per tow of cod aged 3 yr and older varied between 20 and 72 (mean 37.6) in research surveys during the period 1971-1978 and between 96 and 285 (mean 161.0) in surveys during the period 1979-1990 (Hanson *et al.*, 1991). In this paper, I show that this stock has also undergone a significant change in distribution between these periods of low and high abundance.

Material and Methods

Study area

The southern Gulf of St. Lawrence comprises a broad, shallow (usually < 75 m) shelf, the Magdalen Shelf, bordered on the north by the Laurentian Channel, a deep, steep-sided trough with a maximum depth of 535 m (Fig. 1). Vertical temperature and salinity structure changes seasonally (Strain, 1988). Two distinct water layers are present in winter: a surface mixed layer (50-100 m thick), with salinities between 31 and 32 and temperature near the freezing point (-1.5°C), and a deep, warm (4-6°C), saline (near 34.6) layer. In summer, three distinct water layers are present: a thin (10-30 m), warm (15°C), relatively fresh (27-32) surface layer, an intermediate cold layer (-0.5-1°C, salinity 31.5-33), and the deep warm layer. The typical horizontal distribution of water temperature in September is given by Koeller (1981). The intermediate cold layer covers the bottom of much of the central part of the southern Gulf on and around Bradelle Bank. Temperatures increase shoreward from this central area, and with depth along the Laurentian Channel.

Survey procedures

Bottom trawl surveys were conducted in the southern Gulf of St. Lawrence each September from 1971 to 1990. Surveys used a random-stratified design (Fig. 2), with stratification based on depth and geographic region. Station allocation was roughly proportional to stratum area. In addition to the randomly selected stations, 13 fixed stations were fished each year between 1971 and 1987. Surveys were conducted by the stern trawler *E. E. Prince* using a Yankee 36 trawl during the period 1971-1985, and by the stern trawler *Lady Hammond* using a Western IIA trawl during the period 1985-1990 (see Carrothers (1988) for detailed trawl specifications). A comparative fishing experiment in 1985 failed to reveal significant differences in catch rates for cod between the two vessels and gears (G. Nielsen, unpubl. data). Fishing by the *E. E. Prince* was during daylight hours only, while the *Lady Hammond* fished 24 h per day. However, a comparative fishing experiment in 1988 revealed no significant differences between day and night catches of cod (G.Nielsen, unpublished data).

The target fishing procedure was a 30-min tow at 3.5 knots in all years. All catches were adjusted to a standard tow of 1.75 nautical miles. Cod numbers and length frequency distributions were determined for each catch. Otoliths were removed from a length-stratified subsample of each catch for age determination. Bottom temperature was measured at the end of most tows. (Tows without bottom temperature measurements were excluded from all analyses.)

Sample sizes for each year are given in Table 1. Spatial coverage of the southern Gulf was complete in all years except 1978, 1983, 1984 and 1988. Incomplete coverage was due to the occurrence of fixed fishing gear (stratum 21) or the exclusion from analyses of sets without temperature data (other strata).

Statistical analyses

Age composition of the cod catch was calculated for each tow using the RVAN procedure MALKEY (Clay, 1989). This procedure applies a survey-wide age-length key to the length distribution of the catch of each tow. Age-specific cod distribution was described for each year using poisson regression models, following Smith (1990). Separate models were estimated for each age between 3 and 7, and for fish aged 8 or older. Models were of the form

$$E[y_{ij}] = \mu(\mathbf{x}_i),$$
$$Var[y_{ij}] = \Phi\mu(\mathbf{x}_i),$$

where y_{ij} is the number of age j cod caught in sample i, $\mathbf{x}_i$ is a vector of covariates with elements x_{ik}, and Φ is a parameter for extra-poisson variation. A log link was used between the mean and the covariates (McCullagh and Nelder, 1989). Rationale for the choice of a poisson probability model for the number of cod caught in a tow is given by Smith (1990) and Smith *et al.* 1991.

Three models were considered. First, cod catch was related to depth alone (Model A) in order to describe unadjusted depth distributions of cod. Second, effects of depth and temperature were modelled jointly (Model B) in an attempt to disentangle effects of these correlated environmental variables on distribution. Finally, effects of geographic region were also included in models (Model C). All models included both linear and quadratic terms for temperature and (or) depth. That is,

Model A: $\mu(\mathbf{x}) = \exp(\beta_0 + \Sigma\beta_k x_k)$, k=1,2

Model B: $\mu(\mathbf{x}) = \exp(\beta_0 + \Sigma\beta_k x_k)$, k=1,2,3,4

Model C: $\mu(\mathbf{x}) = \exp(\beta_r + \Sigma\beta_k x_k)$, k=1,2,3,4

where x_1 to x_4 are depth, $(\text{depth})^2$, temperature and $(\text{temperature})^2$, respectively. A single intercept β_0 was estimated in models A and B, whereas separate intercepts β_r were estimated for each region r in Model C. Strata were grouped into six broad regions for analyses with Model C (Fig. 3).

Smith *et al.* (1991) suggested that water mass, defined by specific combinations of temperature and salinity, is a better predictor of cod catch than either temperature or salinity alone. Unfortunately, an additional model incorporating water mass could not be included in this analysis because bottom salinity was not measured for a large part (1983-1990) of the time series.

Statistical significance of effects of depth, temperature and geographic region was tested using the change in deviance between hierarchical models with or without terms for the factor tested. This test is equivalent to a likelihood ratio test (McCullagh and Nelder, 1989). For models involving more than one factor (i.e., Models B and C) comparisons were with the full model. For example, for Model C, the significance of depth was tested by comparing the model including region, temperature and $(\text{temperature})^2$ with the full model including terms for these factors as well as depth and $(\text{depth})^2$. All models were estimated using the GLIM software package (Payne, 1987).

Analysis of the 20 yr time series for 6 age groups involved fitting 120 models (for each of the three model types A, B and C). Results of these analyses were summarized by calculating the depths and temperatures of predicted maximum catch for each age and year. These were calculated from the first derivatives of the fitted models with respect to depth or temperature. In one case the predicted curve was monotonically increasing over the depth range encountered in the survey, and in a few cases the curve was montonically decreasing over the encountered depth or temperature ranges. In these cases, covariate values for predicted maximum catch were set at the maximum or minimum values, respectively, encountered in the survey (i.e., they were restricted to the range of values over which the model was fitted). Additional statistical analyses of these summary values were calculated using SAS procedures (SAS Institute, 1982).

Results

Model A - Depth

The effect of depth on cod catch rates was highly significant ($P < 0.001$) in 112 of the 120 age-year combinations and nonsignificant ($P > 0.05$) in only three of the 120 cases (ages 6 to 8, 1978). Over-dispersion (i.e., extra-poisson variation, $\Phi > 1$) tended to be greater for youger cod ($P = 0.0001$, $df=1,99$) and during recent years (1979-1990) of high abundance ($P = 0.0009$, $df = 1,18$; ANOVA with period (71-78 vs 79-90) and year nested within period as factors and age as a covariate; Fig. 4).

Predicted values of catch (scaled by maximum catch) are plotted against depth in Figure 5 for each age group in five survey years. In four of the five years, predicted maximum catches occur at progressively greater depth as age increases. The curves are particularly similar for 1971, 1981 and 1986. In each year, predicted maximum catches were at depths of 60-70 m for age 3 cod, increasing to 120-130 m for age 8^+ cod. In each year, the curves of predicted catch against depth were most sharply peaked for age 3 cod, with the predicted depth distribution becoming progressively wider for older cod. On the other hand, predicted curves differed markedly from the other years in 1976. In this year, maximum catches were in very shallow water (<35m) for all age groups, and there was no tendency for older cod to be distributed in deeper water.

The results of fitting Model A are summarized for all age-year combinations in Figure 6 where depth of predicted maximum catch is plotted against age for each year. A consistent pattern is evident for the period 1979 to 1990. For each year in this 12 year period, older fish were distributed in progressively deeper water. Results are less consistent in earlier years (1971-1978). No positive correlation between depth and age was evident in 1972 or 1975-1977. Cod appeared to be distributed in very shallow water irrespective of age in 1975-1977. The earlier period coincides with a period of low abundance for this stock, and the latter period, one of high abundance. Slope of the age-depth relationship was significantly greater in the period of high abundance than in the period of low abundance ($P = 0.018$; $df = 1{,}116$; Fig. 7A).

Model B - Depth and Temperature

Effects of depth and temperature were both significant in Model B for all 120 age-year combinations (depth: $P<0.001$ in 119 cases and <0.005 in 1 case; temperature: $P<0.001$ in 117 cases, $0.001<P<0.025$ in 3 cases). Estimates of extra-poisson variation showed the same patterns with respect to age and time period as in Model A.

Relationships between cod catch and depth were similar whether estimated in an analysis of depth alone (Model A) or controlling for temperature (Model B). As in the previous analysis, estimated depths of maximum catch, controlling for effects of temperature, were progressively greater for older fish (Fig. 7B) and the slope of this age-depth relationship was significantly greater in the recent period of high abundance than in the earlier period of low abundance ($P=0.002$, $df=1{,}116$). These results imply that these relationships between cod distribution and depth are not an indirect effect of temperature.

Predicted values of catch, scaled by maximum catch, are plotted against temperature in Figure 8 for each age group in five years. Recall that indirect effects of depth on the temperature distribution of cod have been controlled for in this analysis. Results are variable among years. In two years (1976, 1981), younger cod tend to be distributed at warmer temperatures. In three years (1971, 1986, 1990), peak cod catches are predicted for about the same temperature irrespective of age. Spread of the predicted temperature distribution of cod also varied considerably among years. In 1971, 1976 and 1981 predicted catches were high over a relatively wide range of temperatures, whereas temperature distribution was sharply peaked in 1986 and especially 1990 (Fig. 8).

The estimated temperature distribution of cod is summarized in Figure 9 for all 120 age-year combinations. In contrast to the depth distribution, no consistent patterns are evident between the predicted temperature of maximum catch (TC_{mx}) and age. Combining all years, there was no effect of age on TC_{mx} ($P>0.6$, $df=1{,}99$; from ANOVA with factor year and covariate age). However, slopes of the regression of TC_{mx} on age differed significantly among years ($P=0.0001$, $df=19{,}80$). Within years, the relationship between TC_{mx} and age was significant ($P<0.05$) and negative in 5 years, significant and positive in 4 years, and nonsignificant in 11 years. Annual variation in TC_{mx} was highly significantly correlated among age groups of cod (Table 2). TC_{mx} was significantly lower in later years and at higher population sizes (Table 3). For five of the six age groups, annual variation in TC_{mx} was significantly correlated with stratified mean bottom temperature measured during the surveys (Table 3).

Model C: Depth, Temperature and Region

Effects of depth, temperature and region were all highly significant in most analyses with Model C (depth: $P<0.001$ in 113 cases, $P>0.05$ in only 1 case; temperature: $P<0.001$ in 104 cases, $P>0.05$ in 3 cases; region: $P<0.001$ in 118 cases, $P>0.05$ in 1 case). As in the previous analyses with Models A and B, extra-poisson variation was greater at younger ages and in years of higher abundance.

Estimated temperatures of maximum catch showed the same patterns controlling for both depth and region as in the previous analysis, and are not described in detail here. Briefly, temperature distribution was not age-dependent, and maximum catches tended to be in colder water in later years.

As in the previous analyses, depth distribution was age-dependent. However, the age-depth relationship did not differ significantly between periods of low and high abundance after accounting for regional differences in distribution (Fig. 7C). Thus, the change in age-depth relationship between these two periods may be at least partly attributable to broad regional changes in distribution.

To test for an interaction between the effects of region and time period, I fitted poisson models including interaction terms (i.e., depth, temperature, region, period, period_x_region, period_x_temperature, period_x_depth). Interaction terms were significant ($P<0.001$) for all age groups. Changes in the regional distribution of cod between the 1971-78 and 1979-90 periods are shown in Figure 10. This figure shows predicted catch rates in each region, scaled by the maximum catch rate in each year and averaged over years in each of the two periods. In the earlier period, cod were concentrated in the southwestern Gulf (regions CB, MS and GA) and were rare in the central and eastern regions of the southern Gulf (CN, NE and SE). Peak catches were in the Chaleur Bay and Miramichi-Shediac Valley regions for young cod (ages 3 and 4), and in the Miramich-Shediac Valley and Gaspé regions for older cod. Distribution shifted toward the central and eastern regions in the later period. Catches remained high in the Gaspé region during this later period, but declined sharply in the Chaleur Bay region and increased sharply in the central and, to a lesser extent, in the northeast regions for most age groups.

Discussion

Aggregation

A random pattern in space is unexpected for most organisms due to environmental heterogeneity and interaction among individuals. Instead, patterns are generally aggregated (e.g., Taylor and Taylor, 1977; Taylor *et al.*, 1978) and extra-poisson variation is expected in spatial distributions. Spatial behaviour is also generally density-dependent, with degree of aggregation increasing with population density (Taylor and Taylor, 1977; Taylor *et al.*, 1978). In agreement with this general finding, estimated extra-poisson variation was greater at younger (more abundant) ages and in years of greater abundance in this study. Thus, although a probability model with variance proportional to the mean may be adequate for a single age and year (as in most analyses presented here), they may not generally be adequate for analyses combining ages or years.

Temperature

Scott (1981, 1982) listed 2-8 C as the preferred summer temperature range of cod on the Scotian Shelf and in the Bay of Fundy. Scott (1988) reported that the best catches were at temperatures of 4-6 C with cod avoiding very warm (10-12 C) or cold (<2 C) water. On the other hand, in recent March surveys on the Scotian Shelf most age 4 cod were caught at temperatures of 2 C or less (Smith, 1990). In this study, temperature distribution in the southern Gulf of St. Lawrence showed considerable annual variation. In recent years (1981-89), estimated temperatures of maximum catch were mostly within the 2-8 C range. In earlier years, cod tended to be distributed in slightly warmer water (6-10 C) and in 1990 in colder water (1-2 C). This relatively wide annual variation in temperature distribution suggests that temperature preferences of cod are fairly broad. Thus, within limits, variation in the temperature distribution of cod may reflect prevailing environmental conditions more than precise temperature preferences. This view is supported by the correlation between temperature distribution and average bottom temperature in this study.

Tremblay and Sinclair (1985) reported a tendency for older cod to occur at colder temperatures in the southern Gulf of St. Lawrence during the period 1971-1981. I observed no consistent relationship between temperature and age after accounting for effects of depth, suggesting that the tendency reported earlier may have been an indirect effect of depth.

Depth and Regional Distribution

Older cod tend to occur at greater depths in the southern Gulf (Tremblay and

Sinclair, 1985; this study). Separation of age groups by depth was stronger in the period 1979-90 than in 1971-78. This difference between the two periods may be partly due to broad changes in regional distribution. Cod were concentrated in western regions of the southern Gulf in September during the period 1971-78, but were more widely distributed in September during the period 1979-90, with sharp increases in catch rates in central and northeastern regions during this latter period.

Several possible causes can be suggested for these changes in distribution. First, these changes may result from coincident changes in abundance between the 1971-78 and 1979-90 periods, as suggested by Tremblay and Sinclair (1985). Spatial distribution of organisms is the result of two opposing forces: a tendency to congregate in areas of high environmental quality, and a tendency to disperse to minimize competition (e.g., Taylor and Taylor, 1977; Taylor *et al.*, 1978). If the western regions of the southern Guf represent preferred regions of high environmental quality, then expansion of the cod distribution into the central and northeastern regions of the southern Gulf during recent years of high abundance might reflect dispersal into less favoured areas due to increased competition at higher densities. Stronger separation of age groups by depth might also be expected during periods of greater competition (and cannibalism).

Other possibilities are that these distributional changes reflect an earlier migration out of the southern Gulf in recent years (as suggested by Koeller and LeGresley (1981)), a change in the distribution of prey, or some other environmental change. Since both diet and migration are age-dependent, both of the former mechanisms could also produce changes in the separation of age groups by depth. These alternative hypotheses are testable and research to distinguish among them is ongoing.

Acknowledgements

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TABLE 1. Summary of coverage and stratified mean environmental conditions during September bottom trawl surveys of the southern Gulf of St. Lawrence. Strata without coverage were usually fished but were omitted from analyses due to missing bottom temperature data.

Year	Number of sets	Mean Depth (m)	Mean Temperature (°C)	Strata Without Coverage
71	66	78.2	2.6	-
72	70	77.6	2.0	-
73	71	78.0	3.4	-
74	64	76.8	2.4	-
75	67	81.7	3.2	-
76	65	81.1	2.1	-
77	53	81.6	2.2	-
78	59	76.3	3.8	24, 25, 28
79	74	82.3	3.1	-
80	70	79.1	4.9	-
81	68	77.7	3.6	-
82	67	82.5	3.2	-
83	65	83.4	2.2	21
84	89	65.6	1.0	15, 25, 39
85	175	82.7	2.5	-
86	156	82.0	2.2	-
87	139	82.1	2.1	-
88	92	55.7	2.4	15, 21, 25, 37-39
89	164	80.7	2.2	-
90	138	80.5	1.7	-

TABLE 2. Coefficients and probabilities of correlations between ages in the temperature of maximum catch.

Age		3	4	5	6	7
4	r	0.79				
	p	0.0001				
5	r	0.62	0.91			
	p	0.003	0.0001			
6	r	0.50	0.81	0.94		
	p	0.026	0.0001	0.0001		
7	r	0.46	0.77	0.90	0.98	
	p	0.040	0.0001	0.0001	0.0001	
8	r	0.43	0.76	0.85	0.92	0.93
	p	0.056	0.0001	0.0001	0.0001	0.0001

TABLE 3. Coefficients and probabilities of correlations between temperature of maximum catch and year, stratified mean bottom temperature, and population size (from VPA, Hanson et al. 1991).

Age		Year	Stratified Mean Temperature	Population Size
3	r	-0.50	0.51	-0.61
	p	0.024	0.021	0.004
4	r	-0.43	0.51	-0.43
	p	0.059	0.023	0.059
5	r	-0.51	0.53	-0.43
	p	0.021	0.017	0.057
6	r	-0.48	0.49	-0.39
	p	0.034	0.030	0.086
7	r	-0.54	0.45	-0.48
	p	0.014	0.044	0.034
8	r	-0.45	0.31	-0.47
	p	0.049	0.19	0.037

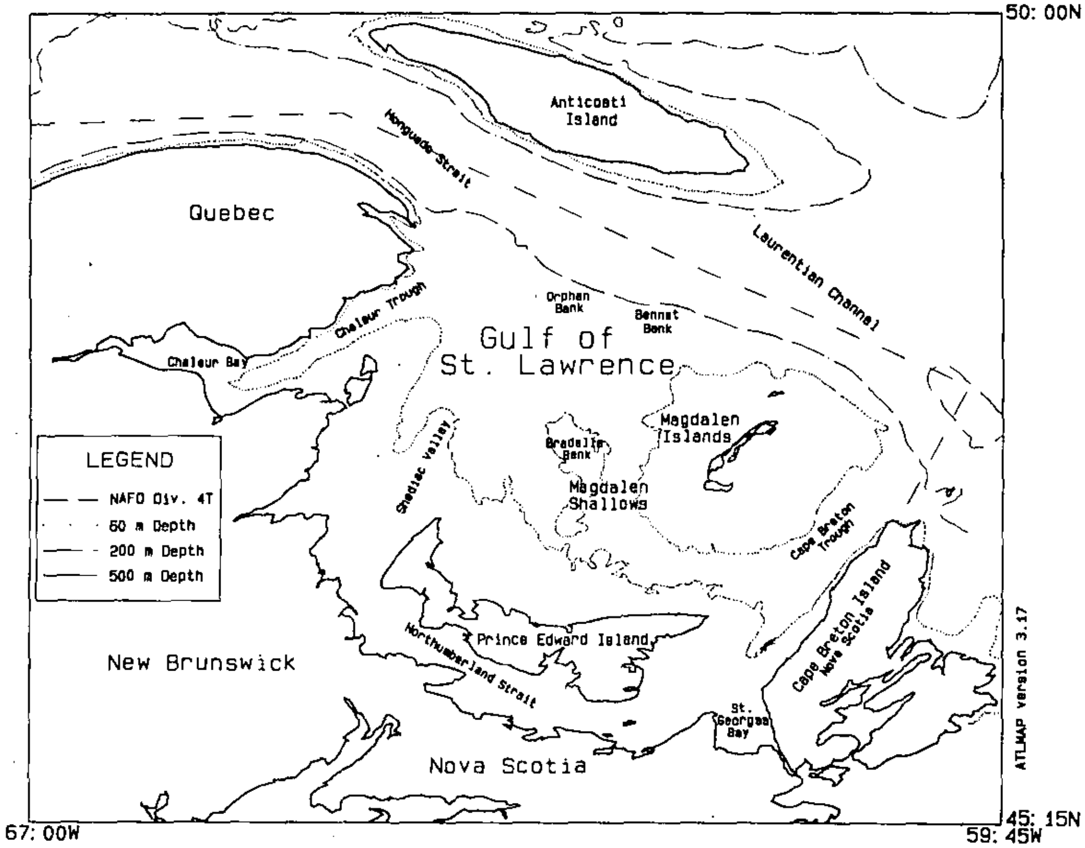

Fig. 1. Bathymetric map of the southern Gulf of St. Lawrence.

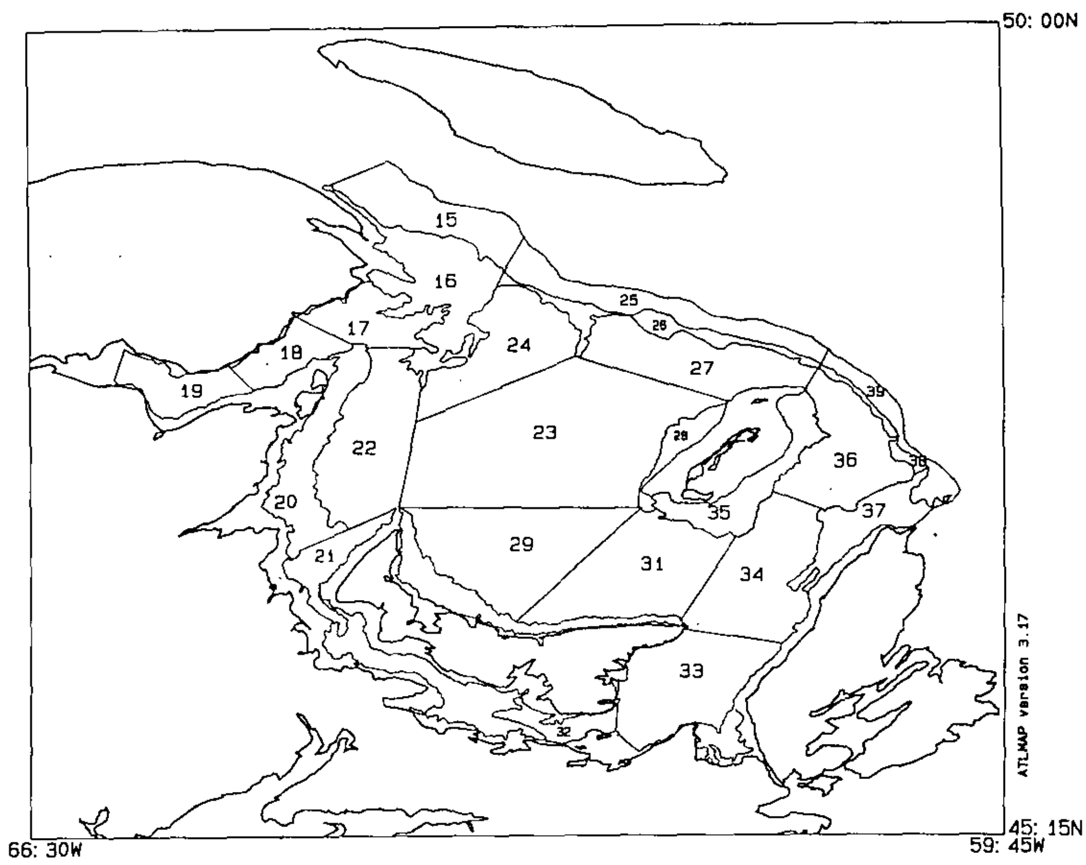

Fig. 2. Stratification map of the southern Gulf of St. Lawrence.

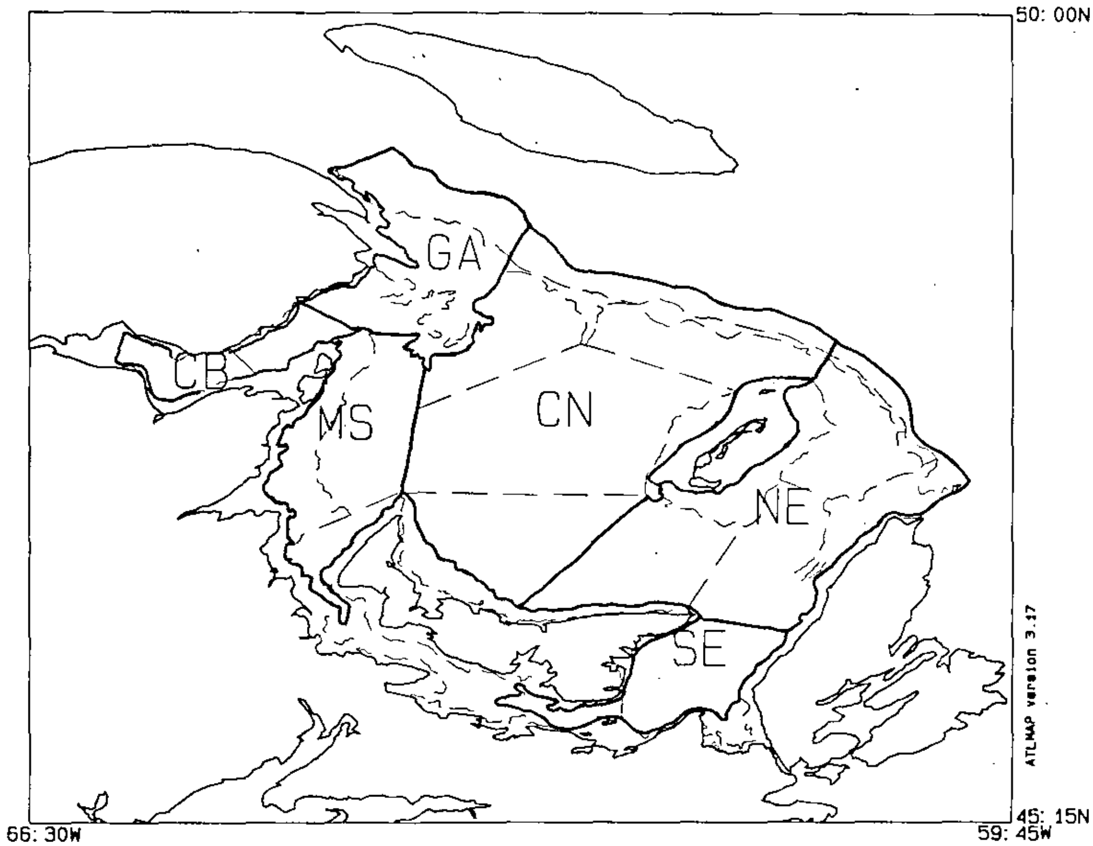

Fig. 3. Map of the southern Gulf of St. Lawrence showing geographic regions used in poisson regression model C. CB = Chaleur Bay, MS = Miramichi-Shediac Valley, GA = Gaspé, CN = central, NE = northeast, SE = southeast.

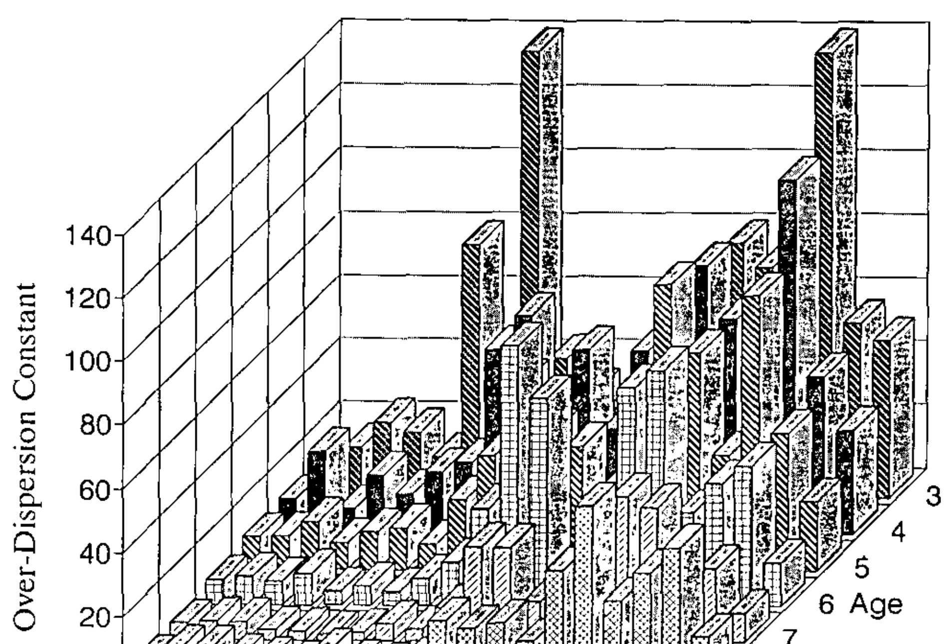

Fig. 4. Estimates of the over-dispersion (extra-poisson variation) constant Theta using poisson regression model A.

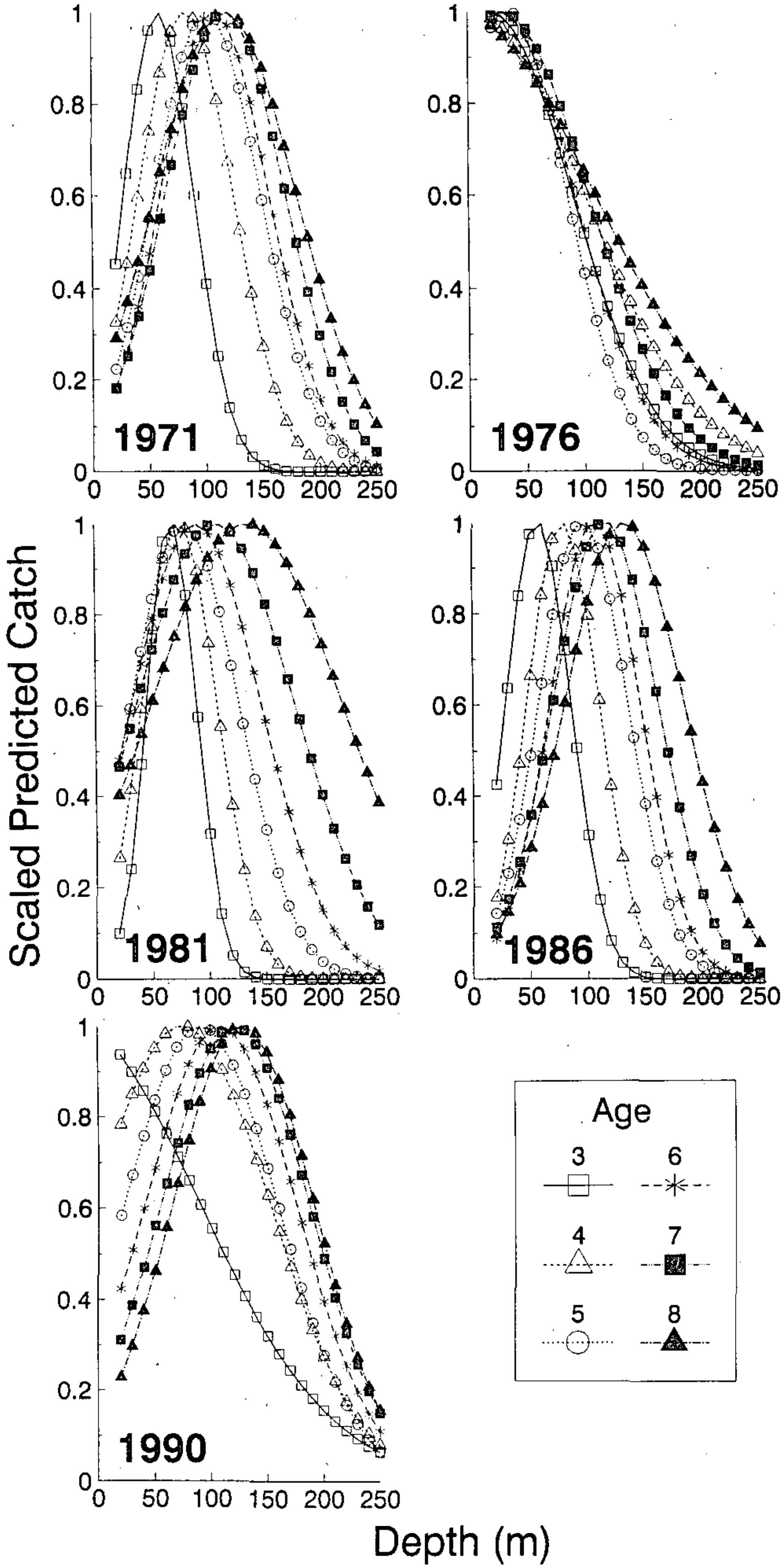

Fig. 5. Predicted values of catch as a function of depth from Poisson model A. Catch has been scaled by the maximum predicted catch for each age and year.

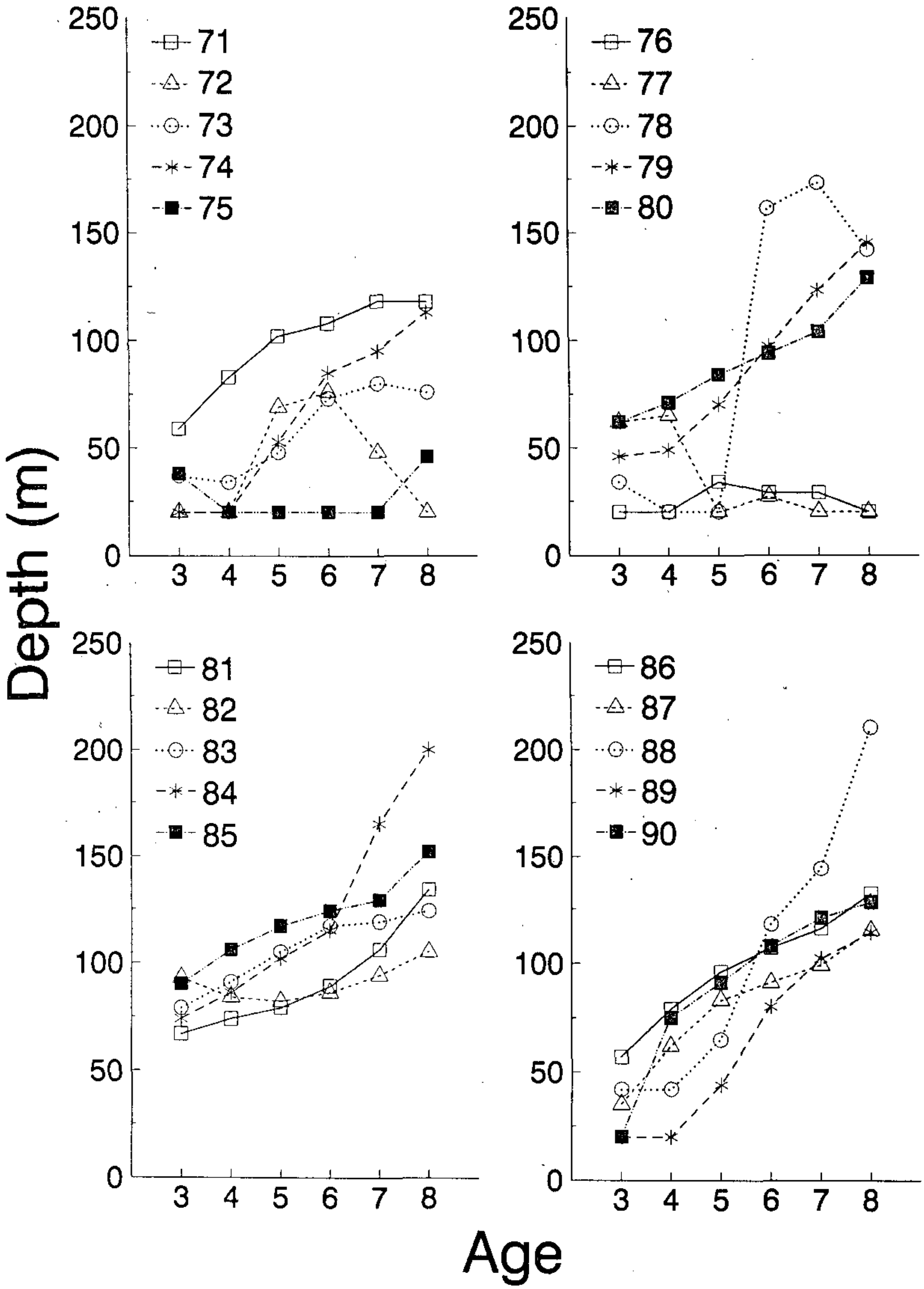

Fig. 6. Depth of maximum predicted catch as a function of age for each year between 1971 and 1990.

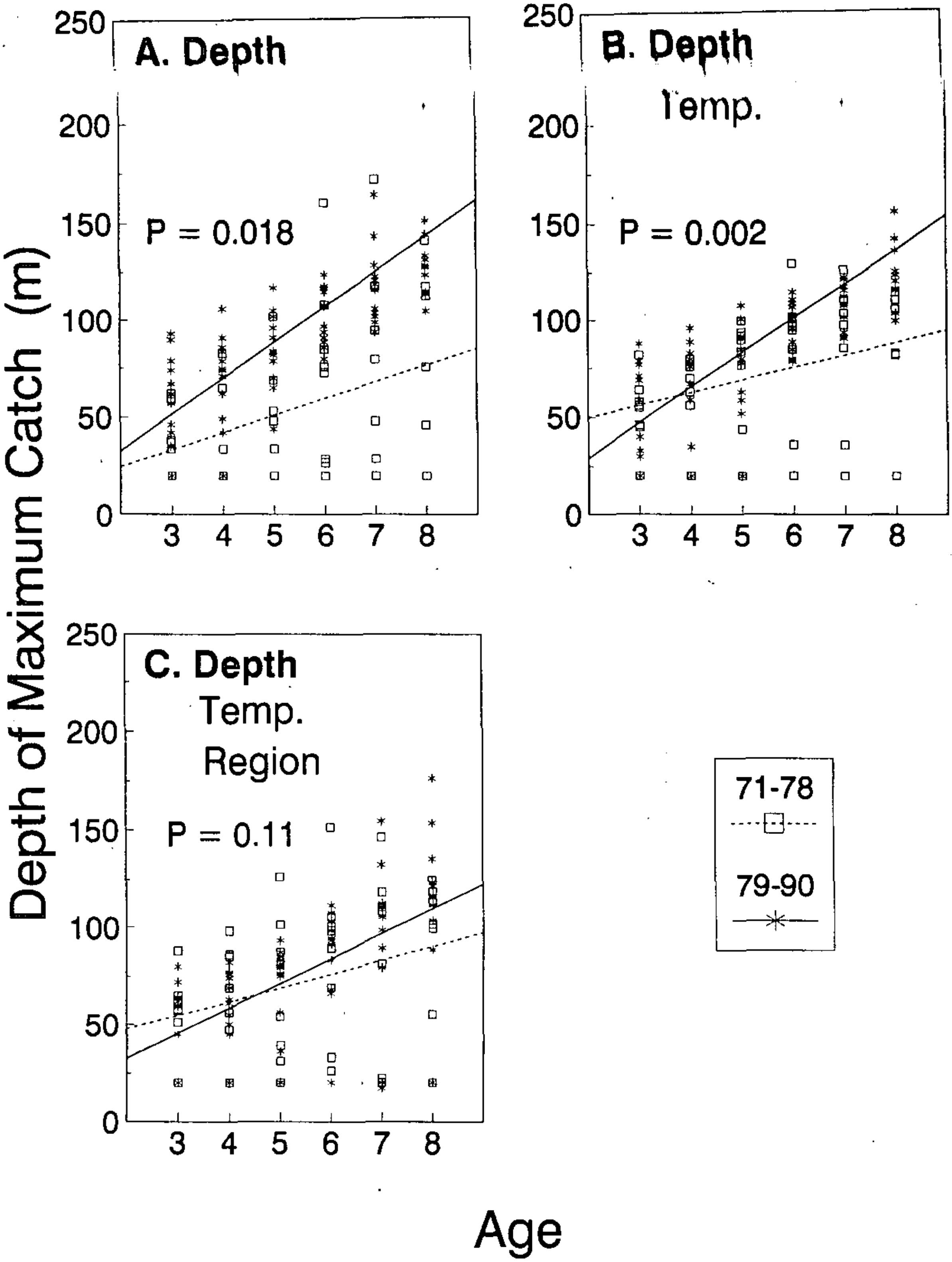

Fig. 7. Regression of the depth of maximum predicted catch against age for the periods 1971-78 and 1979-90, for each of the Poisson models A, B and C.

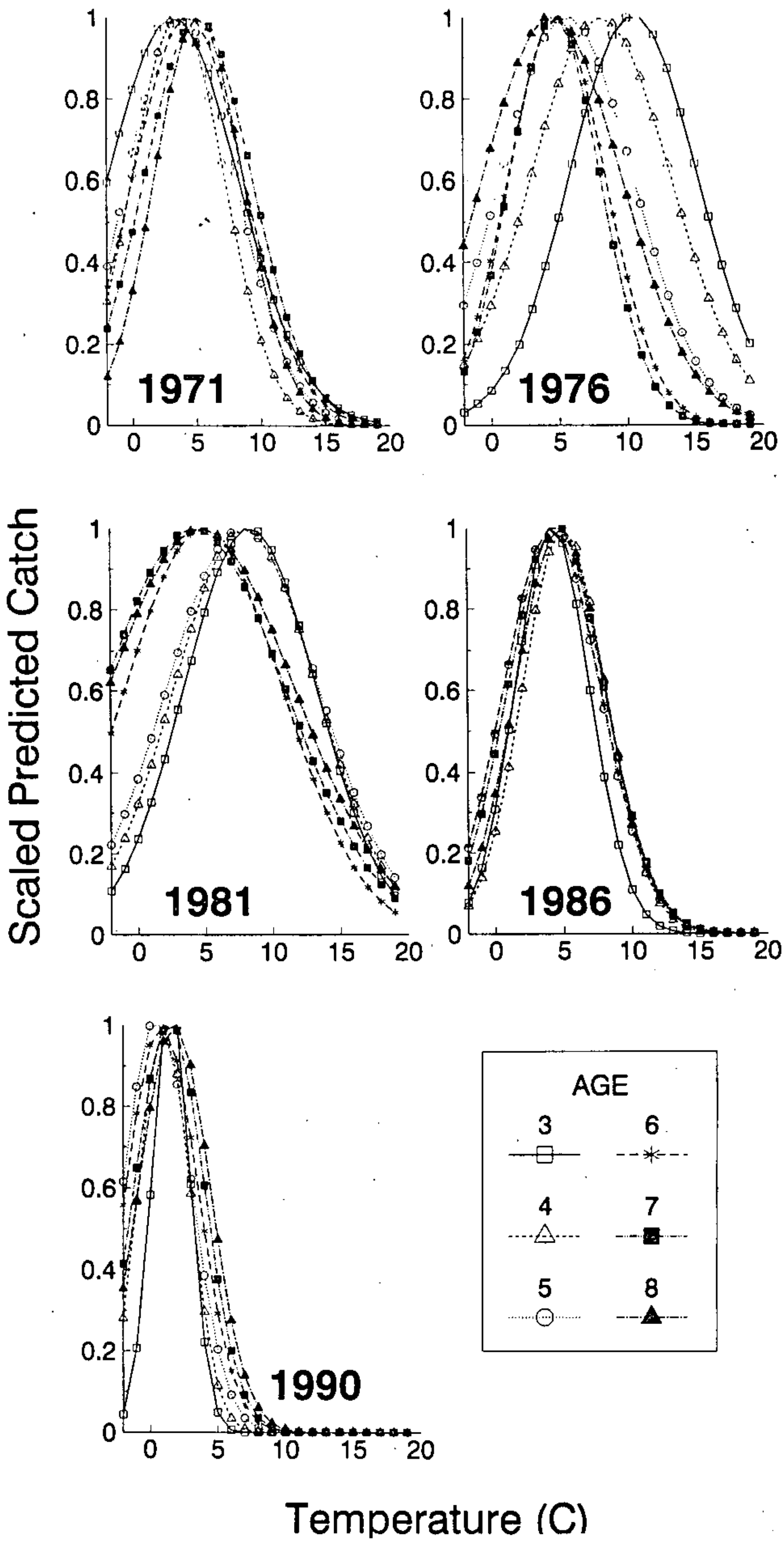

Fig. 8. Predicted values of catch as a function of temperature from Poisson model B. Catch has been scaled by the maximum predicted catch for each age and year.

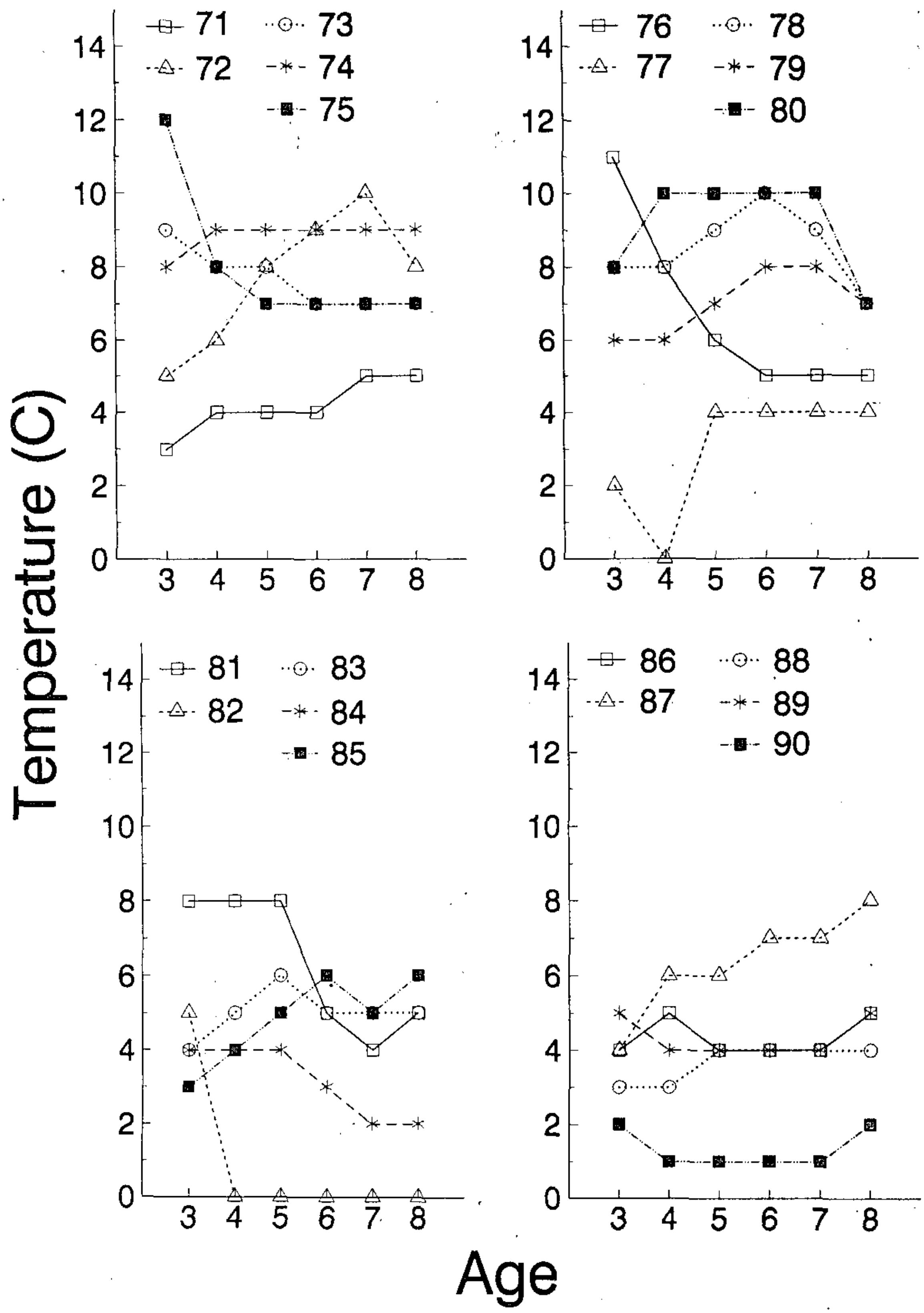

Fig. 9. Temperature of maximum predicted catch as a function of age using Poisson model B.

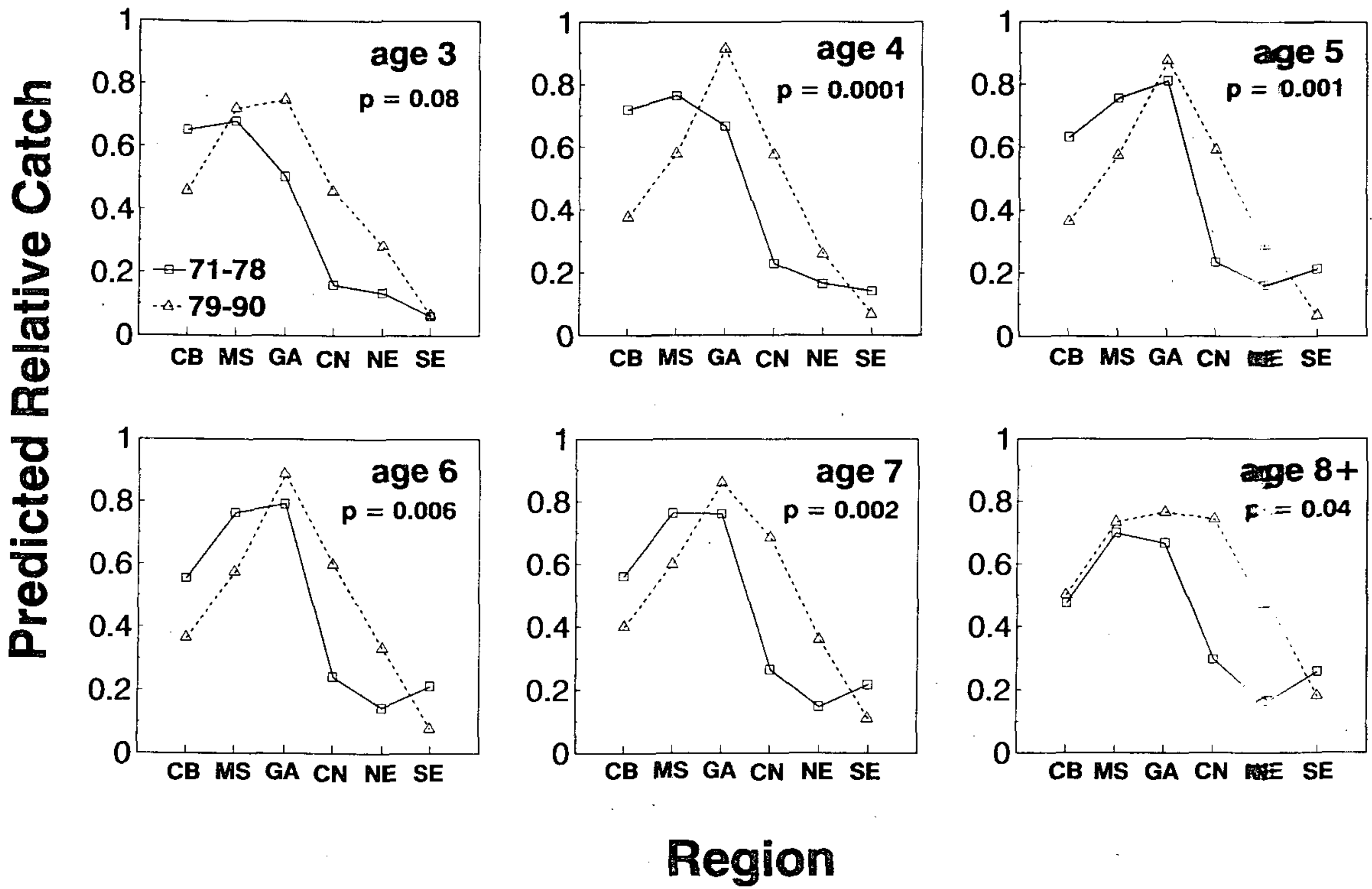

Fig. 10. Predicted relative catch by region for the periods 1971-78 and 1979-90. For each year, predicted catch has been scaled by the maximum predicted value for that year. Probabilities are for the region_x_period interaction from ANOVA of the predicted relative catches with period, region and their interaction as factors.