

## PERSPECTIVES

# On Recruitment and Distribution of Atlantic Cod (*Gadus morhua*) off Newfoundland

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The Atlantic cod (*Gadus morhua*) populations located off Labrador and Northeastern Newfoundland (NAFO areas 2G–3L) have recently declined to the lowest levels of abundance on record. These “northern” cod have historically comprised several geographically recognizable populations with independent migratory life cycles on the shelf from the Grand Banks to Labrador. A reappraisal of past and recent work suggests that fundamental changes have taken place in the population dynamics of these cod during the past several decades. We focus on two key elements: distribution and recruitment. Distributions have become more southerly and recruitment failures prevail. We argue that these features are related and that northerly spawning and warm ocean conditions are prerequisites for strong recruitment. Cold ocean temperatures are associated with southerly distributions and poor recruitment. We propose the “right site” hypothesis, that egg and larval retention and survival are spatially dependent and that in cold years, spawning tends to occur at southerly locations where larval retention will be poor. We make several testable predictions: regeneration of the northern populations will occur slowly at time scales of decades, regeneration of southern populations will occur more quickly given warming conditions, and the 1991–93 year classes will be poor because of southerly distributions.

Ces dernières années, les populations de morues franches (*Gadus morhua*) au large du Labrador et dans le secteur situé au nord-est de Terre-Neuve (divisions 2G–3L de l'OPANO) sont tombées à leurs plus bas niveaux jamais enregistrés. Historiquement, ces morues « du Nord » regroupent plusieurs populations géographiquement distinctes qui ont des cycles migratoires indépendants sur le plateau continental, des Grands Bancs jusqu'au Labrador. Un réexamen des articles récents et antérieurs donne à penser qu'il y a eu des changements fondamentaux dans la dynamique démographique de ces morues au cours des dernières décennies. Prenons deux éléments essentiels : la distribution et le recrutement. Les morues sont maintenant distribuées plus au sud et le recrutement fait défaut. Nous avançons l'hypothèse à l'effet que ces caractéristiques sont reliées, et que le frai dans des eaux nordiques et qu'une température élevée de l'eau sont des prérequis d'un bon recrutement. La froideur de l'eau est associée à des distributions méridionales et à de mauvais recrutements. Nous avançons l'hypothèse « du bon endroit », où la rétention et la survie des oeufs et des larves ont des contraintes spatiales et que, les années, où l'eau est froide, le frai tend à se faire plus au sud, où la rétention des larves est mauvaise. Nous formulons plusieurs prédictions vérifiables : la régénération des populations boréales se fera lentement, en termes de décennies, la régénération des populations méridionales se fera plus rapidement si l'eau se réchauffe, et les classes d'âge 1991–1993 seront peu abondantes à cause de la distribution plus méridionale.

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Atlantic cod (*Gadus morhua*) historically have occupied the coastal shelf from northern Labrador to the southern Grand Banks (Fig. 1A). The cod from northern Labrador to the northern Grand Banks have been termed the “northern” cod stock (NAFO areas 2G–3L) (Fig. 1A), traditionally the most productive cod stock in Atlantic Canada (Rose 1992). In recent times the abundance of northern cod has declined to the lowest levels on record (CAFSAC 1992). Cod have become commercially extinct in the most northerly portion of their former range off Labrador (2GHJ). Under the existing

population dynamics paradigm for the stock, the probable causes of this decline are several, including overfishing by local and foreign vessels, recruitment failures as a result of low numbers of spawning fish and poor environmental conditions, and possible increased mortality caused by a growing seal herd and other factors. The prevailing interpretation (e.g., Harris 1990) suggests that removal of these factors will result in a natural rebuilding and redistribution of the stock to levels and patterns last seen some 30 yr ago (Fig. 1B). In this perspective, we question this interpretation and several of its assumptions. We

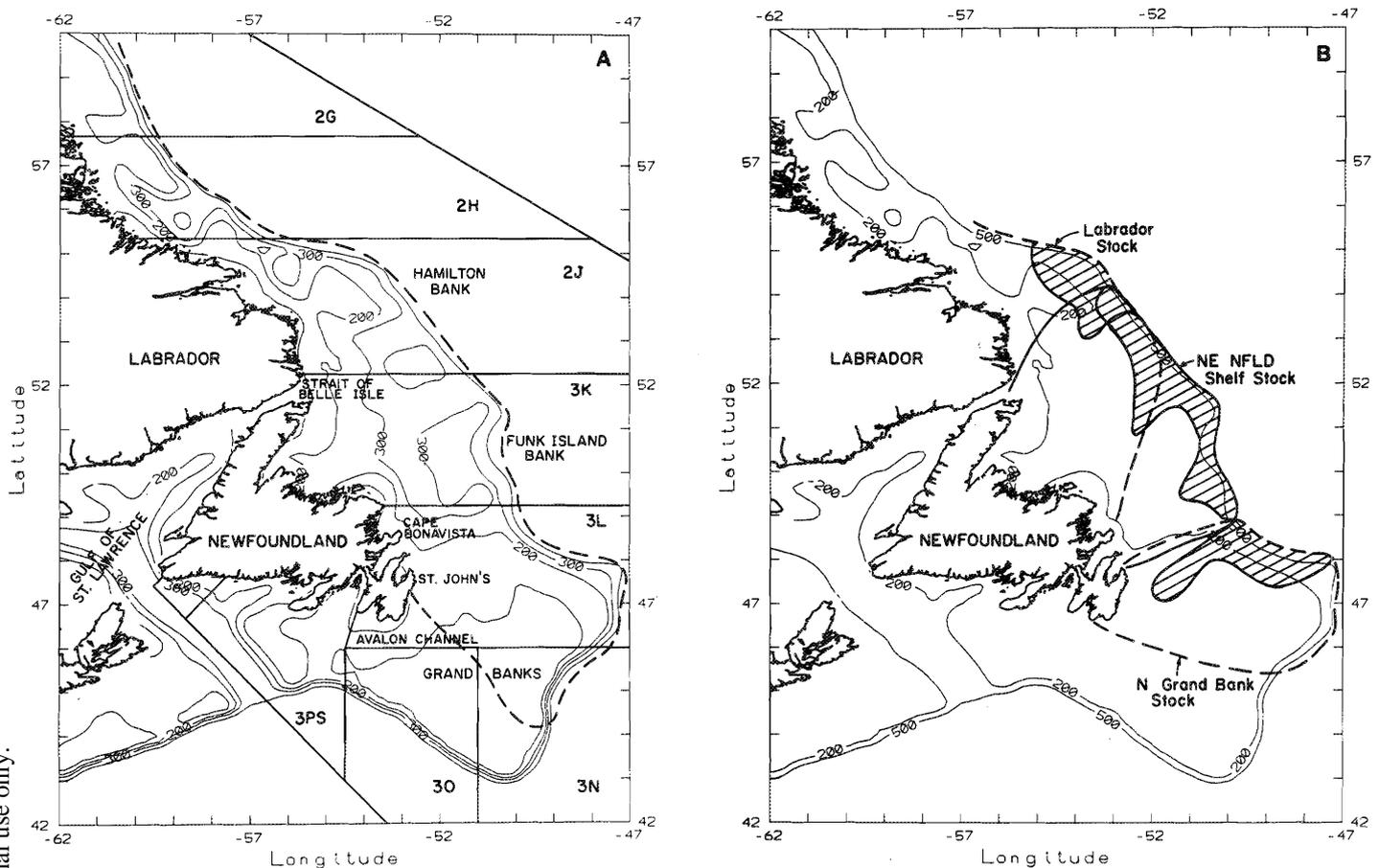


FIG. 1. (A) Bottom topography of the area encompassing NAFO statistical divisions from 2G to 3Ps. Historical range of the northern cod "stock complex" taken from Templeman (1966) is indicated by the broken line. (B) Historic distributions of the Labrador, northeastern Newfoundland, and northern Grand Banks populations. Spawning regions of the different stocks are hatched.

reassess the interactions between stock spatial dynamics and distributions, recruitment, abundance, and environmental fluctuations on the Newfoundland and Labrador shelves and develop an alternative model of recent stock fluctuations.

### Historical Stock Distribution

A fundamental component of fisheries population models and management programs is the distribution of the stock in space and time (Hilborn and Walters 1992). Here, a stock is a management unit whereas a population is a self-sustaining group of organisms whose dynamics, especially recruitment and mortality, are for the most part independent of other populations. A stock may include single or several populations. This definition does not invoke genetic isolation as a prerequisite for population status (see Gaudie 1991).

Population dynamics models employed in research and management of the northern cod have traditionally treated these fish as a single stock (CAFSAC 1992), although there has been wide recognition that the northern cod might form a "stock complex" composed of several populations (Halliday and Pinhorn 1990). In keeping with the single stock notion, recruitment and mortality have often been considered to have no important spatial properties within the full stock area (e.g., Helbig et al. 1992). The Northern Cod Review Panel (Harris

1990) provided a detailed review of the "northern" cod stock as part of an independent review of the management strategy of the Department of Fisheries and Oceans and described the northern cod as a "stock complex". Harris (1990) argued that all regions from northern Labrador (2G) to the southern Grand Banks (3NO) could be considered as one management unit but also recognized that this was an important issue requiring further research.

Several lines of evidence suggest that the "northern" cod has historically included several populations whose summer distributions often overlap because of large-scale shoreward and along shore searches for food. The most longstanding evidence for this view has been derived from 60 yr of cod tagging studies in Newfoundland and Labrador waters and in the Gulf of St. Lawrence. Tagging studies have consistently suggested that local races exist within the range of the "northern" cod.

Thompson (1943) summarized the earliest studies: "On the whole, the evidence from tagging experiments supports the general hypothesis of the existence of local races of cod, the bulk of each of which, in early years of life at least, remain within a region where a specific range of hydrographic and feeding conditions prevails." This hypothesis was supported by more extensive tagging conducted between 1962 and 1966 (May 1966; Templeman 1979). May (1966) suggested that three major groups existed: (1) a Labrador stock that spawns on Hamilton Bank and feeds along the coasts of Labrador and northern Newfoundland, (2) a northeastern Newfoundland population

that also spawns on Hamilton Bank but also southward to Funk Island Bank and feeds in summer along the coast of northeastern Newfoundland, and (3) an eastern Newfoundland population that spawns on the northern Grand Bank and feeds in summer along the coast of eastern Newfoundland. Extensive offshore tagging studies conducted from 1978 to 1981 (Lear 1984) supported May's (1966) hypothesis and provided much additional evidence that the northeastern Newfoundland stock may occupy a large range extending over the entire Funk Island Bank region and as far north as the Hamilton Bank; these data also showed that post-spawning movements tend to be southward from more northerly spawning sites. Tagging studies (1990–92) designed to track the seasonal and annual movements of cod on the northeastern Newfoundland shelf support the earlier work and further indicate that migratory circuits are to a large extent spatially repeated from year to year (Rose 1993).

Northern cod have also been reported to exhibit differing biological properties from the north to the south of their overall range. Thompson (1943) and Templeman (1981) reported that vertebral counts differed between Labrador and Grand Banks fish. Templeman and Fleming (1963) showed that parasitic burdens could be used to characterize cod found in these same zones. These differences suggest limited north–south mixing and therefore geographic stability at scales smaller than those of the full northern cod range. Whether these differences are genetically based remains uncertain. Genetic methods have been suggested for differentiating fish populations, but there is controversy about their validity (Gauldie 1991, 1992; Bentzen 1992). The Ocean Production Enhancement Network (OPEN) and the Northern Cod Science Program (NCSP) are investigating whether there is genetic distinctness among the geographically disparate cod populations from Labrador to the Scotian shelf.

The composite evidence from tagging, biological descriptors, and the work and views of Thompson (1943), May (1966), Templeman (1979), Lear (1984), and Halliday and Pinhorn (1990) suggests that the “northern” cod stock is composed of three geographically based populations (Iles and Sinclair 1982) associated with the Labrador Banks, the northeastern Newfoundland shelf, and the northern Grand Bank (Fig. 1B). All three populations typify North Atlantic cod in that they are migratory and have supported large fisheries. To quote Thompson (1943), “sedentary cod (called “natives” by fishermen) are found all along the coast, but do not as a rule support a large fishery. As a rule, in all regions of the distribution of cod, the fish of the *extended* migration type support the large fisheries.” A summary description of each follows.

#### Labrador

The Labrador cod spawn on the Labrador shelf (Fig. 1B) and migrate in summer to the Labrador coast, at times moving into the Strait of Belle Isle and northern Gulf of St. Lawrence and also to northeastern portions of Newfoundland. The Labrador population almost certainly supplies recruits to more southerly fisheries on the northeastern Newfoundland coast. We propose that recruits are also supplied to the southerly spawning populations on the northeastern Newfoundland shelf and northern Grand Banks. We believe that the Labrador population is the most important to the fisheries because its more northerly distribution provides the best location from which to generate high levels of recruitment. It may also be in the most vulnerable location to changing ocean conditions. The Labrador fish are

accustomed to cold waters (Thompson 1943) and are slow growing with high vertebral numbers (Templeman 1979). This stock was decimated by European trawlers in the 1960's (Harris 1990), though it did partially rebuild during the late 1970's and early 1980's. At present, the population is at the lowest level on record. In the northern reaches (2GH), cod have been commercially extinct since the 1960's.

#### Newfoundland Shelf

The northeastern Newfoundland cod are the most migratory and widest ranging population. They may spawn from Hamilton Bank to the northernmost parts of the Grand Bank depending on their abundance and environmental conditions. This population may recruit well only when spawning occurs in the northern reaches of its range. Recruitment may be as strong as that from the Labrador population when spawning occurs in the northerly part of its range. Fish of this population are midway in growth and meristic characteristics between the Labrador and Grand Banks populations. The northeastern Newfoundland cod migrate in summer to coastal northeastern Newfoundland from the Avalon northward to the Strait of Belle Isle.

#### Northern Grand Bank

The northern Grand Bank population spawns along the northern and eastern slopes of the Grand Bank and migrates in summer along the northeastern slopes of the Bank to the Virgin Rocks area and shoreward to the Avalon Peninsula, and at times northwards to Cape Bonavista. Fish of this population are faster growing and have lower vertebral numbers than fish of the more northerly populations (Templeman 1979). Northern Grand Bank cod are now at relatively low levels.

The historic model of the stock structure of cod on the northeastern Newfoundland and Labrador shelves generates many questions about how such a population pattern could be maintained. The model assumes that widely dispersed progeny congregate with their mother population before they mature. This is not a trivial assumption. Indeed, how can a young cod that was spawned far to the north, drifted southward as an egg, and then spent its entire postdrift life away from its natal area retrace a voyage it made only once as an egg? Templeman (1979) invoked “homing” as the answer. But homing typically assumes a period of juvenile residence in the natal area so that imprinting can occur, as in salmon (Quinn and Leggett 1987). Cod could be genetically predisposed and equipped to return to spawn with their mother population at their natal areas (or at least within broad but distinct regions). However, neither homing nor any navigation mechanisms capable of sustaining such a return migration have been demonstrated for this species. The tagging data suggest that once adult migration patterns are established, they are sustained, but these data are not compelling evidence for homing to natal areas. Juveniles could learn migration routes by following adults back to the spawning regions. But how could juveniles recognize adults of their population, since adults of different populations have overlapping distributions at various times during their life history?

A related but simpler model of the stock structure suggests that populations are sustained by juvenile fish resident in the area of the adult population joining that population. Although the returning juveniles are likely to be progeny of the adult population, at times this may not be the case. Hence, populations are geographically rather than genetically based (although in some cases, genetic differences may have evolved, but their

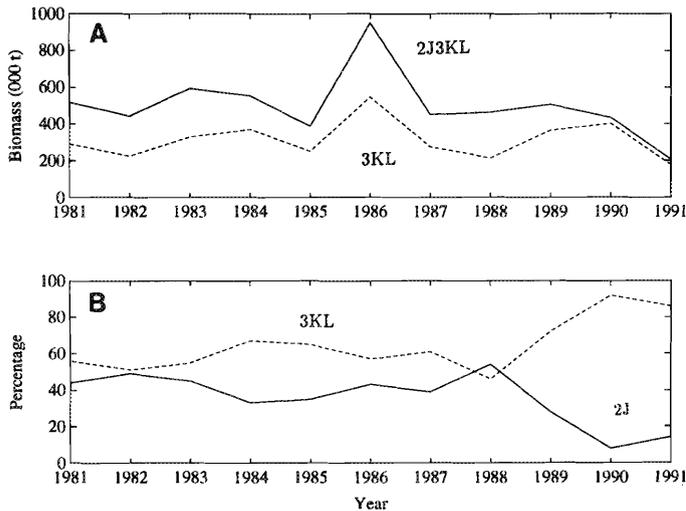


FIG. 2. (A) Trawlable biomass for total "northern" cod stock (NAFO divisions 2J3KL) (solid line) and for the southern region (3KL) (broken line). (B) Percentage biomass in the northern region (2J) (solid line) and in the southern region (3KL) (broken line). Data are from Baird et al. (1992).

importance is unclear). In this model, juvenile cod residing along the Newfoundland and Labrador coast move progressively seaward and closer to the shelf spawning areas as they mature and then join the adjacent adult population. Hence, stock structure will depend to a large extent on the locations at which juveniles mature. For example, juveniles residing near the Labrador coast almost certainly join the Labrador population. But some juveniles spawned on the Labrador shelf might also drift southwards and join the cod population on the northeastern Newfoundland shelf. This model predicts that genetic variation would be higher in southerly populations because drift only occurs southward. Juveniles would be predisposed to learn migration routes from older fish. Once mature, cod would home to spawn to the same region each year by piloting (the use of remembered features and landmarks; Griffin 1955). This model is fully consistent with the tagging and other historic data and descriptions of the stock distribution on the northeastern Newfoundland and Labrador shelves.

Data required to test these alternative models are not available at present. However, we suggest that a better understanding of the stock structures and migratory life histories of cod in Newfoundland waters, and elsewhere, rests on finding answers to some of these fundamental ecological questions.

### Changes in Population Distribution

An examination of the trawl survey data collected during the fall by the Department of Fisheries and Oceans (Baird et al. 1992) suggests that the stock structure evident historically breaks down after 1988 (Fig. 2). Prior to 1988, the proportions of year classes found in 2J, 3K, and 3L remained relatively stable over the life of most of the year classes (Fig. 3). This stability adds further support to the historical interpretation of the stock structure. However, from 1988 to the present, an increasing proportion of the biomass has become concentrated in the southern regions (Fig. 2). Distribution changes are especially evident for older fish. For example, the 1981 year class decreases abruptly in 2J in 1988 and increases unexpectedly in 3K after

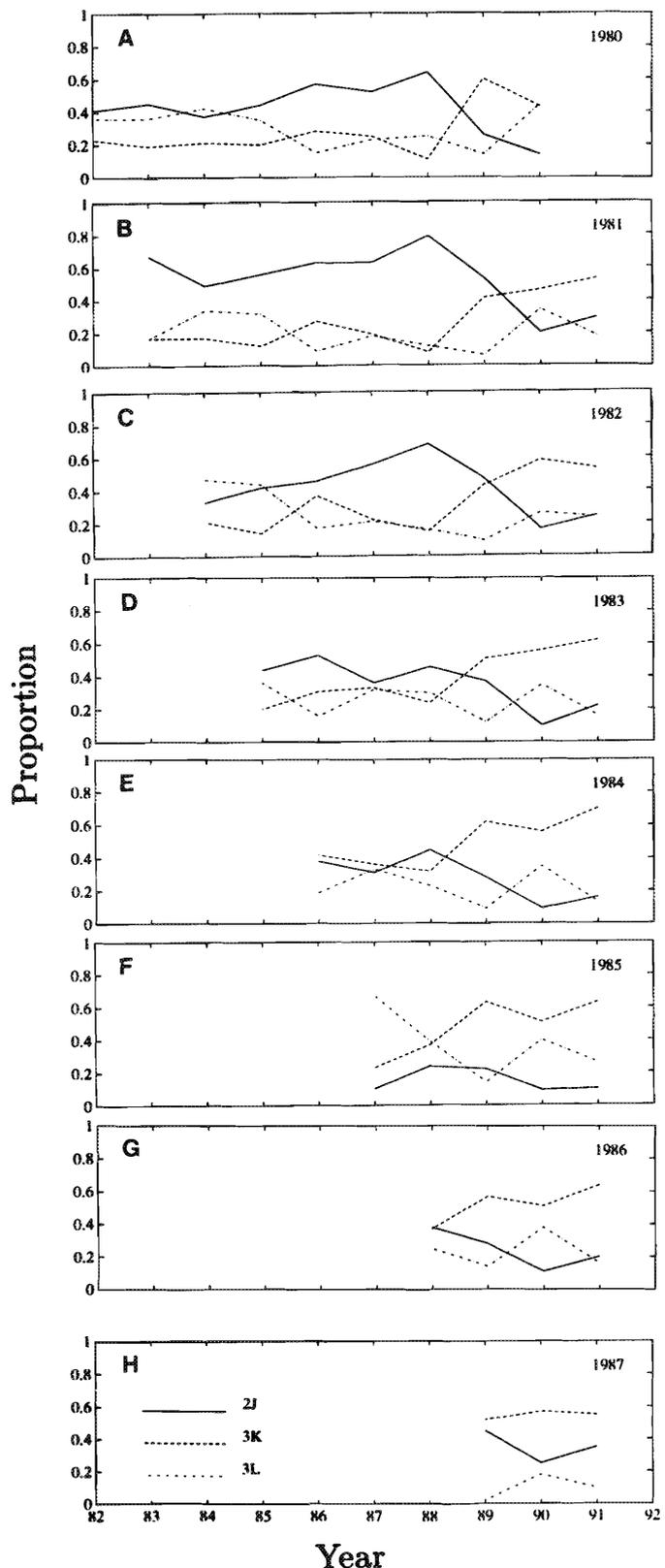


FIG. 3. Relative proportions of year classes spawned from 1980 to 1987 in NAFO divisions 2J, 3K, and 3L, with the year effect removed. Data are from the fall research surveys (Baird et al. 1992).

1989 (Fig. 3). Similar changes can be observed for the 1980, 1982, 1983, and 1984 year classes (ages 8, 6, 5, and 4,

respectively). There is less evidence for redistributions of the 1985–88 year classes (ages 4 and younger).

A key question is whether the distribution changes were caused by fish movements (migratory model) or were simply a consequence of differential fishing mortality (nonmigratory depletion model). The nonmigratory model indicates that cod populations are spatially fixed and were simply “fished-down” from north to south. We believe that fishing precipitated and continues to contribute to the rapid decline in cod abundance in Newfoundland waters in the past decades. However, the disproportionate decline in abundance in the Labrador region (2J) is unlikely to have been caused solely by fishing. Total losses to fishing were greater in the southern regions than in 2J in every year since 1982 (Baird et al. 1992). Moreover, unregulated foreign catches were concentrated in the most southerly part of the range during the 1980’s and early 1990’s. Hence, fishing mortality was likely higher in the south than in the north during this period (Fig. 4). It is conceivable that fishing was responsible for high levels of mortality of the redistributed fish in the southern regions from 1989 onwards. It now appears that most of these emigrants have perished.

We attribute southward migrations of cod to declining sea temperature (Rose et al. 1994). However, it should be kept in mind that temperature may be a proxy for other physical parameters of the ocean (e.g., sea-ice extent) and even biological variables, many of which are correlated at long time scales. For example, capelin distributions (*Mallotus villosus*), like those of cod, appear to have shifted southwards since 1989 (J. Carscadden, Department of Fisheries and Oceans, P.O. Box 5667, St. Johns, NF A1C 5X1, Canada, personal communication). Capelin is the chief food of cod in Newfoundland waters (Lilly 1987), and food shifts influence cod distributions (Beverton and Lee 1965; Rose and Leggett 1990). Thus, deteriorating food supplies for cod in the north could also be a key factor in their movements.

We argue that the stock structure of cod on the northeastern Newfoundland and Labrador shelves could not be considered to be stable except at short time scales (much less than a decade). Spatial patterns and richness (Sinclair and Iles 1989) are regulated by the vagaries of environmental conditions (Iles and Sinclair 1982; Sinclair 1988). Historically, cod populations that formed the “stock complex” (Harris 1990) were likely distributed on many banks from northern Labrador to the Grand Banks. Each “population” was sustained as long as conditions permitted. Smaller populations may have been severely reduced by overfishing. Specific adaptations (genetic) and behaviors (learned) developed to maintain stock and migration patterns (at present, we know little of these mechanisms). In the past three decades, environmental conditions have become less hospitable to cod in the northern reaches of their range in Newfoundland waters. Fish removed first by overfishing and then migration have not been replaced by new recruits. Thus, the more northerly systems have not sustained their once abundant cod populations. Spatial variability in cod populations in northern oceans is not considered unique to Newfoundland waters. Major shifts on cod distributions have been well documented from Greenland and Icelandic waters (Horsted 1989; Hovgård and Buch 1990).

It is noteworthy that our interpretation of stock structures in Newfoundland waters follows the approach of McCall (1990) who proposed that fish populations could become geographically isolated because of varying recruitment success. However, McCall (1990) proposed that fish would redistribute

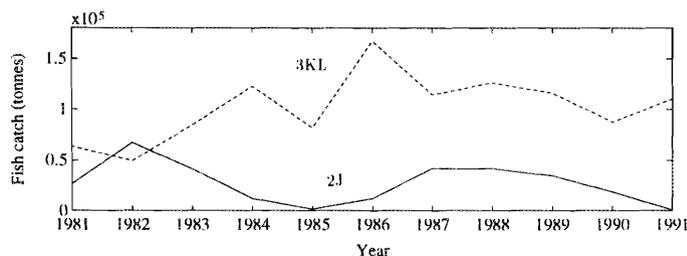


FIG. 4. Offshore fish catch in NAFO divisions 2J (solid line) and 3KL (broken line). Data are from Baird et al. (1992).

naturally as populations increased. Our model differs in that it suggests that density-independent redistribution occurs in response to changing ocean conditions (Sinclair and Iles 1989).

The historical fishery in Newfoundland and Labrador was characterized by remarkably stable catches and also by a large degree of spatial variability (Harris 1990). In particular, the Labrador fishery fluctuated at long time scales (Anonymous 1992). We believe that the overall catch stability was a consequence of large cod populations and the low fishing mortalities of that era. Population fluctuations may not have been detected by the fishery. However, spatial variations were noticed then as now. This is consistent with our model of cod stock dynamics in this region. Accordingly, at times when conditions are best in the north, populations levels will be highest and spatial variations in catch lowest. When conditions are poor in the north, population levels will be poorest and spatial variations in catch highest.

## Recruitment

The current paradigm is that cod from northern Labrador to the northern Grand Bank recruit as a large-scale unit and that smaller scale spatial processes are not important. Koslow et al. (1987) suggested large-scale synchrony of cod recruitment in the Northwest Atlantic. However, more recently, Cohen et al. (1991) reported that the dominant factors for recruitment of cod from Georges Bank to the Labrador shelf operate on more local scales and that recruitment correlations are strongest for neighboring populations. However these data are analyzed, there is evidence of synchrony at large scales but there is also variability at smaller scales. Myers et al. (1993) calculated recruitment separately in regions 2J, 3K, and 3L of Newfoundland waters and while there is some correlation between them, there are also significant differences. Unfortunately, the analysis of Myers et al. (1993) is based on survey data collected in the fall, when the cod populations overlap in distribution; hence, there is some doubt about the independence of recruitment estimates of these separate stocks based on these data. We argue that recruitment varies at smaller scales in response to physical and biological characteristics of specific regions. Here, we test the relationship between available pooled recruitment estimates for 2J3KL cod and physical environmental factors in an effort to shed light on environmental links to ecosystem and population dynamics.

Exploring ocean parameters for causes of recruitment variations is difficult (Shepherd et al. 1984) and there is need for caution. Lapointe et al. (1992), for example, showed the sensitivity of the recruitment estimates derived from the virtual population model. There is evidence that spurious correlations may occur between recruitment and environmental variables because of the influence of the natural mortality term in the

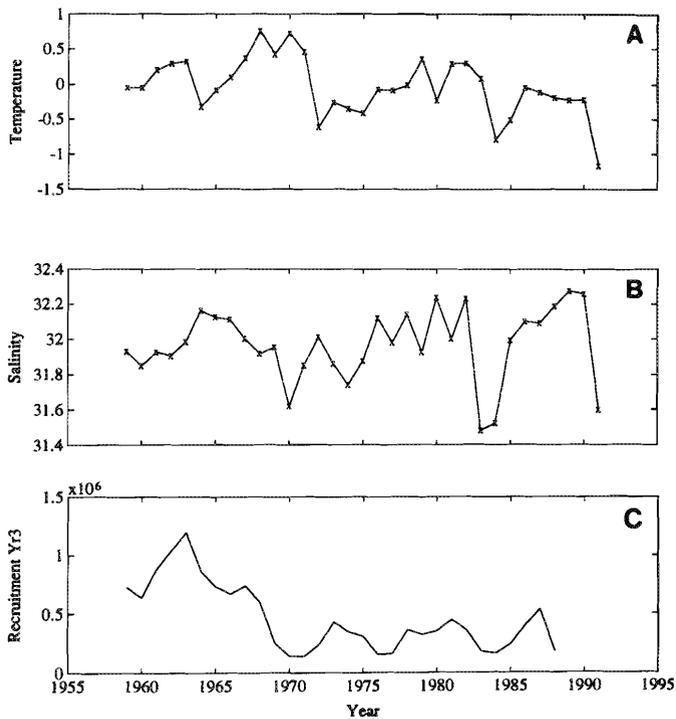


FIG. 5. (A) Temperature and (B) salinity vertically averaged from Station 27 on the inner part of the northeastern Newfoundland shelf (Fig. 1A), with the seasonal signal removed. (C) Recruitment of 3-yr-old cod for the full 2J3KL stock from sequential population analyses (from Baird et al. 1992).

virtual population model (Lapointe and Peterman 1991). In spite of these concerns, we shall explore the best available data, here recruitment estimates from a model analysis of the data.

### Temperature

Studies of interannual variability in the Northwest Atlantic are, for the most part, still at the correlative stage. Large interannual variations in several parameters (e.g., air temperature, water temperature, salinity, wind stress, atmospheric pressure, sea ice concentration) have been observed (cf. Petrie et al. 1992) although the nature of their interactions and the processes involved remain obscure. Some specific process models have been developed and applied to this region. For example, Ikeda et al. (1988) used a two-layer model to show that interannual variations in the position of the ice edge on the Labrador shelf could be related directly to meteorological forcing, and Petrie et al. (1992) demonstrated that wind and air temperatures explain about 50% of the variance in the interannual sea temperatures. In spite of these examples, we still lack a model of the relationship between the primary physical variables of interest.

The difficulties of the correlative approach are evident in an examination of the time series of recruitment of 2J3KL cod (Baird et al. 1992) and temperature and salinity at Station 27

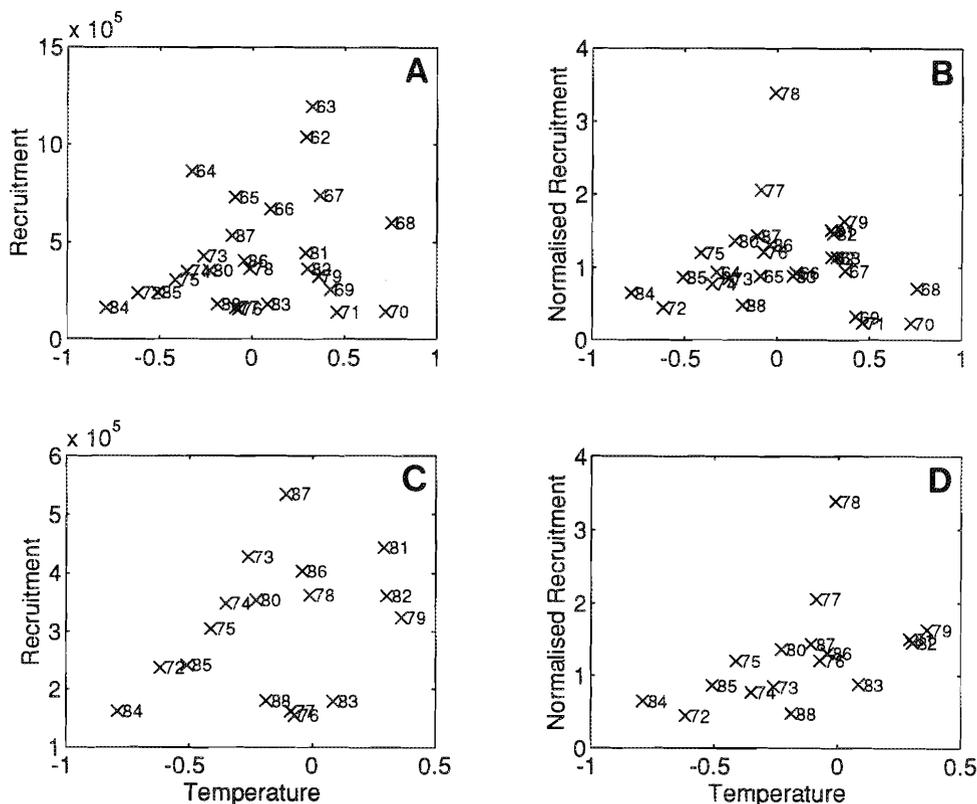


FIG. 6. Recruitment of 3-yr-old northern cod (2J3KL from Baird et al. 1992) versus the mean annual temperature anomaly. The temperature anomaly is obtained from vertically integrating temperature at Station 27 and removing the seasonal signal. The series have been shifted so that recruitment is referenced to temperature in the year of birth. We plot recruitment of year 3 fish as (A and C) numbers and (B and D) numbers normalized by the number of 6+ fish. In Fig. 6C and 6D, we have removed the pre-1972 data.

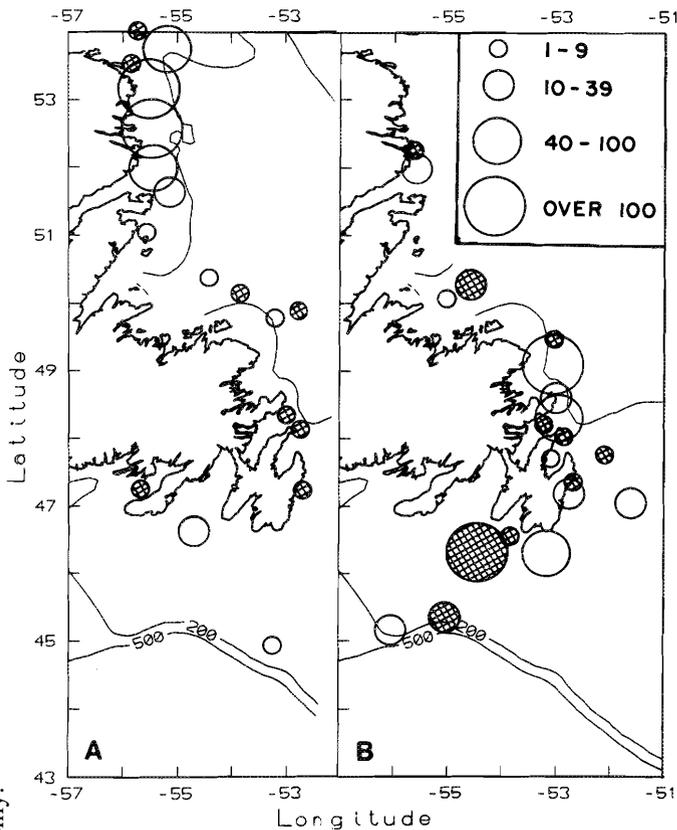


FIG. 7. Cod larval distribution in (A) 1934 (warm) and (B) 1935 (cold) (redrawn from Frost 1938). Open circles are from the spring sampling; cross-hatched circles are from the fall sampling.

(Petrie et al. 1992) on the inner part of the shelf near St. John's (Fig. 5). Correlations may be found between these series ( $p$ 's < 0.05), but it is difficult to interpret lagged correlations in short time series dominated by low-frequency signals. For example, Petrie et al. (1992) showed that air temperature, water temperature, air pressure, wind stress, and sea-ice extent are all correlated on the Newfoundland shelf. Analyses of the recruitment data reveal significant correlations at different lags (e.g., Sutcliffe et al. 1983). However, there are only a few cycles of each series during the roughly 30-yr record. The probability of spurious correlations is high. The declining trend in water temperature during the past 30 yr evident at Station 27 (Fig. 5A) is related to other large-scale phenomena. Recent analysis of atmospheric and sea-ice data clearly shows a  $-0.25^{\circ}\text{C}$  per decade change in Northwest Atlantic temperatures over the last 30 yr (Chapman and Walsh 1993). This decline is a northern anomaly. Temperature is increasing over the North American continent and also over the Northeast Atlantic but appears to be decreasing in waters from Greenland to Newfoundland.

An alternative approach in the analysis of environment and recruitment is to present these data as a scattergram (Ellersten et al. 1989; Loeng 1989). This approach shows that at low temperature, recruitment is always poor (Fig. 6). At high temperatures, no relationship between recruitment and temperature is apparent. If the recruitment data are normalized against stock size, some points change relative position (see Fig. 6B and 6D) but the relationship between cold temperature and poor recruitment remains. We have normalized by spawning numbers (6+ fish) because of an apparent stock-recruitment

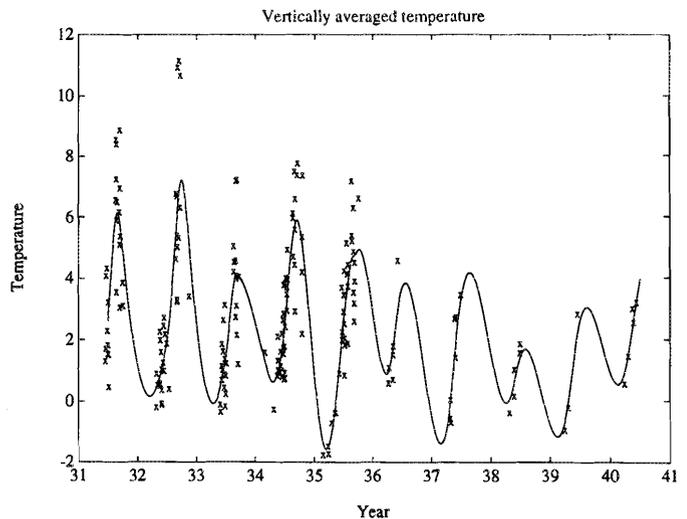


FIG. 8. Temperature on the northeastern Newfoundland shelf. The data shown with crosses have been vertically averaged and are plotted together with a splined smoothing curve.

relationship. Because of incomplete and varied sampling techniques used to collect fish data prior to 1972, there are strong reasons to doubt the quality of these data (Baird and Bishop 1986). We have replotted the recruitment versus temperature anomaly scattergrams without the pre-1972 data to explore the possible influence of these data. Although there are differences between Fig. 6A and 6C and Fig. 6B and 6D, all of the plots show that recruitment is generally low when the temperature anomaly is strongly negative. We do not believe that these results reveal a simple linear relationship between recruitment and temperature, such as might be verified by a regression analysis. Instead, we interpret these scattergrams as showing that temperature acts as a threshold variable for recruitment. Others have carried out regression analysis between recruitment and salinity to show that there may indeed be significant correlations with salinity (Sutcliffe et al. 1983; Myers et al. 1993). Loeng (1989) has shown that Barents Sea cod show similar poor recruitment when their environment is strongly affected by inflows of cold Arctic water (he does not consider a correlation with salinity).

Although the relationship between cold temperature and poor recruitment is not compelling evidence of a causal connection between these factors, we believe that it points to a link between ecosystem changes and population responses. We believe that cold ocean temperatures influence the spatial patterns of cod movements, spawning locations, and the resultant survival of their progeny. We note that previous workers have attributed the cold water - poor recruitment relationship to temporal matches of spawning with food and ice. For example, the Barents Sea cold water - recruitment relationship was proposed to reflect physiological stress and a poor food supply at low temperatures (Ellersten et al. 1989; Loeng 1989). Myers et al. (1993) explored the idea of food limitation (Sutcliffe et al. 1983), but concluded that the pertinent salinity variations were negatively correlated with phytoplankton abundance. Other temporal links, e.g., salinity and sea-ice formation, which could cause larval freezing, were also discounted by Myers et al. (1993).

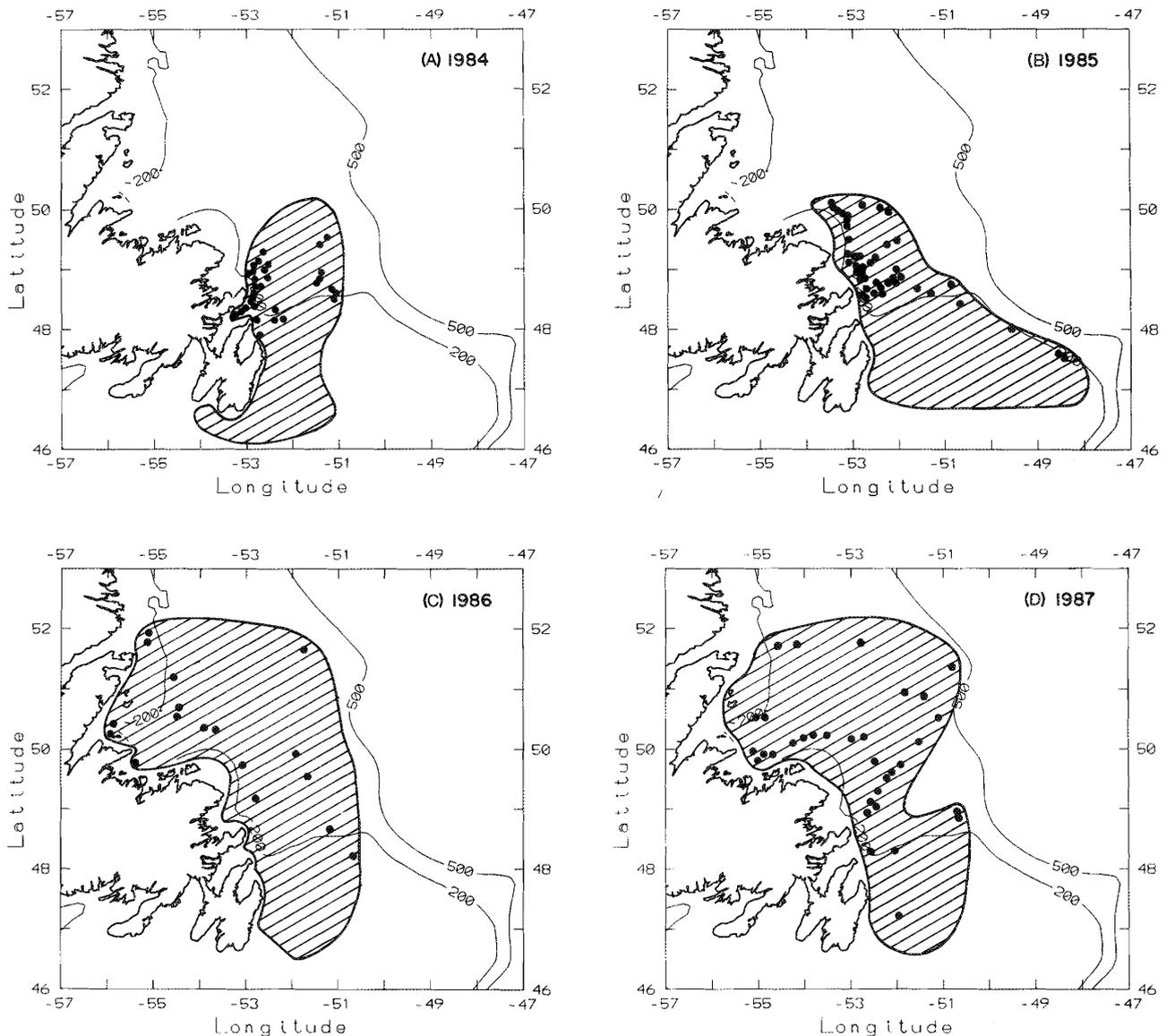


FIG. 9. Spring (early to mid-June) distribution of cod on the northeastern Newfoundland shelf assessed with echo sounders. 1984 and 1985 were cold years (see Fig. 5) with poor recruitment and 1986 and 1987 were warmer years with stronger recruitment (see Fig. 6). The hatched areas are the surveyed areas; each circle represents the occurrence of a cod aggregation with dimensions >1 nautical mile.

### Stock Spatial Dynamics

We propose that the link between thermal conditions and recruitment success in the northern cod is less direct than proposed by Loeng (1989) for the Barents Sea and lies in the spatial dynamics of spawning relative to the stock range and the environment. Recruitment may be determined as much by the relative distribution of the fish as by their absolute abundance. For example, in the dynamic Labrador and northeastern Newfoundland shelf current system, egg and larval drift and probable settling sites will not be independent of the location of spawning. Northern and shoreward spawning would be expected to be more successful than seaward and southward spawning because of the drift patterns for eggs and larvae on the shelf (Helbig et al. 1992). Could a link between cold temperature and poor recruitment be found in the distributions of spawning adults? We examined several data sources to explore this hypothesis. The first was cod egg and larval distribution data (Fig. 7) reported for the early 1930's (Frost 1983) combined with

oceanographic and fishery data reported by Thompson (1943). These data suggested that interannual variations in the egg and larval distribution patterns along the Labrador and Newfoundland coast were associated with variable thermal conditions on the northeastern Newfoundland shelf. In 1935, water temperatures were much colder ( $<0^{\circ}\text{C}$ ) than in 1934 on the Newfoundland shelf (Fig. 8). At the time, thermal conditions were believed to be associated with the relative strength of the cold-water Labrador current (Thompson 1943). In 1934, a relatively warm year, cod larvae were concentrated in the northern portion of the range off Labrador. Although no comprehensive data on adult cod distribution are available for this era, trap fishery catches, which reflect overall available biomass (Rose and Leggett 1988, 1989; Rose 1992), were recorded in detail. In 1934, the spring trap fishery was strong in northern Labrador and weak in southern Labrador. Similarly in 3K, the trap fishery was strongest in the north and failed entirely south of Cape Bonavista. This pattern in the trap fishery suggests that adult cod were

distributed in the postspawning period in the northern parts of their ranges in the warm year 1934. This pattern changes abruptly in 1935, a cold year in which larvae were concentrated in the southern ranges off eastern Newfoundland, Thompson (1943) interpreted these larval distribution data as reflecting the stronger flows of the Labrador current in 1935 which could have carried eggs and larvae further southward, but there is no evidence that cold years and strong flows are correlated. We suggest that differing spawning distributions may have played a large role in producing these very different larval distribution patterns. As evidence of a more southerly spawning distribution in 1935, the best fishing was found "well to the south — e.g. at Bay Bulls (on the east coast of the Avalon Peninsula), the water temperature being too low further north in this cold year" (Thompson 1943).

We also examined fisheries acoustic data collected by the Department of Fisheries and Oceans describing spring (post-spawning) cod distributions on the northeastern Newfoundland shelf for 1984–87 (Fig. 9). These years included two very cold years, 1984 and 1985, with poor recruitment and two warmer years with strong recruitment (at least in 3K). We found that in the colder years (1984 and 1985), cod were relatively abundant in the southern reaches of their range in early June (the northern reaches could not be surveyed because of ice conditions). During the warmer years (1986 and 1987), cod were distributed widely in the northern portions of their range at the same time of year and were less frequently observed and less widely distributed in the southern ranges than in 1984 and 1985. Differences in overall abundance could not account for the observed pattern differences because total biomass (>>3 yr) differed by only 20% and the biomass of older fish (>>7 yr) did not differ between these years (Baird et al. 1992). Note that sampling was not equivalent in all years, and we do not know where spawning occurred. Still, these data add support to the hypothesis that in cold years, cod will be found in more southerly locations.

Examination of offshore fishing success from 1981 to 1986 when fishing distributions were uncontrolled indicates that catches peaked in 2J in 1982 (Fig. 4) when ocean conditions were warm and strong recruitment prevailed (Fig. 5) and then declined during 1984–85 (cold water and poor recruitment), rebounding in 1986. The opposite pattern is evident in catches from 3K. Although these patterns may be partially driven by fleet dynamics and ice conditions, it seems unlikely that fishermen would bypass large concentrations of cod in 3K to fish in the more distant 2J zone. An alternative interpretation is that the major cod concentrations were not present in 3K during the winter months until 1984. We note that interpretation of the catch data (Fig. 5) since 1987 is confounded by the imposition of controls on fishing distribution beginning that year.

To further investigate a possible spatial basis for the recruitment–temperature link, we examined distributions during the 1960's when recruitment was on average double the levels observed during the 1980's. It was obvious that the higher levels of recruitment during the 1960's were associated not only with more abundant stocks but more northward distributions of cod (Harris 1990) which in turn coincided with warm ocean conditions (Fig. 5). Were the high levels of recruitment during this era solely the result of the high abundance levels? Or did the northward distribution and spawning of the stocks during the 1960's (Postalakii 1972) enhance recruitment success across the full range of the stock and hence help sustain high levels of abundance, at least for a time, even in the face of heavy fishing

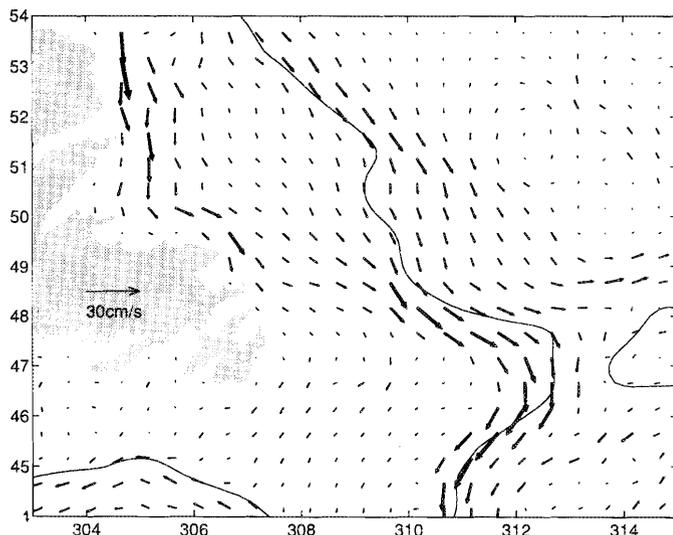


FIG. 10. Spring surface circulation for the northeastern Newfoundland shelf derived from a diagnostic model applied to the northeastern Newfoundland shelf (deYoung et al. 1992). This plot shows the inshore branch of the Labrador current, on the inner part of the shelf, and the outer branch, located at the shelf break (see Fig. 1B). The 500-m isobath is indicated by the solid line.

mortality imposed by European-based trawlers?

The weight of the evidence suggested the hypothesis that cold water temperatures might influence cod spawning locations. If this is true, then it is likely that the variations in distribution result from cumulative exposure to thermal variations over the previous spring and fall. At these times, cod undertake cross-shelf migrations to feed (spring) and to return to the offshore wintering grounds (fall) (Templeman 1966; Rose et al. 1991). Hence, during these travels, fish are directly exposed to any interannual variations in seasonal temperature signals. Our view differs substantially from the cold-water barrier hypothesis (Templeman 1966; Lear et al. 1986) that attempts to explain variations in the migration patterns and inshore catches of cod. We propose that at the large-scale, cod respond to the cold water after integrating over a migration cycle. Thus the fish migrate through the cold intermediate layer, but redistribute southwards before the next spawning season in response to this cold water and in search of warmer conditions in which to mature. Thus, they move south because there is warmer water across the shelf to the south.

Cod are highly sensitive to small temperature changes (Harden-Jones and Scholes 1974), although they are able to produce an antifreeze protein that enables them to adapt to cold water (Goddard et al. 1992). The spatial response would be to interannual rather than immediate conditions and could be mediated by growth and maturation cycles. Thus, variability in thermal conditions on the shelf could be reflected in spawning locations even though waters having temperatures for spawning (3–5°C) occur all along the shelf edge at depths greater than 300–400 m. Dadswell et al. (1987) postulated a similar thermal mechanism for migrating American shad (*Alosa sapidissima*). However, if northerly spawning is critical for good recruitment in northern cod and spawning occurs along the shelf edge, where water depths are 300–500 m (Fig. 1B) and temperatures are  $\geq 3^{\circ}\text{C}$  even in cold years, then why do cod not just move north to spawn along the shelf edge even in cold years? The answer may

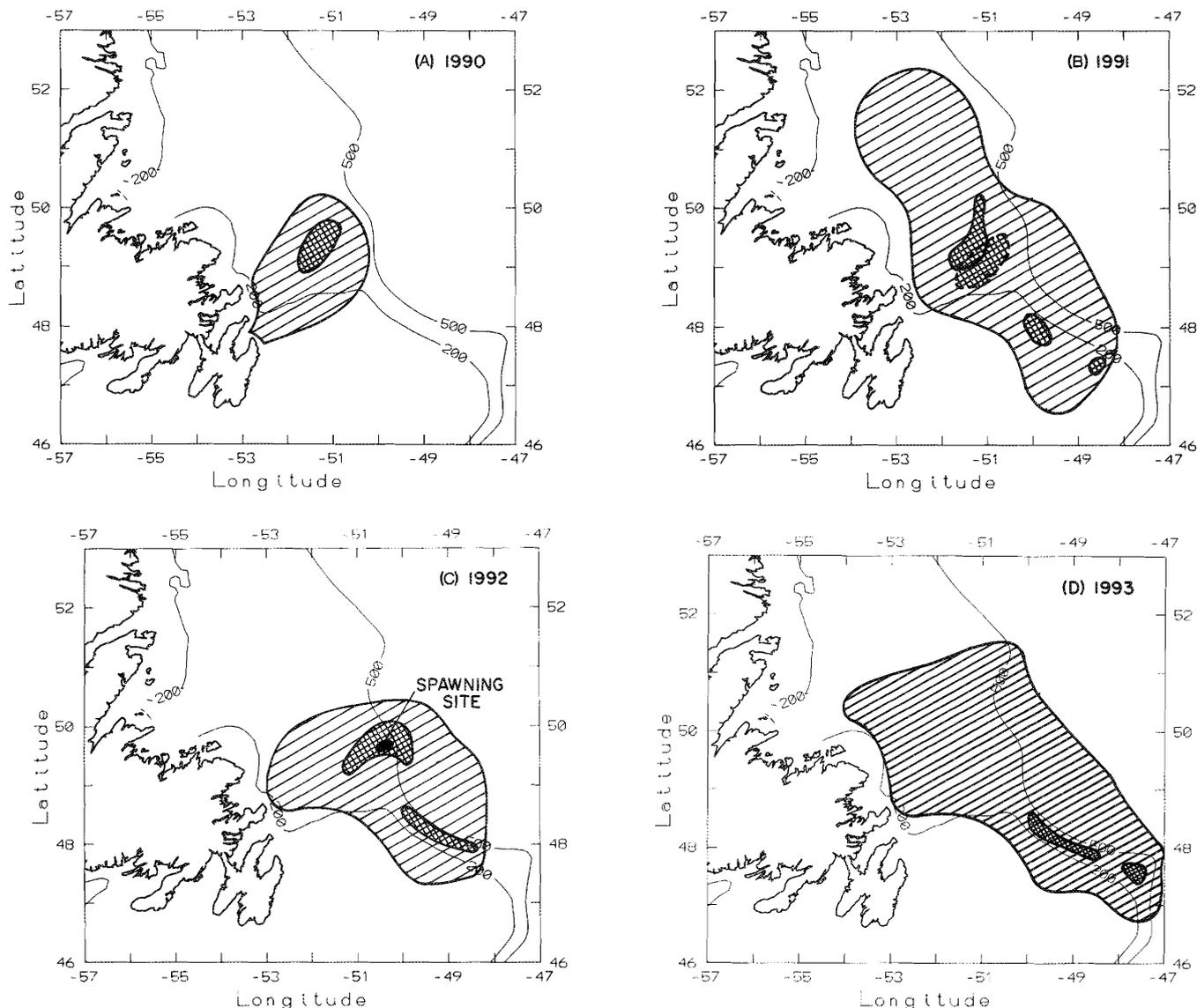


FIG. 11. Maps of the (A) 1990, (B) 1991, (C) 1992, and (D) 1993 generalized spring distributions of adult cod on northeastern Newfoundland shelf. Cross-hatching indicates where fish were acoustically detected and biologically sampled within the overall survey area (hatched). The site where spawning was observed in 1992 is marked.

be that a major portion of cod spawning occurs shoreward of the shelf break where waters are more variable relative to the interannual signal than at the shelf break itself. Shoreward temperatures may at times be much cooler than cod prefer in the prespawning and spawning period. It is noteworthy that recent observations have shown that cod do spawn well shoreward of the shelf break in waters with temperatures of 2.5°C (Rose 1993). Analyses of historical distribution patterns also indicate that cod may spawn at locations well shoreward of the shelf break (Hutchings et al. 1993).

#### Right Site Hypothesis

We propose that the distribution of spawning cod on the northeastern shelves plays an important role in determining recruitment; we call this dependence the "right site" hypothesis. This is a variant of the spatially based recruitment model advanced by Iles and Sinclair (1982). We suggest that in cold years, cod on the northeastern Newfoundland and Labrador shelves are

likely to be distributed in the southerly portions of their ranges. A southerly distribution pattern and spawning would result in short residence times for eggs and larvae and a decreased probability of larval settling in a favorable area on the shelf (Helbig et al. 1992). Hence, cold years would be unlikely to yield high levels of recruitment. In warm years, spawning would take place in the more northerly reaches of the range. Hence, warm years would result in longer egg and larval residence times on the northeastern Newfoundland shelf and higher probabilities of larvae being advected shoreward to a favorable settling ground. On the northern Grand Banks, spawning sites in cooler years would likely be distributed eastward to deeper warmer waters at the eastern edge of the Grand Banks. In warm years, these fish would spawn on the northwest edges of the Bank in shallower waters. It follows that during warm years, there is the potential for much higher recruitment at the egg and larval stage than in cold years for all populations of Newfoundland cod.

Gadoid stocks have been shown to occupy an area in rough

proportion to their abundance (Crecco and Overholtz 1990; Gordoa and Duarte 1991; Rose and Leggett 1991). The densities of spawning aggregations have been observed to be relatively constant on the northeastern shelf (G. Rose, unpublished data). Hence, northward distributions and spawning are likely to be facilitated not only by warmer ocean conditions but by high levels of abundance which cause cod to be distributed over a wider area. By chance alone, a more abundant stock is more likely to spawn at the right site. In contrast, a smaller stock is more likely to have to put all its eggs in one basket by spawning in a contracted spawning area. This effect would compound the influence of stock size on recruitment.

### Egg Dispersion

Cod eggs are released at the bottom, rise to the surface, and mature in about 30–40 d at temperatures typical for their historical spawning areas, from the north end of the Grand Banks to the north end of the Labrador shelf (Fig. 1B). The exact time at which the larvae settle to the bottom is not known but larvae are in the surface waters (0–50 m) for at least several weeks after hatching. Helbig et al. (1992) developed a model of cod egg dispersion on the Newfoundland shelf driven by a simplified circulation field and meteorological forcing. The primary circulation field in this region consists of mean southward flow made up of the inner and outer branches of the Labrador current (Fig. 10). Eggs released anywhere on the shelf are likely to be carried southward (Greenberg and Petrie 1988). This conclusion can be drawn from mean current data and is supported by drifter studies on the northeastern Newfoundland Shelf (Venkatesh et al. 1990; Helbig et al. 1992).

The right site hypothesis states that the location of spawning is important to recruitment success. We assume that the longer the eggs can stay on the shelf the greater the probability that they will survive to the larval stage and beyond (deYoung and Davidson 1994). If eggs are carried off into the North Atlantic, then they are lost to the stock (Sinclair and Iles 1989). To test these ideas, we have run advection-diffusion models using the circulation diagram shown in Fig. 10. These studies have shown that residence times are lowest for eggs released at the southern part of the northeastern Newfoundland shelf and near the shelf break. Residence time is highest for eggs released in the northern part of the range and on the inner part of the shelf. Between 48 and 49°N, near the shelf break, there is a southeasterly transport that carries the positively buoyant eggs off the shelf.

There was an intensive effort in 1991 and 1992 to locate cod eggs on the northeastern Newfoundland shelf. The average concentrations during June 1991 over the spawning sites in the northeastern Newfoundland shelf were approximately 1 egg/m<sup>2</sup> (J. Anderson, Department of Fisheries and Oceans, St. John's Nfld., personal communication). On the Scotian shelf, egg densities are roughly 50 egg/m<sup>2</sup> (Hurley and Campana 1989; Brander and Hurley 1992). In Norway, where eggs are concentrated in a coastal region, densities greater than 100 egg/m<sup>2</sup> have been observed (Ellertsen et al. 1981; Sundby 1983). How many eggs do we expect to find on the Newfoundland shelf? If there were 10<sup>8</sup> fish spawning (a minimum number according to the SPA and consistent with a detailed acoustic mapping of the spawning school in June 1992 (Rose 1993)) and each fish lays 10<sup>6</sup> eggs, then over this spawning period there should be roughly 10<sup>14</sup> eggs released. The surface layer is roughly 50 m deep, the width of the shelf is 200 km, and the length of the sea area potentially holding eggs is given by multiplying the mean current

speed of 0.2m/s by the time of spawning, 60 d, to give approximately 1000 km; hence a total area of 2 × 10<sup>11</sup> m<sup>2</sup>. Dividing the total egg numbers by the volume indicates a concentration of 500 eggs/m<sup>2</sup>, much larger than observed. There are, however, many factors that could influence the observed concentration, in particular egg mortality. Nonetheless, these data are consistent with the hypothesis that eggs in the southern region have short residence times on the shelf and are advected off the shelf; hence the low observed concentrations in 1991 and 1992.

There is an indication from these data that egg concentrations are lower than expected on the Newfoundland shelf. Although egg production may be stable over a wide range of spawning-stock biomass, as suggested by Rothschild and Fogarty (1989), egg success can still be an important factor in recruitment. Furthermore, a breakdown in the egg production density-dependent stability may provide a mechanism for a contribution to population collapse (Rothschild 1986). The relationship between egg production and stock biomass for cod is unknown.

### Postspawning Distributions, 1990–93

Detailed studies were conducted on spawning and post-spawning distributions of northeastern Newfoundland cod in the springs of 1990, 1991, and 1992. Cold conditions prevailed throughout this period, culminating in 1991 when cold waters blanketed much of the shelf. Coincident with these low temperatures, cod were observed to be highly aggregated in the most southerly reaches of their range where warm waters persist (Fig. 11). Cod in spawning condition were located in 1991, 1992, and 1993 in this southern range; a major spawning event was observed in 1992 (Fig. 11C). In 1990 the southerly moving cod had spawned at an unknown but more northerly location. Cod of the Labrador stock declined dramatically during this period. If we are correct in believing that southerly spawning yields poor recruitment, the observed southerly distributions of the stocks in 1991, 1992, and 1993 predict poor recruitment. Thus, based on our model, we suggest that the prognosis for both the Labrador and northeastern Newfoundland cod stocks is poor for at least the next decade.

### The Future

We conclude that the current paradigm of the natural rebuilding and redistribution of the "northern" cod is inappropriate. These cod were fished to low levels by the mid-1970's and did rebuild rapidly until the mid-1980's (Harris 1990). What is different now? Although the biomass levels at the start of the moratorium on fishing in the spring of 1992 did not differ greatly from those observed in that earlier era, distribution patterns differed greatly. Through the late 1970's and early 1980's, mature fish were present in relatively large numbers to the north in the Labrador population (2J) (Fig. 2). In contrast, mature fish have been virtually absent there since 1990. Moreover, cod on the northeastern Newfoundland shelf (3K) have become concentrated in the most southerly part of their range since 1989. Hence, we believe that the past will not predict the future because conditions have changed from any previously observed.

A key question for rebuilding the cod stock on the Newfoundland and Labrador shelves concerns the fate of the northern (2J) fish that migrated southward between 1989 and 1991. On the one hand, if migratory behavior and spawning region are genetically determined and the northern fish differ

from the more southerly populations on the northeastern Newfoundland shelf (3KL), then perhaps when environmental conditions improve the remnant of the Labrador population will reestablish historic population and migration patterns (assuming sufficient genetic stock has survived). On the other hand, if historic population and migration patterns are geographically and behaviorally based, then it may take several generations and several decades to reestablish migration patterns in the northern regions by recolonization.

In conclusion, predictions of future performance of the northern cod stock based on our model suggest a longer rebuilding time as compared with those of existing models. We offer several specific predictions:

(1) Biomass levels will continue to decline, until a northward shift in distribution occurs, as a consequence of a lack of recruits from the north and continued fishing mortality from foreign fleets.

(2) Regeneration of the northern populations that historically inhabited the Labrador shelf and banks will occur slowly, at scales of decades. Their current numbers represent remnant populations which will take generations and warming ocean conditions to rebuild. There may have been an irreversible loss of genetic material from these populations.

(3) Regeneration of the present southern populations will occur much more quickly given warming ocean conditions which will enable these fish to spawn to the north (as in the 1960's) and at more shoreward locations.

(4) The 1991, 1992, and 1993 year classes will likely be poor in abundance because of cold temperatures and the southerly distributions of cod. We believe that the year classes will be even smaller than would be predicted from the stock-recruitment relationship and the low stock numbers.

(5) Although oceanographic predictions are somewhat unreliable, present indications are that we are enduring a period of local cooling in the North Atlantic (Chapman and Walsh 1993); hence, we can expect continued poor recruitment until stock range and biomass expand to the northerly areas. Improvement in this prognosis will be heralded by a northward and shoreward shift in distributions from the present southerly and seaward pattern.

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