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Distributions of Atlantic cod and American plaice during the
September 1996 survey of the southern Gulf of St. Lawrence and
their relation to historical patterns

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Abstract

We described the distributions of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) in September 1996 using data from the annual bottom-trawl survey, and compared these distributions to those observed in earlier years. Catches of age-0 cod were less extensive than in 1995. The highest catches occurred in the area south of the Miramichi estuary. Age-1 cod were widely distributed in inshore areas between Miscou Island and western PEI. Catches of age-2 cod were sparse in 1996. Catches of age-3 and -4 cod were highest in shallow water off Miscou Island and northwest of the Magdalen Islands, and in deeper water southwest of St. Paul's Island. Densities of older cod were highest in a band extending from Chaleur Bay, through the Shediac Valley, north of PEI and throughout the northeastern region of the southern Gulf. Densities of age-5 cod in 1996 were relatively high in inshore areas of the western region and low over much of the central Magdalen Shallows. This resembled distributions in recent years (1993-1995) and during the low abundance period of the mid-1970s, and contrasted with distribution during the high abundance period in early 1980s. Even though conditions were cold in 1996, cod occupied relatively warm water in 1996, as they had in recent years and in the mid-1970s. This contrasts with the cold temperatures occupied by cod in the early 1980s, when conditions were warm but abundance was high. As in recent years, an unusually high proportion of cod occurred in eastern regions of the southern Gulf.

Distribution in 1996 was similar for small and large plaice, with one concentration in the central Shallows and a second in eastern regions of the southern Gulf. Plaice distribution in 1996 resembled that in 1994 and 1995, showing a marked eastward shift compared to plaice distributions in the 1970s and 1980s. Indications of the eastward shift were apparent as early as 1991-1993. Recent declines in plaice biomass have been confined to western strata of the survey.

Résumé

Nous avons décrit les répartitions de la morue de l'Atlantique (*Gadus morhua*) et de la plie canadienne (*Hippoglossoides platessoides*) en septembre 1996 en nous fondant sur les données du relevé annuel au chalut de fond et avons comparé ces répartitions à celles observées au cours des années précédentes. Les captures de morues d'âge 0 ont été moins élevées qu'en 1995. Les plus importantes ont été réalisées au sud de l'estuaire de la Miramichi. Les morues d'âge 1 étaient largement réparties dans les zones côtières situées entre l'île Miscou et l'ouest de l'I.-P.-É. Les captures de morues d'âge 2 ont été clairsemées en 1996. Celles des morues d'âges 3 et 4 ont été les plus élevées dans les eaux peu profondes situées au large de l'île Miscou et au nord-ouest des îles-de-la-Madeleine et, dans des eaux plus profondes, au sud-ouest de l'île St. Paul. Les densités de morues plus âgées étaient les plus importantes dans une bande s'étendant de la baie des Chaleurs, en passant par la vallée Shediac, au nord de l'I.-P.-É. et à la partie nord-est du sud du Golfe. Les densités de morues d'âge 5 étaient relativement élevées dans les zones côtières de la région ouest mais faibles dans la plus grande partie des hauts-fonds des îles-de-la-Madeleine. Cette répartition est semblable à celle notée au cours des dernières années (1993-1995) et pendant la période de faible abondance du milieu des années 1970 et diffère de celle notée pendant la période de forte abondance du début des années 1980. Les températures ont été froides en 1996 et les morues se rencontraient dans des eaux relativement plus chaudes, comme au cours des dernières années et au milieu des années 1970. Au contraire, les morues se trouvaient dans des zones froides au début des années 1980, lorsque les températures étaient plus élevées et l'abondance plus grande. Comme au cours des dernières années, une proportion anormalement élevée de morues se trouvait dans les zones est du sud du Golfe.

La répartition de 1996 était semblable pour les petites et les grandes plies, une concentration se trouvant dans les hauts-fonds du centre et une autre dans l'est de la partie sud du Golfe. La répartition de la plie de 1996 ressemblait à celle de 1994 et 1995 et présentait un décalage marqué vers l'est comparativement aux années 1970 et 1980. Des indices de ce déplacement vers l'est étaient visibles dès 1991-1993. Les récentes baisses de la biomasse des plies se limitaient à la strate ouest du relevé.

Introduction

The geographic distribution of individuals in a population reflects their environmental preferences and the results of intra- and interspecific interaction. Changes in distribution may reflect changes in environmental conditions (e.g., deYoung and Rose 1993), changes in environmental preferences (e.g., Swain and Kramer 1995), changes in the distribution or abundance of prey, competitors or predators, or changes in the relative abundance of stock components, and can have important implications for fisheries production and management.

The two dominant groundfish species in the southern Gulf of St. Lawrence are Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*). Plaice distribution during the September feeding season in the southern Gulf remained remarkably stable throughout the 1970s and 1980s despite wide variation in plaice abundance (Swain and Morin 1996, 1997). However, plaice distribution in September 1994 and 1995 showed a sharp shift toward eastern regions of the southern Gulf compared to distributions of the 1970s and 1980s (Swain 1996). In contrast to plaice, cod distribution in the southern Gulf varied substantially during the 1970s and 1980s. This interannual variation in cod distribution is consistent with a density-dependent redistribution of the population as predicted by optimal foraging theory (Fretwell and Lucas 1970, MacCall 1990) and bioenergetic considerations (Swain and Kramer 1995). Cod geographic range expanded as abundance increased from the mid 1970s to the early to mid 1980s (Swain and Sinclair 1994). Cod distribution shifted from warm inshore waters in the mid 1970s to relatively cold waters at intermediate depths in the early to mid 1980s (Swain 1993, Swain and Kramer 1995). This shift in distribution is consistent with the bioenergetic prediction that fish should occupy colder water at higher levels of abundance in order to reduce metabolic costs when food rations are low (Swain and Kramer 1995). Recent shifts in distribution back to the low-abundance pattern, with peak densities in warm shallow waters, provide additional support for the hypothesis that cod distribution is density-dependent during the feeding season in the southern Gulf (Swain 1996). Variation in cod abundance in the southern Gulf is confounded with variation in environmental conditions, but recent analyses indicate that, for all but the youngest (age-3) cod, variation in distribution is more closely related to density-dependent changes in environmental preferences than to density-independent responses to changes in environmental conditions (Swain 1997). However, cod distribution differed between the low abundance periods of the 1970s and 1990s in one respect: like plaice, a higher proportion of cod has occurred in eastern regions of the southern Gulf in recent years (Swain 1996).

The purpose of this report is to describe the distributions of cod and plaice during the September 1996 bottom-trawl survey of the southern Gulf and relate these distributions to those observed in earlier years.

Methods

These analyses use data from the bottom trawl survey conducted in the southern Gulf of St. Lawrence each September since 1971. In 1996, the survey was conducted September 3-26 and comprised 208 successful tows. In order to be comparable with results for the 1971-1983 period, results reported here exclude strata 401-403, which have been fished only since 1984.

Cod Geographic Distribution

Cod distribution was mapped for each age from 0 to 8+ yr using the same methods as in recent assessments. Cod density was estimated at each point on a 11.75 × 9.75 km grid using the 5 nearest sample points weighted by the inverse of the squared distance between grid and sample points. Contours were drawn at the same levels as in previous years (e.g., Sinclair et al. 1996). Interpolation and contouring was done using SURFER (Golden Software 1991).

For age-5 cod, distribution in 1996 was compared with that in a low-abundance period in the 1970s (1973-1975), a high-abundance period in the early 1980s (1980-1982) and a recent period of low abundance (1993-1995). In order to emphasize changes in distribution rather than changes in abundance, we used a measure of local density U_{ij} that was adjusted for variation in overall population size:

$$U_{ij} = Y_{ij} \frac{\bar{Y}_i}{\bar{Y}_i}$$

where Y_{ij} is the catch in tow j in year i , \bar{Y}_i is the stratified mean catch rate in year i , and \bar{Y}_i is a scaling factor (approximately equal to the average stratified mean catch rate in surveys since 1971). \bar{Y}_i was 25. We mapped the log-transformed catch rate $L_{ij} = \ln(U_{ij} + 1)$ because spatial continuity was stronger and more easily modelled on the log scale (e.g., see variograms in Swain 1996). For each case, we calculated variograms and fitted spherical models to these variograms using GS⁺ (Gamma Design 1994). We estimated fish density at each point on a 11.75 × 9.75 km grid using ordinary point kriging, calculated using the MATLAB program COKRI (Marcotte 1991). Interpolations used the five nearest neighbours. Contours were drawn using SURFER.

Plaice Geographic Distribution

The 1996 distributions of two size classes of plaice (≤30 and ≥31 cm total length) were mapped using the same methods as in recent assessments. Interpolation onto the 11.75 × 9.75 km grid was calculated using kriging as described above, with weights based on relative variograms calculated using GEOEAS.

For commercial-sized plaice (≥31 cm total length), distribution in 1996 was compared to that in earlier years using the same methods as described above for age-5 cod. As

described above for cod, plaice density was adjusted to the same average value (70 fish/tow) in each year for these comparisons.

East/West Biomass

We estimated trawlable biomass of cod and plaice (all ages/sizes) in each stratum by multiplying the mean weight per standard tow in a stratum by the number of trawlable units in the stratum. For each year, we calculated the trawlable biomass in western strata (415-429) and eastern strata (431-439). Plaice catches by the *E. E. Prince* were divided by 0.642 to make them equivalent to catches by the *Lady Hammond*. This conversion factor was derived from an analysis of weights caught by the two vessels in the 1985 comparative fishing experiment (G. A. Poirier, unpublished analyses). Although comparative fishing experiments in 1985 and 1992 revealed differences in fishing efficiency among the *E. E. Prince*, *Lady Hammond*, and *Alfred Needler* in terms of numbers of cod caught (Nielsen 1994), analyses in terms of the weight of cod caught failed to reveal significant differences in fishing efficiency among these vessels (G. A. Poirier, unpublished analyses) and no adjustments have been made here to weights of cod caught to account for the vessel changes in 1986 and 1992.

Cod Temperature Distribution

We compared cod temperature distributions between 1996 and earlier periods with contrasting levels of abundance or environmental conditions using cumulative distribution functions (cdf's; Perry and Smith, 1994). We calculated the cdf (in %) for temperature as follows:

$$f(t) = 100 \sum_{h=1}^L \sum_{i=1}^{n_h} \frac{W_h}{n_h} I \quad \text{where } I = \begin{cases} 1, & \text{if } x_{hi} \leq t \\ 0, & \text{otherwise} \end{cases} \quad (1)$$

where t is a level of temperature, W_h is the proportion of the survey area in stratum h , n_h is the number of trawl tows in stratum h , x_{hi} is the bottom temperature at the end of tow i in stratum h , and L is the number of strata. We similarly calculated the cdf for cod catch in relation to temperature:

$$g(t) = 100 \sum_{h=1}^L \sum_{i=1}^{n_h} \frac{W_h}{n_h} \frac{y_{hi}}{\bar{Y}} I \quad \text{where } I = \begin{cases} 1, & \text{if } x_{hi} \leq t \\ 0, & \text{otherwise} \end{cases} \quad (2)$$

where y_{hi} is the number of cod caught in tow i in stratum h and \bar{Y} is the stratified mean catch per tow. Using these cdf's, we calculated the estimated percent of the survey area and the percent of cod occurring in 1°C bins of bottom temperature. We calculated these statistics for 1996 and for the three previous periods used to illustrate variation in the geographic distributions of cod, 1973-1975 (low abundance, intermediate environment), 1980-1982 (high abundance, warm environment), and 1993-1995 (low abundance, cold environment). For the three multi-year periods, cod catch rates were adjusted for interannual variation in overall population size as described above. For each period, we assessed the significance of temperature selection by cod using randomization tests (Perry and Smith, 1994). The test statistic was the maximum absolute vertical distance between

$f(t)$ and $g(t)$, calculated at 0.5°C intervals between -2.0 and 20.0°C. For each test, cod catches were redistributed randomly among temperatures 2999 times, following the procedure described by Perry and Smith (1994). The proportion of the random permutations (including the observed data) with a test statistic equal to or greater than that of the observed data gives the probability of the observed difference between cod and available temperature distributions under the null hypothesis that cod are distributed randomly in relation to temperature. We also calculated median temperatures available in the environment and occupied by cod using $f(t)$ and $g(t)$, evaluated at 0.1°C intervals.

Results and Discussion

Cod Geographic Distribution

The largest catches of age-0 cod in September 1996 were in the area south of the Miramichi estuary and west of Northumberland Strait (Fig. 1). Smaller catches of age-0 cod occurred in inshore areas north of PEI, east of PEI off Beach Point and in the St. Georges Bay area. Catches of age-0 cod were considerably less extensive in 1996 than in the 1995 survey. In particular, the large catches of age-0 cod seen in the Chaleur Bay area in 1995 were not seen in 1996.

Age-1 cod were widely distributed in inshore waters in a band from Miscou Island to western PEI (Fig. 2). Catches of age-1 cod were considerably more extensive and widely distributed in 1996 than in recent years (Sinclair et al. 1995, 1996). This is consistent with the large catches of age-0 cod in several areas of the southern Gulf in 1995 (Sinclair et al. 1996). Catches of age-2 cod were sparse in 1996, with the highest concentration northwest of the Magdalen Islands. Catches of age-3 and age-4 cod were highest in shallow water off Miscou Island and northwest of the Magdalen Islands and in deeper water near the Cape Breton Trough. Catches of these ages were also moderately high in areas west and north of PEI and southeast of the Magdalen Islands. Densities of older cod were highest in a band extending from the Chaleur Bay and Miscou areas, through the Shediac Valley and off the Miramichi Estuary, along the north shore of PEI and throughout the northeastern region of the southern Gulf between the Magdalen Islands and Cape Breton. Peak densities occurred off Miscou Island, north of the Magdalen Islands and west of St. Paul Island. Substantial concentrations also occurred in Chaleur Bay, west of Bradelle Bank, north of PEI and southeast of the Magdalen Islands. In western areas, cod concentrations tended to extend further out into the central Shallows than in recent years, though densities remained low over much of the central Shallows. The cod concentrations depicted as extending to the edge of the survey area along the Laurentian Channel north and east of the Magdalen Islands are misleading in Figure 2. These concentrations reflect high catches in the 80-160 m depth range. Nearby tows in deeper water closer to the edge of the survey area caught few cod.

Figure 3 compares the distribution of age-5 cod between 1996 and a low-abundance period in the 1970s, a high-abundance period in the 1980s and recent years when abundance was again low. In the low-abundance period in the 1970s, cod densities were

highest in inshore areas of the southwestern Gulf and low in the central Magdalen Shallows. In the high-abundance period in the 1980s, distribution expanded into the central Shallows and peak densities shifted offshore to intermediate depths. In recent years of low abundance, distribution in western regions shifted back to the pattern of the mid 1970s, with peak densities in inshore areas and few cod over the central Shallows. However, distribution in recent years differed from that in the mid 1970s in that a higher proportion of cod occurred in eastern regions of the southern Gulf in recent years than in the earlier period. Distribution in 1996 resembled that in the 1993-1995 period, with densities relatively high in inshore areas of the western region and low over much of the central Shallows, and with a relatively high proportion of cod distributed in eastern areas between the Magdalen Islands and Cape Breton. One notable feature of the distribution in 1996 was the absence of cod off the Gaspé Peninsula, an area where densities have historically been relatively high.

The changes in distribution displayed in Figure 3 are consistent with the hypothesis that cod distribution is density-dependent, expanding and shifting into colder water at intermediate depths as abundance increases (Swain 1993, Swain and Sinclair 1994, Swain and Kramer 1995). An alternate hypothesis, consistent with hypotheses proposed to explain changes in the distribution of northern cod (de Young and Rose 1993, Rose et al. 1994), is that these changes in distribution in the southern Gulf reflect a response by cod to environmental change, with cod avoiding areas of cold water. Bottom waters in the southern Gulf are coldest over the central Shallows, an area of low cod density in the mid 1970s and in recent years. Variation in bottom temperatures are consistent with this hypothesis, with relatively cold conditions in recent years and relatively warm conditions in the early 1980s. However, a recent analysis that jointly tested effects of abundance and environmental variation on cod distribution and accommodated autocorrelation in distribution, supported the hypothesis of an environmental effect on cod distribution only for age-3 cod (Swain 1997, and unpublished analyses). For older cod and for the 3+ population, this analysis supported the hypothesis that distribution is density-dependent but provided no support for an effect of variation in the extent of cold bottom water on cod distribution.

Plaice Geographic Distribution

Distribution in the southern Gulf was similar for both small and large plaice in September 1996 (Fig. 4). Two concentrations were present, one in the central Shallows with an arm extending eastward to the area between PEI and the Magdalen Islands, and one in the eastern region with centers of concentration between PEI and St. Georges Bay and between Cape Breton and the Magdalen Islands. Densities were highest in the western concentration on the central Shallows for smaller plaice and in the eastern concentration between PEI and St. Georges Bay for larger plaice.

Distribution in 1996 resembled that in 1994 and 1995 and differed sharply from that seen in most years earlier in the time series (Fig. 5). Plaice distribution was similar throughout the high-abundance period in the 1970s and the low-abundance period in the 1980s (Fig.

5; Swain and Morin 1996). Densities were highest in Chaleur Bay and northwestern areas of the central Shallows, with a smaller concentration in eastern areas between PEI and Cape Breton. Distribution in 1994-1996 showed a marked eastward shift with a striking decline in plaice densities in Chaleur Bay and northwestern regions off the Gaspé Peninsula. Although less marked, this eastward shift in distribution is also evident in the 1991-1993 period.

East/West Biomass

The percent of the cod trawlable biomass occurring in eastern strata has tended to increase since 1971 (Fig. 6). Declines in cod biomass in the late 1980s and early 1990s were steeper in the western strata than in the eastern strata. In recent years, biomass has fallen to levels similar to those of the early to mid-1970s in the western strata but has remained well above the earlier low levels in the eastern strata. In 1996, biomass appeared to increase in eastern strata but not in western strata, resulting in the highest value in the time series for the percent of trawlable biomass occurring in eastern strata.

In 1995 and 1996, the percent of the plaice biomass occurring in eastern strata was the highest in the time series (Fig. 6). Plaice biomass has fluctuated less widely in the eastern strata than in the western strata, neither rising as sharply as the western biomass in the early 1970s nor falling as sharply as the western biomass in the early 1980s. Recent declines in plaice biomass have been confined entirely to the western strata (Fig. 6).

Factors underlying variation in the distribution of cod and plaice between western and eastern grounds in the southern Gulf are not well understood. Possible contributing factors include changes in the relative abundance of eastern and western stock components, responses to changes in patterns of fishing activity or in the distribution of prey, competitors or predators, and effects of delayed spring migrations into the southern Gulf in the early 1990s when ice persisted unusually late in the Gulf (Swain, 1996).

Cod Temperature Distribution

Figure 7 compares the available temperature distribution and cod temperature distribution between 1996 and three earlier periods. Environmental conditions were warm in 1980-1982 (a high-abundance period for cod), moderately cold in 1973-1975 (a low-abundance period), and very cold in 1993-1995 (also a low-abundance period). Cod temperature distribution was coldest in the 1980-1982 period even though environmental conditions were warmest in this period. Cod temperature distribution was most sharply skewed in the 1980-1982 period, with a high percentage of cod occurring in the 0-1°C temperature range. A higher percentage of cod occurred in relatively warm water in the 1973-1975 and 1993-1995 periods. Environmental conditions were again cold in 1996, but cod occupied relatively warm water. A relatively high percentage of cod occurred in the 1-2°C temperature range at age-3, and in the 1-4°C temperature range at ages 5 and 7. These results are consistent with the hypothesis that cod temperature distribution is density-

dependent, with a higher proportion of cod occupying cold water when abundance is high (Swain and Kramer 1995). This relationship is predicted from bioenergetic considerations. The optimum temperature for growth decreases as food ration decreases (Brett et al. 1969, Elliott 1975, Woiwode and Adelman 1991). Thus, fish should occupy colder temperatures as abundance increases in order to reduce metabolic costs as ration decreases (assuming that food ration is density-dependent). Density-dependent temperature distribution provides a possible explanation the density-dependent shifts in geographic distribution observed for cod in the southern Gulf.

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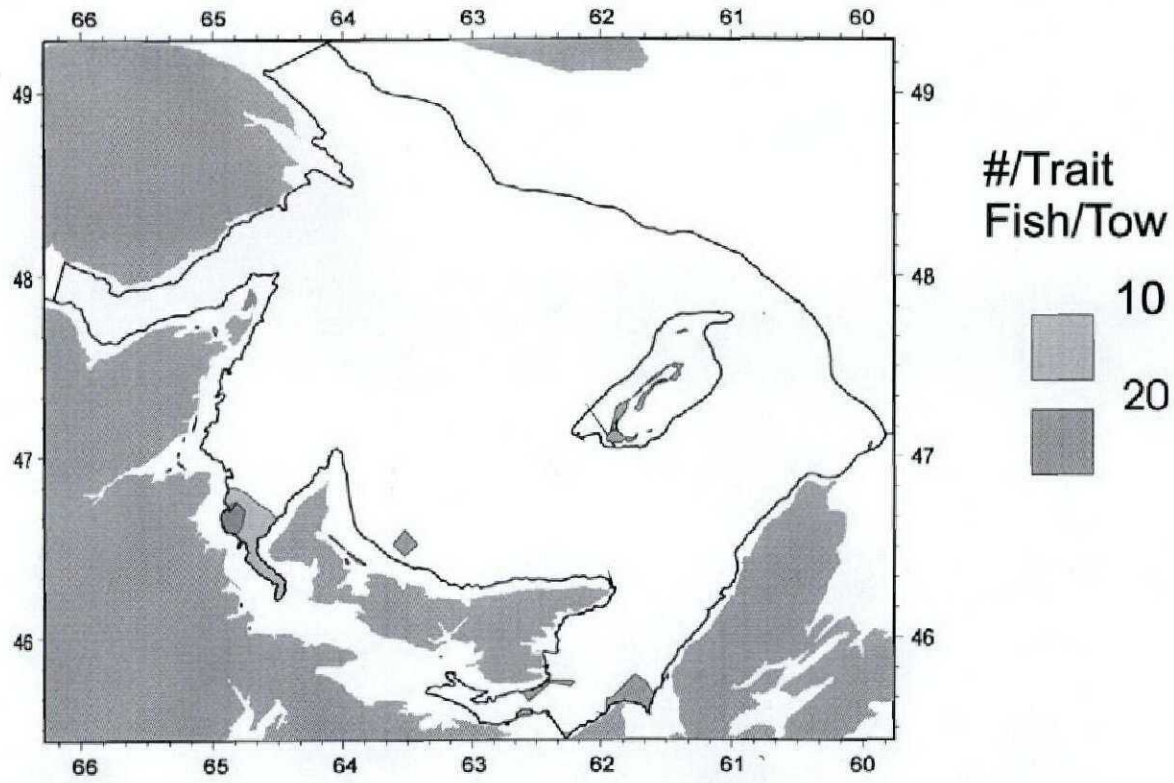


Figure 1. Geographic distribution of age-0 cod during the 1996 September survey of the southern Gulf of St. Lawrence.

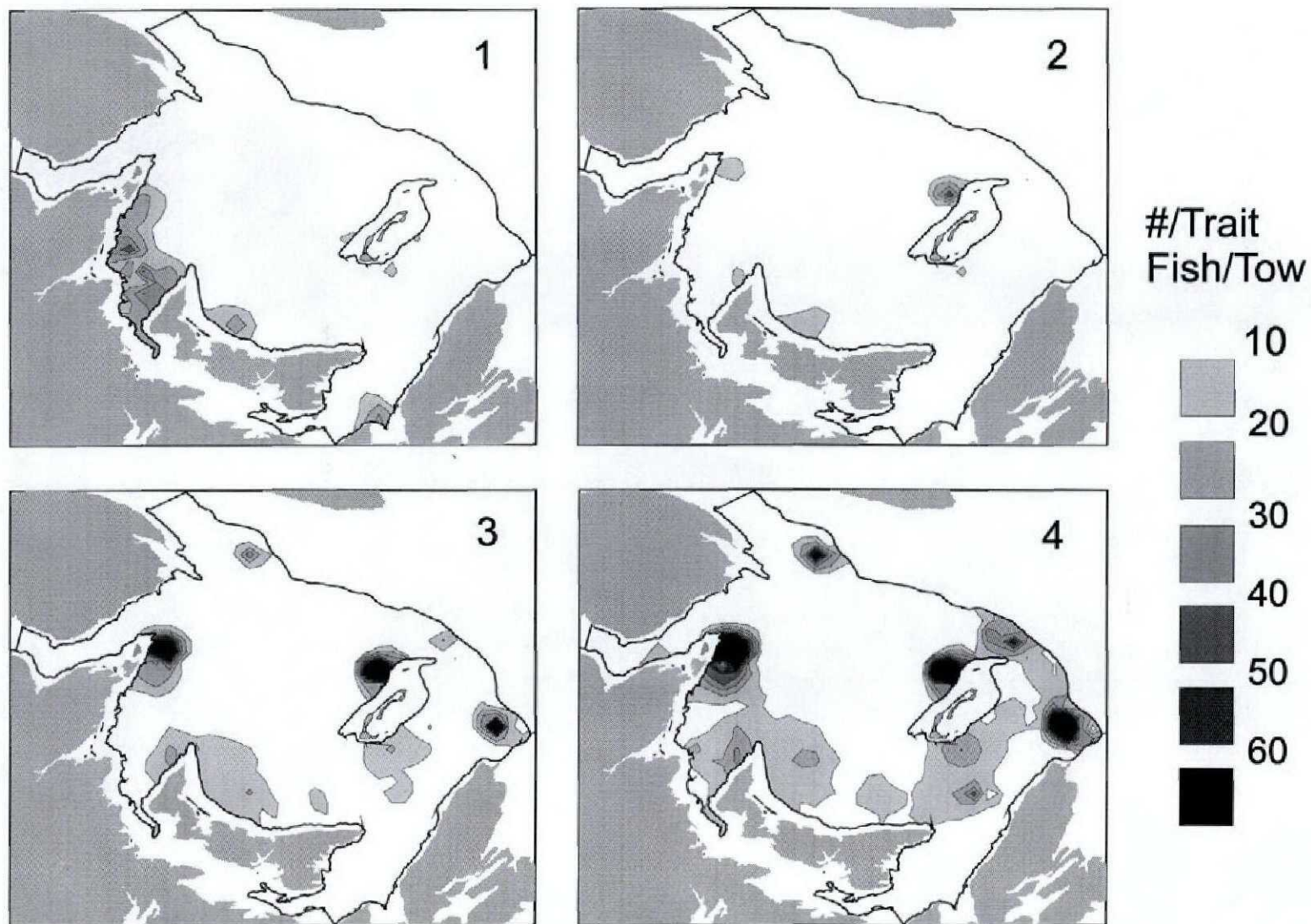


Figure 2. Geographic distribution of cod by age (1-8+ yr) during the 1996 September survey of the southern Gulf of St. Lawrence.

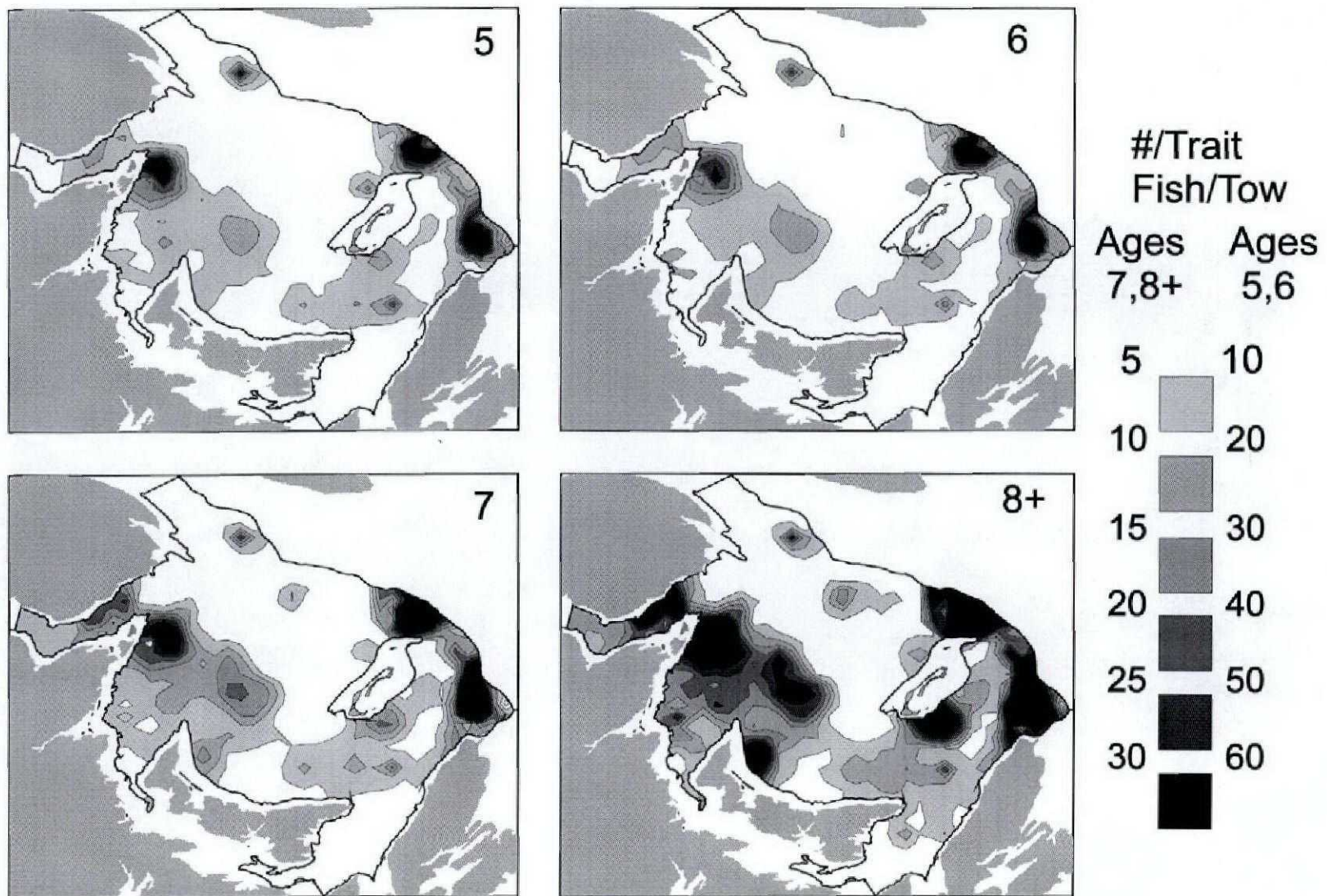


Fig. 2. cont'd.

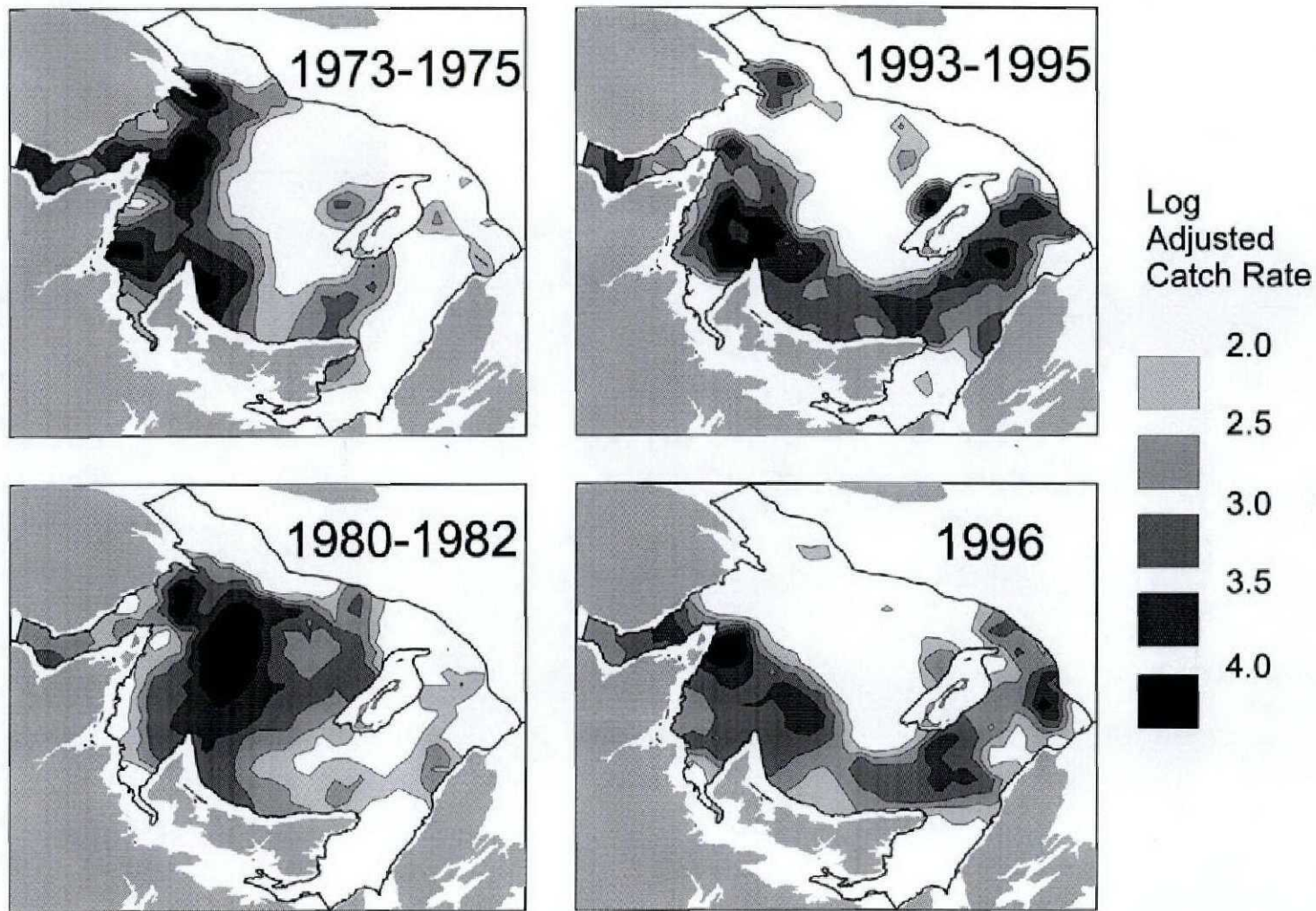


Figure 3. Distribution of age-5 Atlantic cod in September in the southern Gulf of St Lawrence during a low-abundance period in the 1970s, a high-abundance period in the 1980s, and in recent years. Catch rates are adjusted to the same average level (25 fish/tow) in all years.

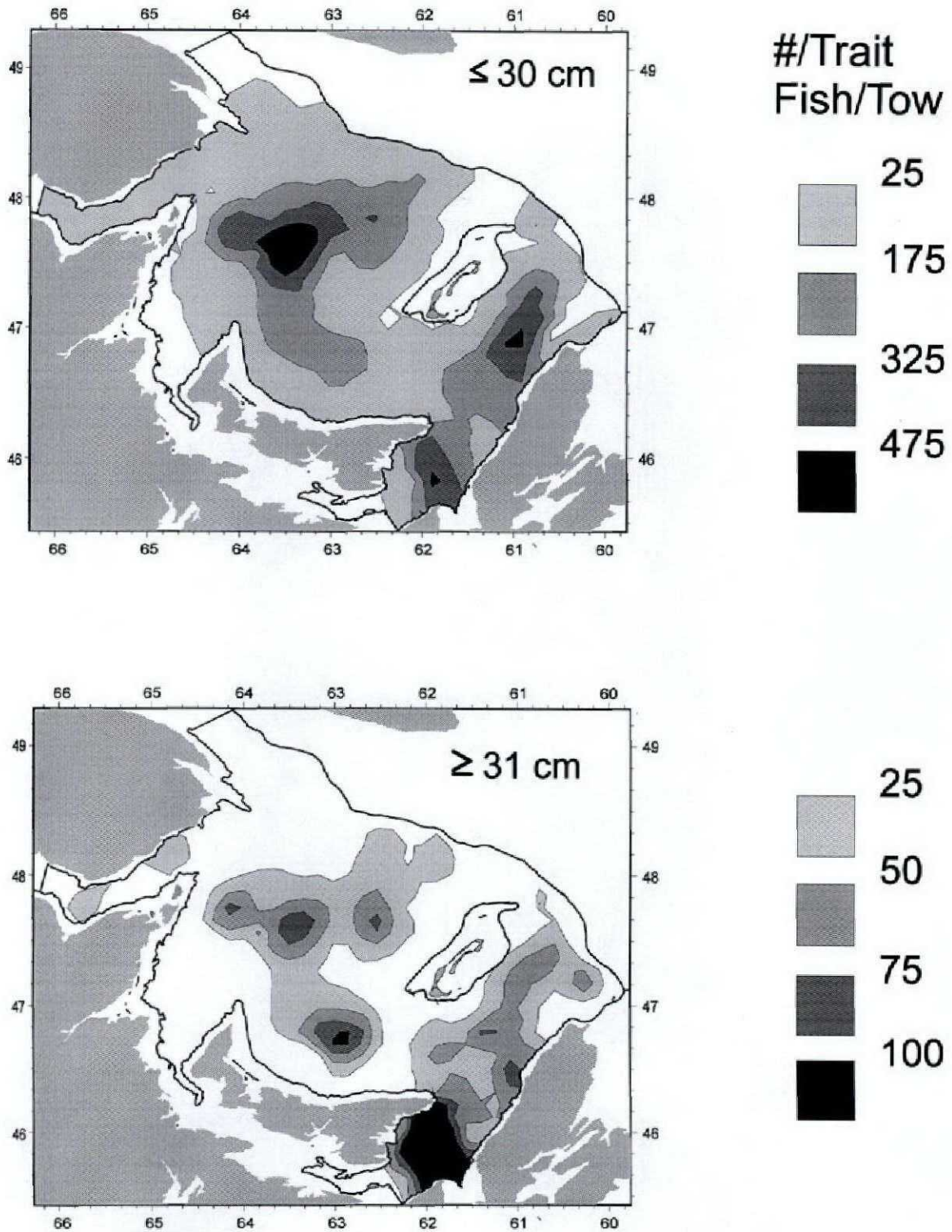


Figure 4. Geographic distribution of American plaice in the southern Gulf of St. Lawrence, September, 1996. Distribution is shown separately for small and large plaice.

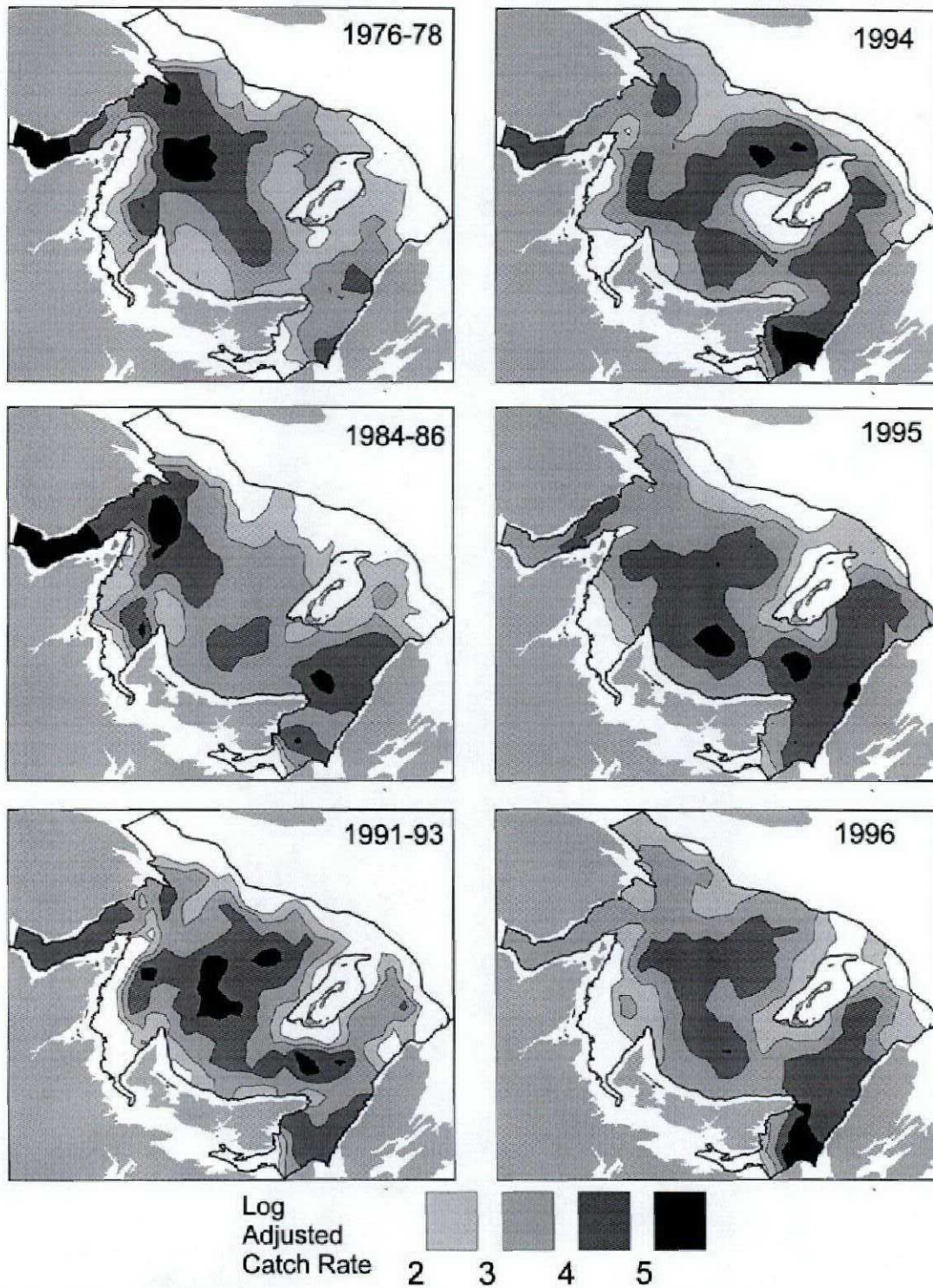
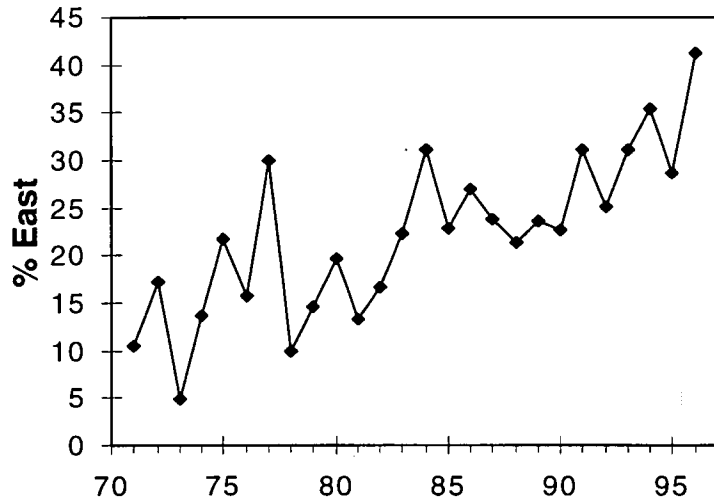


Figure 5. Distribution of commercial-sized American plaice (>30 cm total length) in September in the southern Gulf of St. Lawrence in selected periods. Abundance was relatively high in the 1976-1978 period and relatively low in the other periods. Catch rates are adjusted to the same average level in each year (70 fish per standard tow).

Cod Trawlable Biomass



Plaice Trawlable Biomass

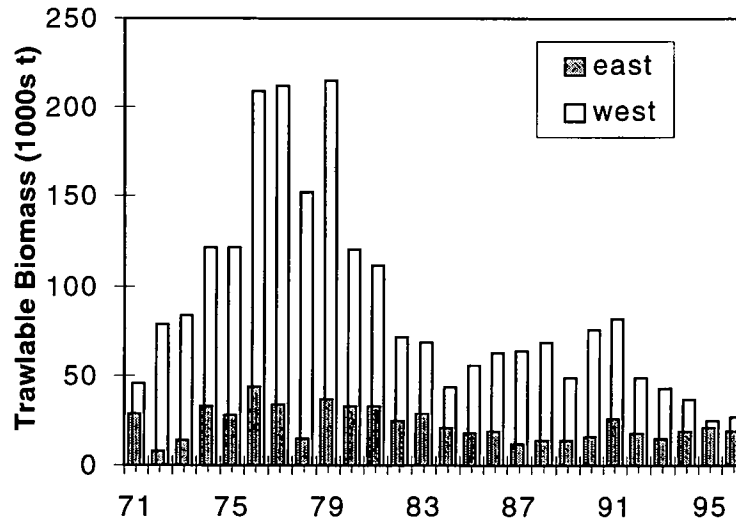
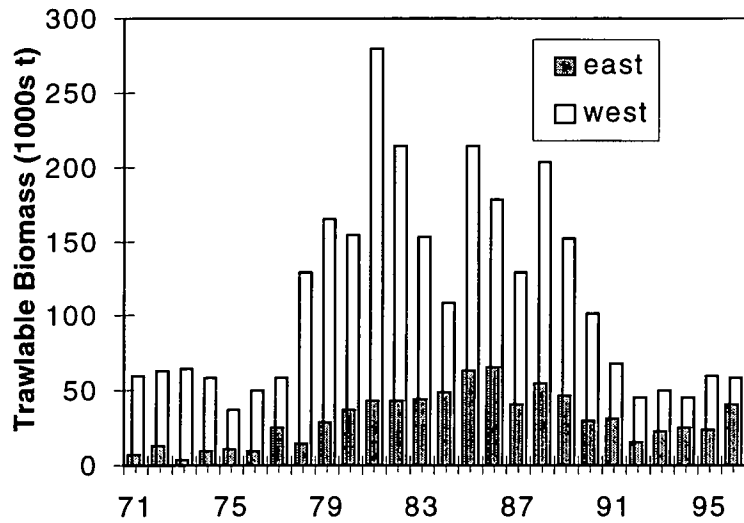
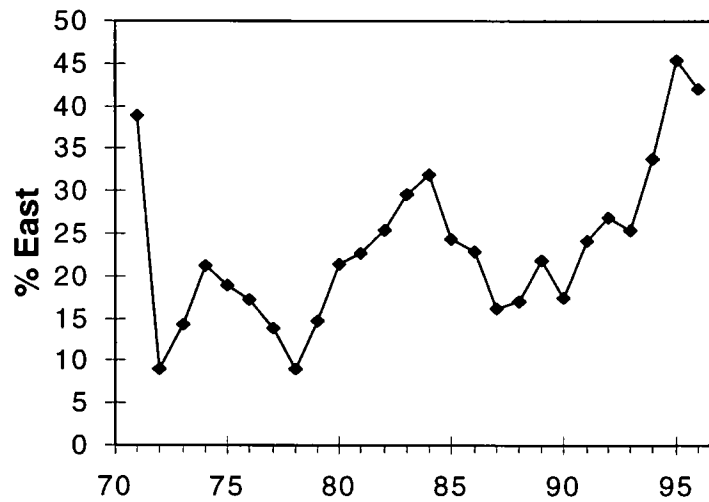


Fig. 6. Distribution of cod and plaice trawlable biomass between eastern (strata 431-439) and western (strata 415-429) regions of the southern Gulf of St. Lawrence.

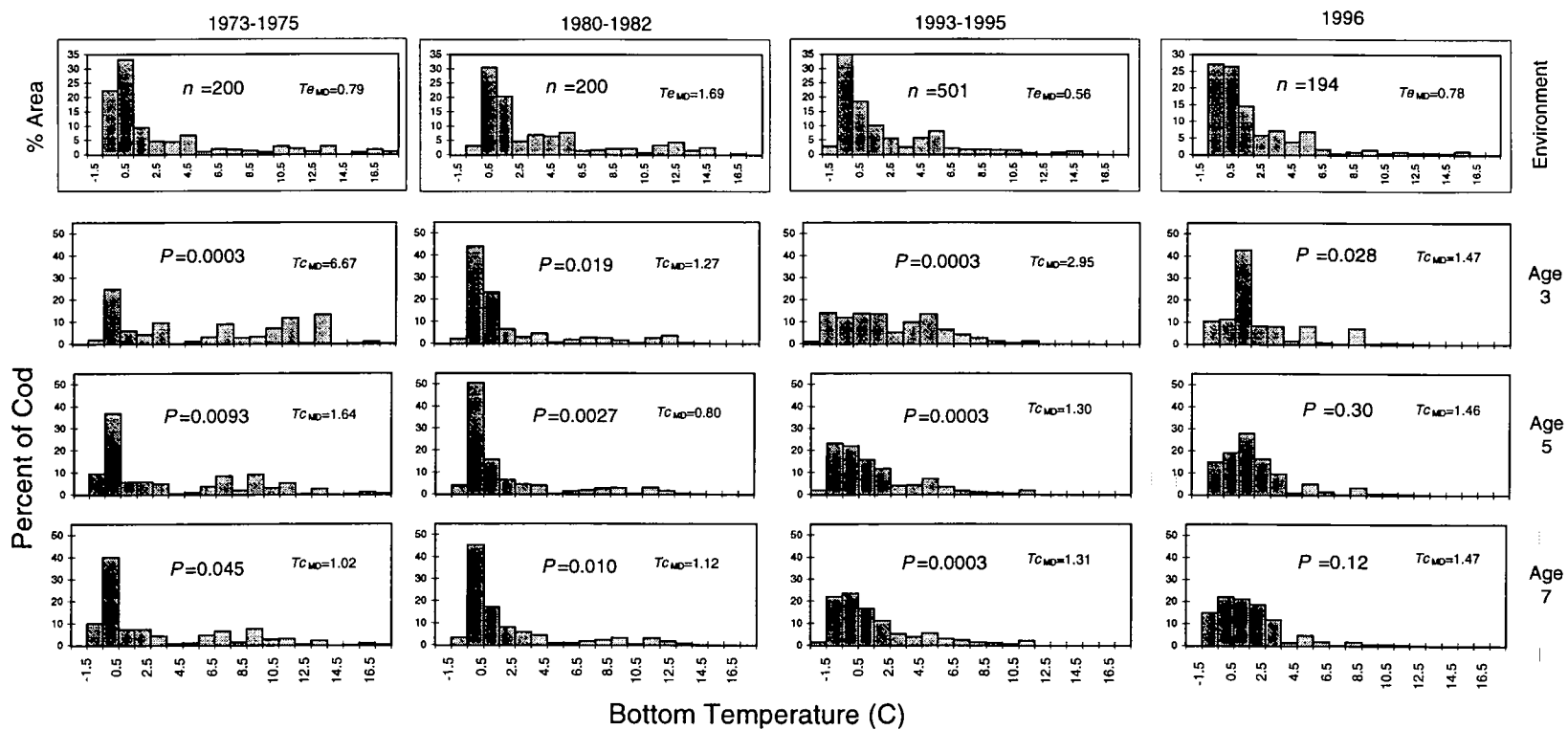


Figure 7. Bottom temperatures available in the environment and those occupied by cod in 1996 and in three earlier periods. n is the number of tows, P gives the significance of temperature selection by cod according to the randomization test described in the text, Te_{MD} is the median temperature available in the environment, and Tc_{MD} the median temperature occupied by cod.