PERSPECTIVE

Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean

G.A. Rose, B. deYoung, D.W. Kulka, S.V. Goddard, and G.L. Fletcher

Abstract: Research on northern cod (*Gadus morhua*) from 1983 to 1994 indicated that a southward shift in distribution in the early 1990s was real and not an artifact of sequentially fishing down local populations. In the early 1990s, seasonal fishery and survey data showed distribution changes where there was no fishery, and large tonnage and densities (450 000 t, densities fourfold higher than 1980s levels) appeared in the south concurrent with declines in the north. All fishery, acoustic, and trawl survey indices increased in the south, while the stock declined. Southern-caught cod in the early 1990s exhibited northern characteristics: (*i*) antifreeze production capacities above historical norms and equivalent to those of northern fish, (*ii*) vertebral counts above historic norms and equalling northern counts, and (*iii*) declines in size-at-age to levels associated with northern fish. The cause of the shift is thought to be a combination of abiotic (climate) and biotic (capelin (*Mallotus villosus*)) environmental changes and cumulative long-term fisheries effects on cod behavior. The shifted distributions increased vulnerability to Canadian and foreign fisheries and led to a rapid decline in abundance, both before and after the moratorium on fishing in Canadian waters in 1992. Rebuilding will occur in three steps: environmental restoration, recolonization by adults, and enhanced recruitment across the shelf.

Résumé : Des travaux de recherche sur la morue franche (*Gadus morhua*) réalisés de 1983 à 1994 ont montré que le déplacement apparent des populations de morue vers le sud au début des années 90 était bel et bien réel et non pas un artefact qui serait lié à une diminution progressive des populations locales due à la pêche. Au début des années 90, les données de la pêche saisonnière et des campagnes d'échantillonnage ont montré que des changements se produisaient dans la distribution des morues même en l'absence de pêche, et un fort tonnage et de grandes densités (450 000 t, densités quatre fois supérieures à celles des années 80) ont été observés dans le sud tandis qu'on observait des déclins dans le nord. Tous les indices des pêches, des relevés acoustiques et des échantillonnages au chalut se sont accrus dans le sud tandis que le stock déclinait. Les morues capturées dans le sud au début des années 90 avaient des caractéristiques des morues du nord : (*i*) capacités de production d'antigel supérieures aux moyennes historiques et équivalentes à celles des morues du nord, (*ii*) nombres de vertèbres supérieurs aux moyennes historiques et égalant les nombres observés chez les morues du nord et (*iii*) baisses de la taille selon l'âge à des niveaux comparables à ceux observés chez les morues du nord. On pense que ce déplacement serait dû à une combinaison de changements environnementaux abiotiques (climat) et biotiques (capelan (*Mallotus villosus*)) et aux effets cumulatifs à long terme de la pêche sur le comportement de la morue. Le déplacement des populations vers le sud a accru leur vulnérabilité à l'égard des pêches canadiennes et étrangères et a entraîné un déclin rapide de l'abondance de la morue, tant avant qu'après l'imposition en 1992 du moratoire sur la pêche dans les eaux canadiennes. Pour qu'il y ait reconstitution des populations, il faudra qu'il y ait restauration de l'environnement, recolonisation par des adultes et accroissement du recrutement sur toute la plate-forme.

[Traduit par la Rédaction]

Introduction

Polarized arguments about the effects of fishing and the environment on fish stocks are common in the fisheries literature (for reviews, see Parsons and Seki 1995; Larkin 1996). The recent declines of the "northern" cod (*Gadus morhua*) off northeast Newfoundland and Labrador have rekindled such debate (Mann 1993; Hutchings and Myers 1994). On

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the one hand, environmental conditions and water temperatures approached the severest ever recorded in the late 1980s and early 1990s in Newfoundland waters (Colbourne et al. 1997a). By the early 1990s, cod size-at-age and growth were reduced (Bishop et al. 1993; Krohn et al. 1997), recruitment was generally poor (Drinkwater and Mountain 1997), and distribution and migration patterns were changing (Rose 1993; deYoung and Rose 1993). Moreover, other elements of the ecosystem were not stable during this period. For example, capelin (*Mallotus villosus*) declined and retreated southward (Frank et al. 1996), noncommercial species shifted seaward (Gomes et al. 1995), and northern species such as pandalid shrimp (*Pandalus* spp.) and Arctic cod (*Boreogadus saida*) expanded their ranges southward and increased in abundance well beyond previously recorded levels (Drinkwater and Mountain 1997). On the other hand, overfishing has been epidemic since the 1950s and is thought to be the major cause of the declines of many Northwest Atlantic fish stocks (Sinclair and Murawski 1997). There is general agreement that decades of overfishing, beginning with the foreign fisheries of the 1950s and 1960s, and continuing through the 1970s and 1980s primarily with Canadian fisheries, precipitated a severe decline in the northern cod that culminated in the lowest abundance levels known by the early 1990s (deYoung and Rose 1993; Hutchings and Myers 1994). The fisheries could also have contributed, directly or indirectly, to the observed changes in other aspects of the ecosystem (Jennings and Kaiser 1998).

Larkin (1996) suggested that catastrophic stock declines may result from the co-occurrence of detrimental factors, be they fishery or environmental (the inverse could be applied to abrupt increases, such as have recently occurred with shrimp, Arctic cod, and snow crab (*Chionoecetes opilio*) in Newfoundland ecosystems). Larkin's (1996) view recognizes the complexities of interactions in marine environments. For example, climatic or oceanographic factors may affect productivity at different, perhaps longer, time scales than do most fisheries (Brander 1997). As a consequence, the same level of fishing might impact commercial fishes and ecological communities differently under differing environmental conditions. Hutchings (1996) implied that such environmental hypotheses about the northern cod were suspect because they might be attractive to those who assert that the collapse was environmentally driven. However, there should be no abrogation of management responsibility for the success or failure of fisheries implied in such hypotheses (by blaming failures on environmental down-turns). To the contrary, consideration of the environment implies that management has broader responsibilities than traditionally acknowledged, including consideration of "ecosystem" processes and how these may affect both productivity and vulnerability of stocks and communities to fishing.

The northern cod ecosystem historically encompassed a vast area from the northern Labrador Shelf to the Grand Bank (Fig. 1). Stock declines occurred first in the north (NAFO division 2GH, hereafter 2GH; other NAFO divisions cited similarly) in the late 1950s, 1960s, and 1970s and then in the midnorth (2J) in the late 1980s and early 1990s. As the decline proceeded, the relative abundance of cod shifted southward (Atkinson et al. 1997), and age structures collapsed (Bishop et al. 1993). The southern region retained the

majority of the extant biomass in the mid-1990s, and in the late 1990s, the southern coastal area enjoyed the greatest stock rebuilding (Lilly et al. 1999).

The declines of northern cod in the 1960s followed massive fisheries on the northern spawning grounds prosecuted primarily by Russian and other then eastern block countries (Travin and Pechenik 1963). Reported catches broached 500 000 t in several years in the mid-1960s (a maximum of >800 000 t reported in one year). Although no direct estimates of cod biomass from that era exist, simulation models suggest an historic biomass in the range of 2.5–3.5 million t (Fahrig et al. 1998). The northern cod is among the least productive of the major cod stocks (Brander 1994). A harvest of approximately 10% of the biomass is likely to be sustainable (approximately half of $F_{0.1}$) and is consistent with traditional total catches of 150–300 000 t·year^{-1} (Harris 1990). Natural fluctuations in productivity may have been substantial as a consequence of the northern climatic range of this stock (Mann 1993; Fahrig et al. 1998). The late 1950s and 1960s were punctuated by warm ocean conditions favorable for growth and perhaps recruitment (Drinkwater and Mountain 1997) and by northerly cod distributions (deYoung and Rose 1993). The extraordinarily high catches of the mid-1960s indicate high levels of abundance and accumulated productivity. However, the northern cod did not sustain the harvests of the 1960s, even in the short term (Harris 1990), and by the early 1970s was in rapid decline. Potential long-term effects of these fisheries on spawning stock distribution and productivity may be significant but are difficult to assess. Nevertheless, deYoung and Rose (1993) presented evidence that cod were still widely distributed in the north, at least to Hamilton Bank, in the aftermath of this debacle and attributed the relatively rapid rebuilding of northern cod in the late 1970s and early 1980s, despite low spawning biomass, to comparatively warm conditions and the maintenance of northerly spawning off southern Labrador.

deYoung and Rose (1993) hypothesized that adult cod shifted their distribution southward in the late 1980s and early 1990s, a view supported by several additional studies (Gomes et al. 1995; Kulka et al. 1996; Atkinson et al. 1997; Warren 1997). Southerly distribution shifts were hypothesized to increase the likelihood of poor recruitment (deYoung and Rose 1993) and, because of the southerly location of the major fisheries, to have contributed to the rapid decline of this stock in the late 1980s and early 1990s (Rose et al. 1994). Alternatively, Hutchings and Myers (1994), reinforced by Hutchings (1996), discounted the shift hypothesis and argued that apparent distribution changes were solely the result of local overfishing, first in the north and then proceeding southward.

The importance of whether real distribution shifts occurred relates not only to a reconstruction of historical events but also to attempts to project and manage the rebuilding of the northern cod. If cod did shift southward under adverse conditions, they might be expected to expand their range northward once conditions improve and hence recolonize the key northern spawning grounds. Under these assumptions, protection of seemingly isolated southern populations may be critical to the rebuilding of the full stock. Alternatively, if no movement occurred in the past, but populations simply collapsed in place (Hutchings and Myers

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Fig. 1. Newfoundland region and the northern cod ecosystem. The tagging site in May 1991 is indicated by a star, and the location of cod aggregations in the winter and spring of 1993 is indicated by a cross.
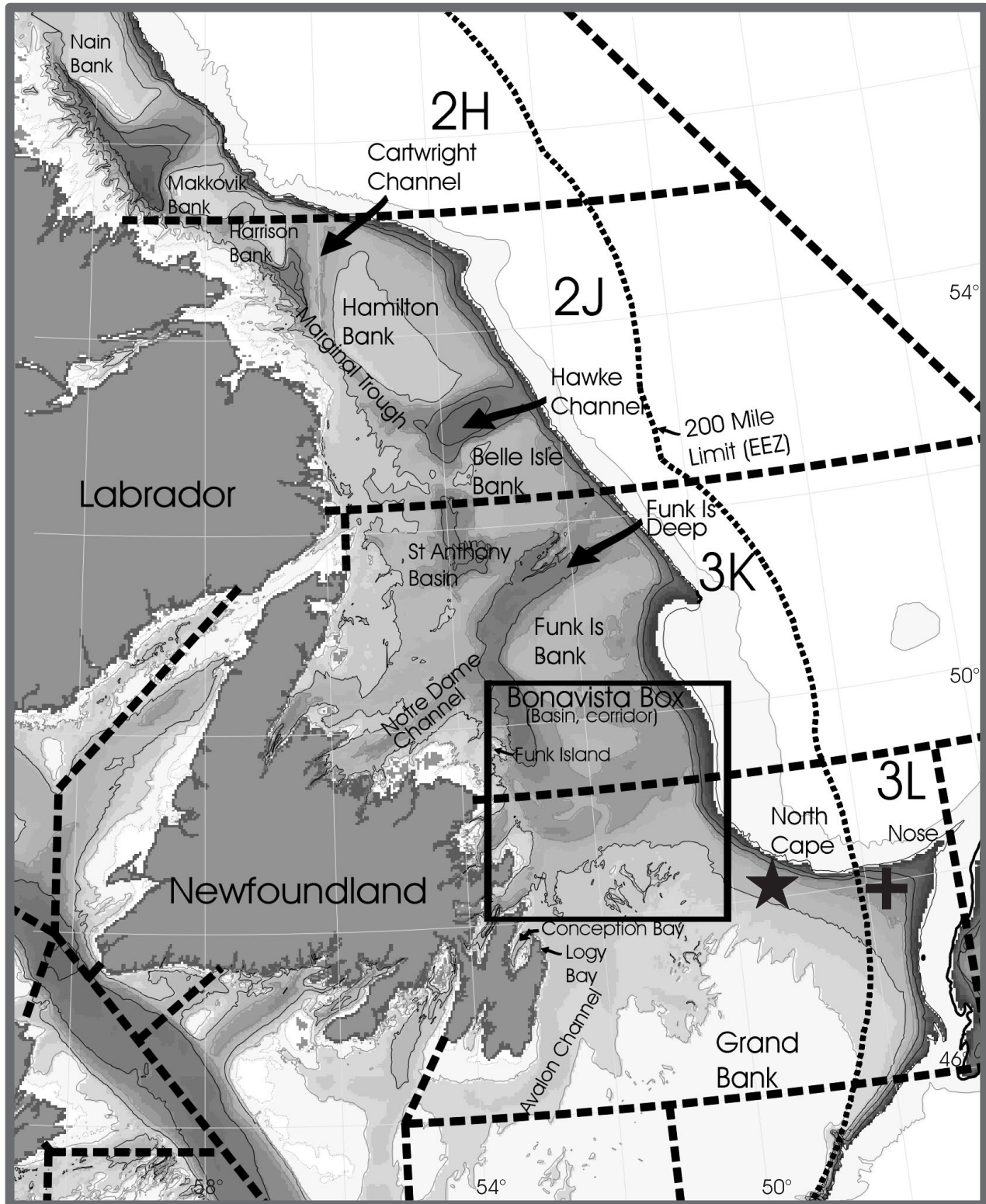
1994; Hutchings 1996), a checkerboard of discrete and spatially rigid populations is implied, and there is less reason to protect locally rebuilding populations as they recover.

The shift hypothesis generates several predictions:(*i*) cod distribution changes did not follow fishing activity in the late 1980s and early 1990s (in the extreme case, distributions changed in the absence of a fishery), (*ii*) large numbers of cod were present in the southern ranges beginning in the

late 1980s and early 1990s as densities abruptly increased above historical levels, (*iii*) availability of cod to the fisheries in the south increased after 1989 (and decreased in the north) independent of declining abundance, and (*iv*) northern fish were present in the southern area in the early 1990s. In addition, the shift hypothesis is consistent with the occurrence of further declines in adult abundance after the moratorium on fishing in the Canadian exclusive economic zone (EEZ) in 1992 because the southern fishery outside the Canadian EEZ was not under moratorium. The alternative hypothesis, of local depletion, predicts fish distribution changes that follow fishery concentrations, no buildup of cod in the southern range after 1989, no increase in availability in southern waters, and no northern fish in the southern range in the early 1990s. Declines in abundance after 1992 are inconsistent with the local depletion hypothesis, unless some other mortality factor is considered.

In this paper, we examine the predictions of the shift hypothesis, address the question of what happened to the northern cod in the late 1980s and 1990s, and discuss our findings as they relate to stock rebuilding. We present data from sea and laboratory research on cod distribution, migration, physiology, and oceanographic conditions, integrated with published documentation from Department of Fisheries and Oceans (DFO) surveys and the inshore fisheries. Our "view from the ocean" is built therefore upon direct observation and experimentation conducted at sea during the most recent decline of the northern cod.

Methods

DFO has conducted bottom-trawl surveys using a stratified random design since 1978 (Bishop et al. 1993). Most fishing sets were accompanied by a near-bottom temperature measurement. The methods underpinning these surveys are well known and described (Doubleday and Rivard 1981).

Acoustic searches for cod were conducted annually in May to early July from 1983 to 1994 in the area bounded by $48°00.0'$ and $50°00.0'$N and $050°00.0'$ and $053°00.0'$W (this region approximates the southerly cross-shelf migration route for this stock, called the Bonavista corridor, after Rose (1993)) (Fig. 1). From 1983 until 1989, the chief purpose of the work was to tag cod (echosounders were used to locate cod aggregations), whereas from 1990 until 1992, tagging and more formal acoustic surveying were undertaken together. In 1993 and 1994, only acoustic surveying was done. The RV *Gadus Atlantica*, using towed 49- and 38-kHz transducers, undertook the acoustic surveying in all years and used an Engels 145 otter trawl to capture cod. Some additional tagging was conducted from the RV *Lady Hammond* in 1991 and the RV *Petrel V* in 1992. In all years, the same strategy was used: echosounders were used to locate cod aggregations, and then, short-duration (5–15 min) fishing sets were undertaken on those aggregations (catches >90% cod in all cases). In 1993 and 1994, no tagging was undertaken as a consequence of the moratorium on fishing (July 1992), but fishing sets were conducted in the same fashion.

The echosounding record was not uniform from 1983 to 1994, and uncertainties about calibration in the early years disallowed the use of standard acoustic integration techniques (MacLennan and Simmonds 1992). However, scientific echosounders were used (Simrad EK400, Biosonics 102), and good-quality echograms existed for all years. The distribution of cod was in most cases amenable to counting techniques. A method was developed to quantify these signals as to relative cod density based on a visual counting scheme. First, all cod aggregations supported by fishing sets were identified on the echograms from the decade of data. For each aggregation identified, a minimum of five randomly placed "sampling windows" were placed over the echogram, and all single echoes within the window were counted. If echoes overlapped, counts were estimated (comparisons between counts and integrated densities in the fully calibrated data of the later years indicated that counts underestimated biomass, especially at higher densities). To normalize sampling volumes, a variation of the "duration in beam" technique was used (Crittenden et al. 1988). The width of a minimum of five fully formed single fish echoes was measured to the nearest 0.1 mm on the echogram (this width will be a function of vessel speed, depth, and fish size). All counted densities were then "normalized" to the mean width of the single fish trace. This technique provided a measure of the relative local densities of cod that was for the most part free from calibration and system related biases and could be used to compare the 1983–1994 data.

Acoustic data from 1990 to 1994 were collected with scientific echosounders calibrated according to standard methods with a 38-mm tungsten carbide standard target (Foote et al. 1987). Migrating cod aggregations are near monospecific (Rose 1993). Species identifications were made on the basis of target strength and echogram interpretations supported by directed fishing. Data were integrated over either 100 or 1000 m, scaled using a target strength to mean length model for cod (Rose and Porter 1996), and represented as fish per square metre based on 1-km transect segments. Segments from each surveyed aggregation were then randomly sampled at a decreasing rate until autocorrelation was not significant ($P > 0.05$). Mean abundance and SE were estimated from Monte Carlo sampling of the density data at that rate with *n* being the number of samples at which autocorrelation was not significant. Confidence intervals thus include sampling variance only. Error from detectability (Lawson and Rose 1999) and target strength is thought to be minimal because cod were distributed well off the bottom (to 150 m) during most of this work (see Rose 1993), and target strength experiments were conducted as a part of this research (Rose and Porter 1996).

Fishery data have been collected through an observer program on Canadian fishing vessels since 1980 (Kulka and Firth 1987). Prior to 1987, approximately 20% of vessel-days were monitored. Since 1987, there has been 90–100% coverage in the winter fishery. The full data set used here includes a total of 275 488 otter trawl sets made during the winter–spring fishery (January–July of 1981–1992) in 2J, 3K, and 3L (the northern cod). The subset of the data for the Bonavista corridor comprises a total of 65 702 sets made from January to July of 1981–1992. Each set was monitored as to location, duration, gear type, depth, and catch by species. Catch data were standardized by vessel, gear type, duration, and month prior to analyses (for full details, see Kulka et al. 1996).

In June 1994, acoustically identified cod aggregations were sampled using otter trawls at three sites within the historic range of the northern cod (Hawke Channel, Notre Dame Channel, and the Bonavista Basin) and from the north cape of the Grand Bank (Fig. 1). Vertebral columns from randomly selected fish from the catch from each aggregation were frozen at sea, subsequently thawed and X-rayed, and vertebral numbers counted. We followed the method of including the last urostylar vertebrae (Templeman 1981). Blood samples for genetic analyses were taken from 50 fish from each aggregation. The results of subsequent analyses have been reported by Ruzzante et al. (1998).

Adult cod (45+ cm) were monitored for antifreeze production over 14 winters between 1980 and 1994. Cod were collected annually from Conception Bay and south of Logy Bay on the eastern Avalon during the summer and fall (July–September) by commercial fishers prior to the moratorium in 1992 and by scuba divers from the Ocean Sciences Centre, Memorial University of Newfoundland, thereafter. Each winter, only cod caught in the preced-

Fig. 2. Density of fishing effort and catch rate (t·h^{-1}) from the offshore winter trawler fishery for northern cod for 1981, 1983, 1985, and 1987.
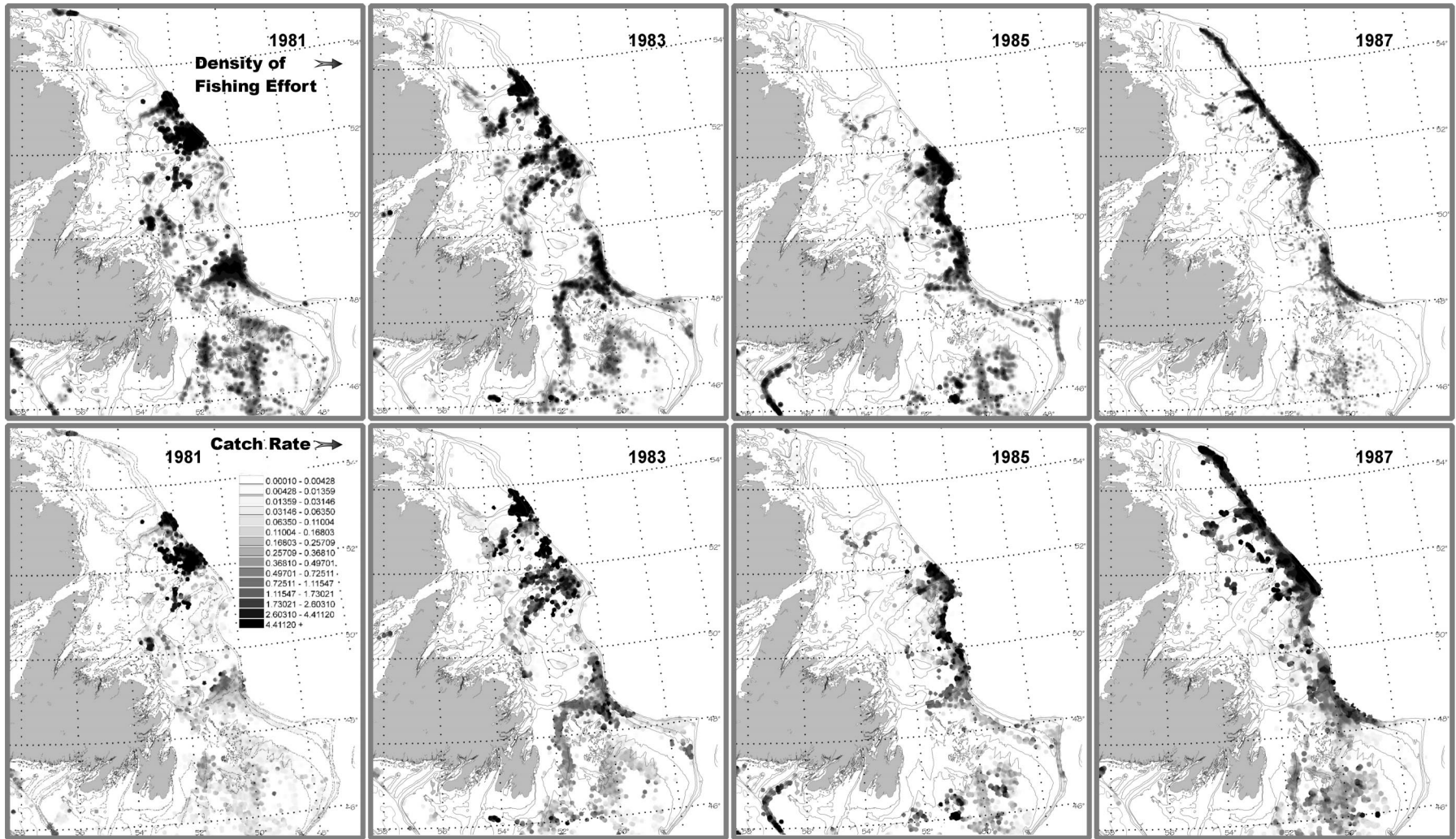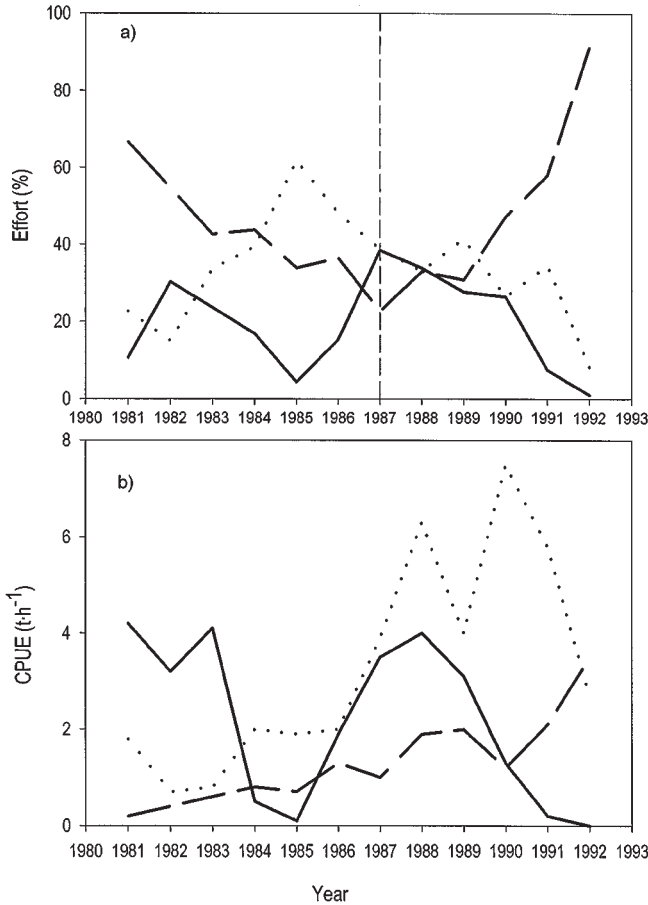

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Fig. 3. (*a*) Percentage of fishing effort and (*b*) mean CPUE for the offshore winter trawler fishery for northern cod in 2J (solid line), 3K (dotted line), and 3L (dashed line) from 1981 to 1992. The vertical dashed line represents introduction of the one third rule that attempted to disperse effort evenly over the three regions.

ing summer were monitored for antifreeze production. Cod were held in experimental tanks (either a 40 000-L raceway or one of three cylindrical tanks of approximately 2000–2700 L) and were exposed to seasonally ambient conditions of temperature and photoperiod throughout the experiments. Tanks were supplied with seawater pumped continuously from approximately 10 m depth in Logy Bay (Fig. 1). Water temperatures were recorded several times a week while the cod were under investigation. Cod were fed chopped capelin twice weekly throughout, and each experiment was terminated at some point during the summer.

Blood samples were taken at approximately monthly intervals over the winter cycle (December–June in most years). Blood samples (1–2 mL) were withdrawn from a caudal blood vessel using 3-cm^3 syringes with 21- or 23-gauge needles. Sampling was quick (<1 min) and no anaesthetic was used. Samples were injected into Vacutainers containing sodium heparin (Becton Dickinson) and held on ice for a short period prior to centrifuging at 4000 × *g* for 10 min. The plasma was then removed from the cells and stored frozen at –20°C until analysed for antifreeze activity.

In common with many teleost species inhabiting high latitudes, Atlantic cod produce antifreeze glycoproteins (AFGPs) that interact with ice crystals in a noncolligative manner to inhibit ice crystal growth, lower the plasma freezing temperature, and increase the fishes' ability to withstand exposure to extreme low temperatures (Fletcher et al. 1987; Davies and Hew 1990). The freeze-

depressing action of AFGP is between 200 and 300 times greater than would be predicted based on the number of antifreeze molecules in solution (i.e., colligative properties) alone (DeVries 1988). However, since the AFGPs have no influence on the melting point (other than the expected colligative effects), a solution containing antifreeze will have a lower freezing point than melting point. This difference between the freezing and melting points is termed thermal hysteresis (TH). TH is directly proportional to the concentration of antifreeze in solution and is used as a direct measurement of antifreeze activity.

Analysis of antifreeze activity within each plasma sample was carried out using a nanolitre osmometer (Clifton Technical Physics, New York) according to the method of Kao et al. (1986) in which a small volume of plasma containing a single ice crystal is cooled and heated in a controlled and quantifiable manner. By microscopic observation of the resultant growth and shrinkage of the ice crystal, the freezing and melting points, and hence TH, of the plasma sample can be determined. Standard solutions used to calibrate the osmometer commonly give TH readings of approximately 0.07°C; thus, such values indicate that antifreeze is absent from the plasma.

Results

Did cod distribution changes follow high levels of fishing?

Offshore trawler fishing effort during the 1980s was widely distributed over the stock area from 2J to 3L, although areas of concentration varied from year to year (Fig. 2). Mean annual effort was highest in the south and lowest in the north in the 1980s and until the moratorium in mid-1992 (Kruskal–Wallis test, *P* < 0.05; mean number of sets per year were 4034, 3503, and 2452 in 3L, 3K, and 2J, respectively, excluding 1992 when this fishery was truncated in February) (Fig. 3*a*). Effort was also more variable among years to the north, especially in 2J (coefficients of variation for 2J, 3K, and 3L were 0.9, 0.5, and 0.4, respectively). A management measure introduced in 1987 resulted in a more even dispersion of effort over the full stock range for a few years (the so-called one third rule) (Fig. 3*a*). However, from 1990 to 1992, effort again shifted to 3L. In contrast with effort, catch-per-unit-effort (CPUE) in 3L was the lowest of the regions in the early 1980s, while CPUE was much higher in 2J (Fig. 3*b*). In 1984 and 1985, CPUE in 2J declined but rebounded to levels comparable with those of the early 1980s from 1986 to 1989. From the mid-1980s until 1992, peak CPUE shifted southward, with maximums in 1988 in 2J, 1990 in 3K, and 1992 in 3L. CPUE remained high in 3L (the highest on record for this region) until the moratorium in 1992. Annual CPUE and effort were not significantly correlated in any region, but correlation was stronger in the north (*P* values for 2J, 3K, and 3L were 0.06, 0.07, and 0.89, respectively).

The period from 1988 to 1994 encompasses the most recent decline of the northern cod and the proposed distribution shift (Fig. 4). The fall trawl survey, winter fishing CPUE, and spring acoustic survey data all show declines in the spatial extent of high densities of cod, and southward shifts, during this period. However, in the fall of 1988 and the winter of 1989, cod were still distributed over the full stock range from north to south and across the shelf.

An increasing concentration of fish in the southern zone (southern 3K and northern 3L) is initially evident in the fall survey of 1989 and the following winter fishery of 1990

Fig. 4. Sequential data from the fall DFO research vessel survey (kg·tow^{-1}), the winter fishery (t·h^{-1}), and the spring acoustic/trawl survey (fish·m^{-2}) from 1989 to 1994.

Fig. 4 (*concluded*).

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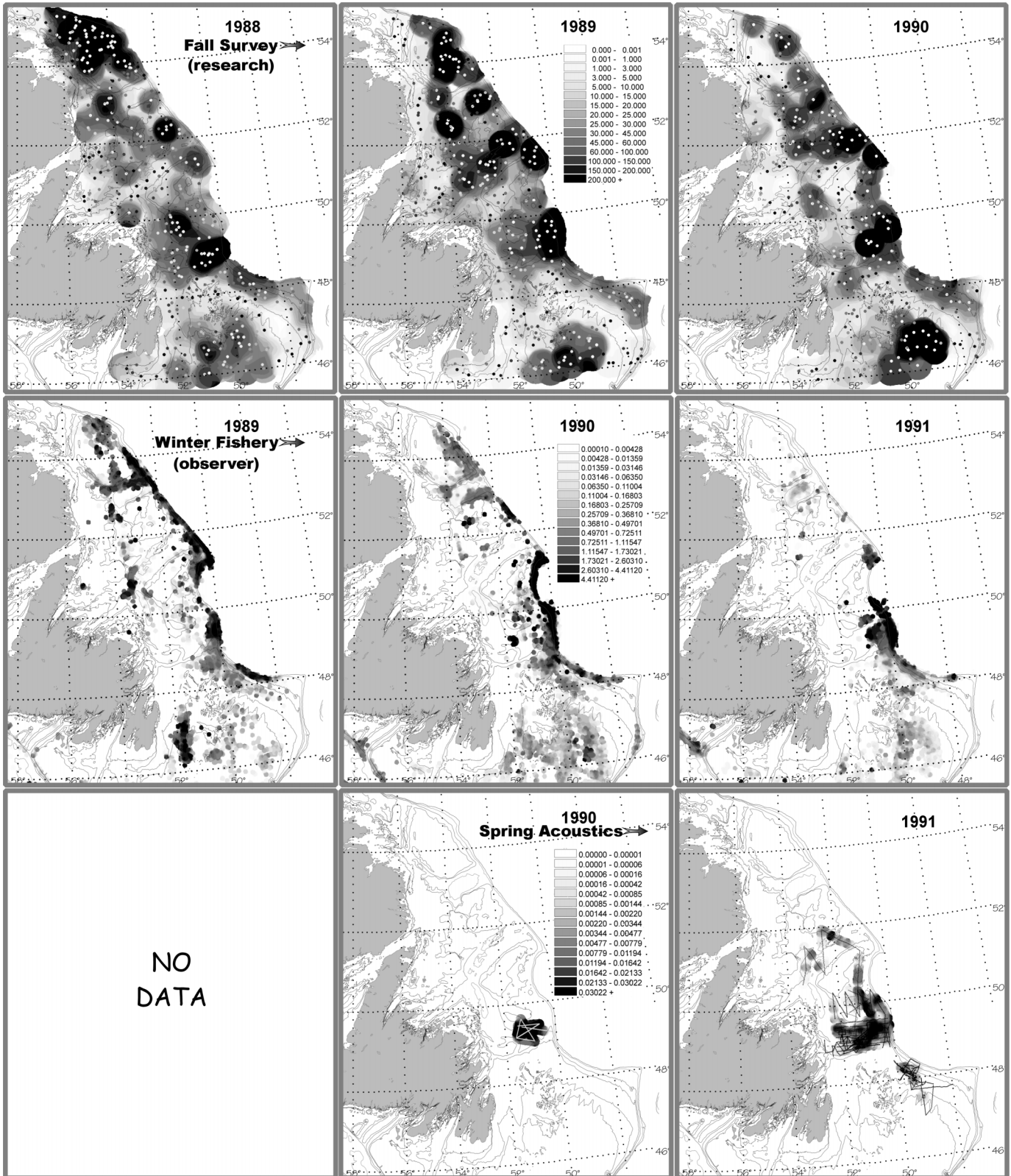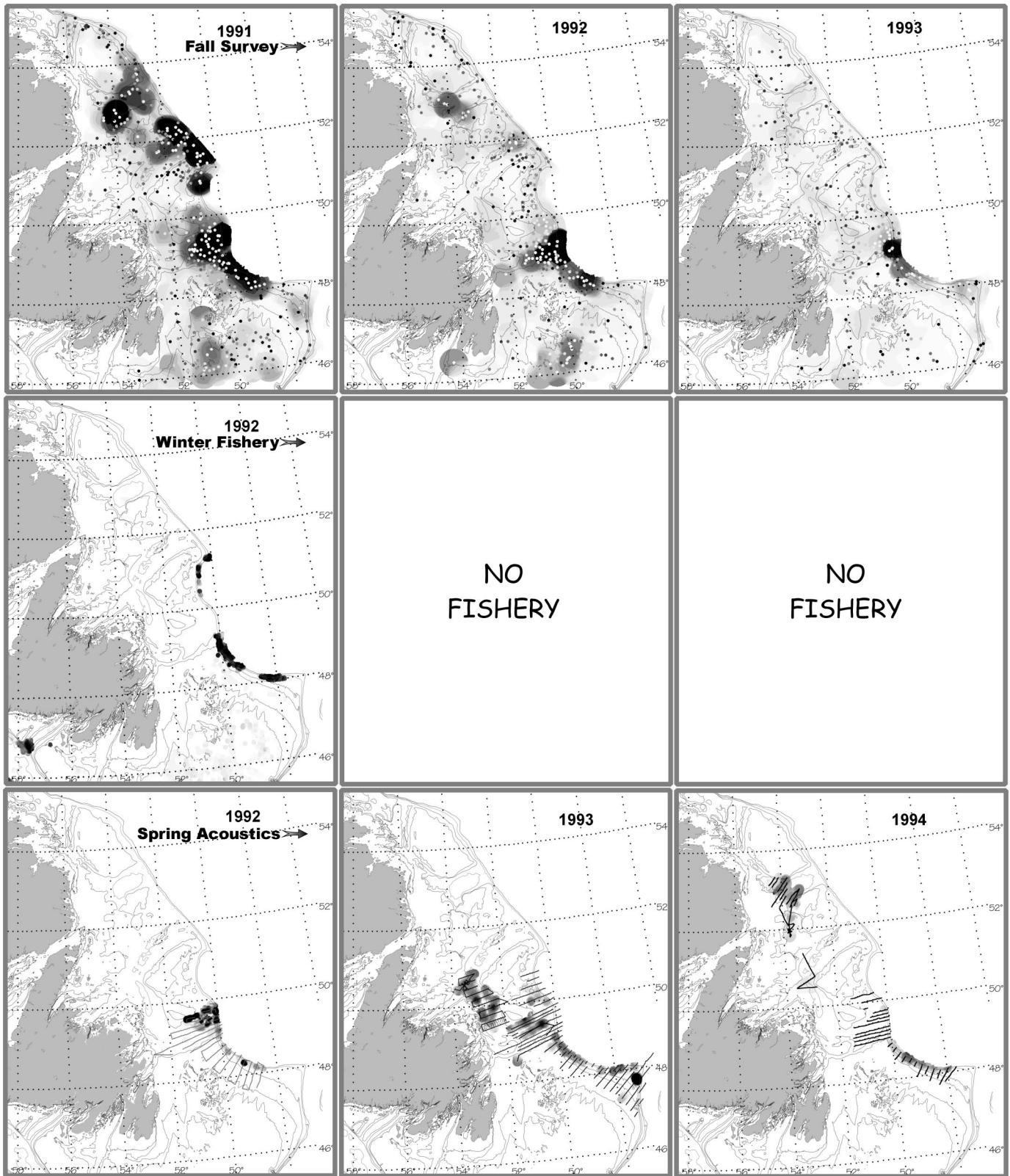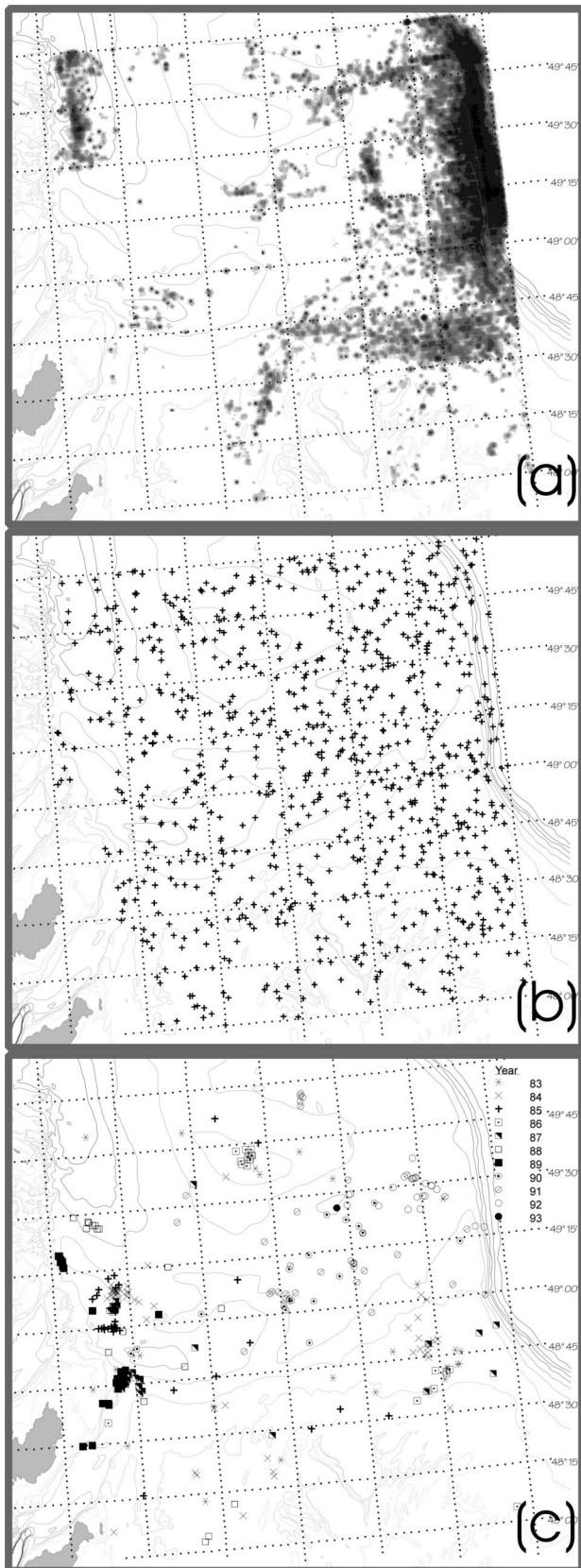**Fig. 5.** Bonavista corridor study area (*a*) winter fishery trawl sites, (*b*) fall trawl survey fishing sites, and (*c*) spring research fishing sites for 1983–1993. Only the spring data are shown by year (no spatial patterns exist in the other series).

(Fig. 4). CPUE in 2J declined precipitously in winter 1990 but reached its highest value on record further south in 3K (Fig. 3*b*). Spring surveys in 1990 confirmed the existence of very high densities in southern 3K and northern 3L (Fig. 4). The fall 1990 survey showed fewer fish in the north relative to earlier surveys, but a broad distribution from north to south was still evident. However, in the following few months, the 1991 winter fishery failed completely in the north, while CPUE remained elevated in the south. The 1991 spring survey again confirmed the presence of high densities of fish in the south. The 1991 fall survey located much reduced densities but still a broad distribution from north to south except in northern 2J. The 1992 winter fishery took virtually no fish from the north and, despite very high CPUE in the south, was closed in February 1992. The 1992 spring survey showed very high densities of cod in the south over a reduced area. The 1992 fall survey indicated a further decline in the north and one area of concentration in the south (the same area of concentration earlier indicated by the spring surveys and winter fisheries). There was no cod fishery within the Canadian EEZ in 1993. The 1993 spring survey found high densities of cod well to the southeast and outside the EEZ. No concentrations were found inside the EEZ. The 1993 fall survey indicated additional declines in the north and south. The 1994 spring survey found further declines over the southern range, and virtually no cod were located within the main migration corridor in use from 1990 to 1992. Distributions of cod on the Grand Banks (46–47.5°N) also declined beginning in the fall of 1991.

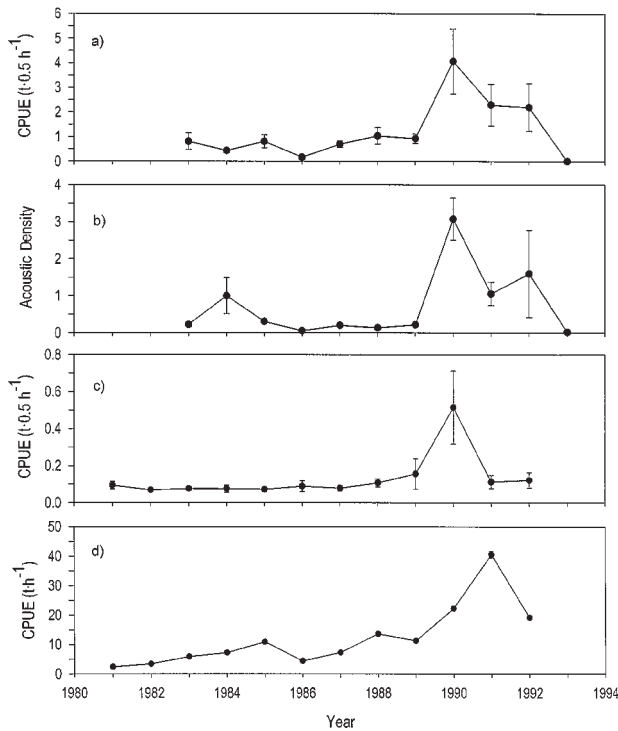## Did fish abundance and density increase in the southern range after 1989?

From 1983 to 1994, commercial and survey fishing sets, and sets directed at cod aggregations during acoustic and tagging experiments, were widely distributed in the Bonavista corridor study area (Fig. 5). In the acoustic-tagging data, sets and aggregations tended to be concentrated within years. Mean standardized annual catch rates ranged from 100 to 500 kg·0.5 h^{-1} and did not differ from 1983 to 1989 (Duncan's multiple range test, $P > 0.05$) (Fig. 6*a*). However, in 1990, catch rates quadrupled and remained significantly above historical levels through 1991 and 1992 ($P < 0.05$). In 1993 and 1994 (not shown), catch rates fell to levels below those of 1983–1989.

Mean acoustic densities of the same cod aggregations in the Bonavista corridor showed a pattern similar to the catch rates with respect to the increases after 1989 and the decline in 1993, but the magnitude of the variations was greater (up to an order of magnitude) (Fig. 6*b*). In addition, densities were higher from 1983 to 1985 than during the years 1986–1989 (Duncan's multiple range test, $P < 0.05$).

Mean annual catch rates from the DFO fall survey within the Bonavista study area were similar through the 1980s but increased five- to sixfold in 1990 (Fig. 6*c*). Catch rates declined to levels similar to those of the 1980s after 1990. Commercial CPUE became elevated in 1990 (there is some evidence of an earlier trend), peaked in the winter of 1991, and remained high in 1992 (Fig. 6*d*).

Acoustic biomass estimates of cod in June in the Bonavista corridor declined from approximately 450 000 t in 1990 to 100 000 t in 1992 (Table 1). After 1992, both distri-

Fig. 6. (*a*) CPUE from directed fishing sets during spring research (standardized to a 30-min tow), (*b*) acoustic densities for the aggregation fishing during the spring research, (*c*) CPUE from the fall trawl surveys, and (*d*) CPUE from the winter fishery in the Bonavista corridor from 1981 to 1993 (mean and 95% CI).

Table 1. Acoustic biomass estimates for cod in the Bonavista corridor in June of 1990–1994.

	Biomass (t)	SE
1990	450 000	60 000
1991	300 000	35 000
1992	100 000	10 000
1993	20 000	3 000
1994	2 000	1 000

Note: SE values are based on transect sampling error only.

adult or juvenile cod could be found anywhere on the northeast shelf or northern Grand Bank inside or outside the EEZ by trawl or acoustic surveys (Fig. 4).

In the inshore trap fisheries, total catch in the southern range (3L) in 1990 was the highest on record for the period 1975 until the moratorium in 1992 (Fig. 7*a*). Availability increased three- to four-fold in 1990 and 1991 over the values recorded in the 1980s (Fig. 7*b*). In contrast, in the northern range of the stock (2J), both catches and availability declined steeply after 1989.

Were "northern" fish present in the southern ranges?

From 1980 to 1991, a consistent pattern of antifreeze production in relation to temperature and time of the year was observed in adult cod caught during the previous summer off the Avalon Peninsula (Fig. 8*a*). In all years, antifreeze was absent from the plasma in late summer – fall. As water temperatures declined to 0°C and below (end of December – January), production of antifreeze was initiated so that small but measurable quantities appeared in the plasma by early January. Levels rose throughout the winter, reaching mean peak values of TH towards the end of March. Water temperatures generally rose above 0°C during April, and, coincident with this, antifreeze began to be lost from the plasma. By June–July, summer plasma freezing points of approximately –0.7°C were again the norm and TH readings were again at or below 0.07°C.

During this period (1980–1991), the highest mean levels of TH (mean TH ± 1 SE) were observed in March of 1982 (0.462 ± 0.024°C, $n = 13$), 1989 (0.462 ± 0.049°C, $n = 10$), and 1991 (0.461 ± 0.024°C, $n = 10$). Between 1980 and 1991, only three fish out of a total of 218 sampled during the months of peak antifreeze levels (March and April) developed antifreeze concentrations giving TH values >0.6°C (Table 2). These three fish were all caught in the summer of 1988 and developed their peak TH levels in March 1989.

During the winter of 1991–1992, cod caught in the summer of 1991 exhibited a pattern of antifreeze production unlike any previously observed (Fig. 8*b*). Production was initiated considerably earlier in the year at higher ambient temperatures. By the beginning of January, antifreeze levels were already high, at the time when antifreeze would typically be just appearing in the plasma. By late January, a mean TH of 0.432 ± 0.044°C was recorded, and levels continued to rise to a peak of 0.798 ± 0.1°C by late April 1992. This was 73% higher than the highest mean level recorded over the preceding 10 years. As in previous years, levels de-

bution and abundance continued to decline (Fig. 4; Table 1). In 1993, postspawning adults could be located only to the southeast of the Bonavista corridor and north cape areas on the nose of the Grand Bank outside the Canadian EEZ (Fig. 1).

In May 1991, a large cod aggregation was tracked for 5 days as it moved eastward along the north cape of the Grand Bank toward the EEZ limit. After the tracking experiment, 2200 cod from this aggregation were tagged in relatively shallow and cool waters (approximately 200 m, 0°C) and released (Fig. 1). Only three tags have ever been returned (one from a lone Canadian vessel fishing nearby a few days after tagging). By contrast, tagging experiments conducted a few weeks later but further to the north and in deeper and warmer waters (>350m, 3–4°C), where fish are known to have ventured to inshore Newfoundland (Rose 1993), have had tag returns of 15–20% (see Taggart et al. 1995).

In 1992, the extant northern cod were concentrated at the offshore margins of the Bonavista corridor (Fig. 4). However, in February 1993, a DFO acoustic survey failed to locate any fish in this corridor. The same survey reported the location of a large cod concentration (no firm estimate) approximately 50 km outside the Canadian EEZ on the nose of the Grand Bank (J. Baird, Northwest Atlantic Fisheries Centre, St. John's, Nfld., personal communication) (Fig. 1). In June 1993, a more comprehensive survey of this region located a single aggregation of adult cod spanning 8 km (acoustic estimate 20 000 t) approximately 50 km from the winter location and 40 km outside the EEZ. By 1994, few

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Fig. 7. (*a*) Catches of the trap fisheries in 3L (solid circles) and 2J (open circles) and (*b*) index of the overall availability of fish to the trap fisheries in 3L and 2J (data from Bishop et al. 1993).
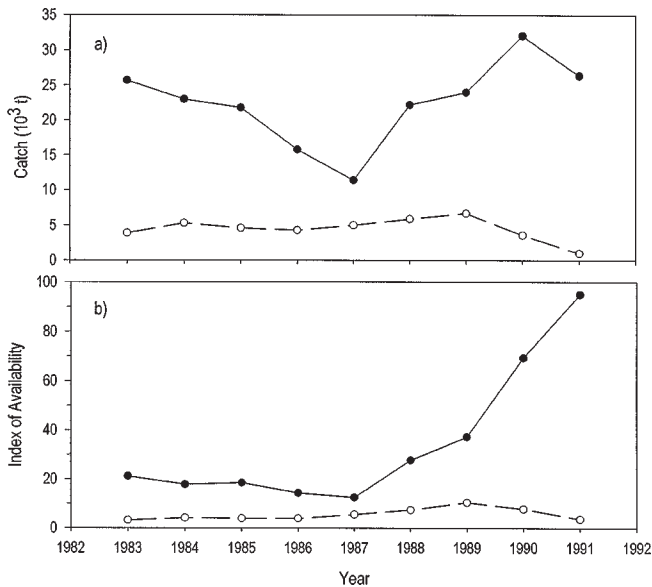
clined after April and antifreeze was gone from the plasma by July.

In 1992–1993, 1993–1994, and 1994–1995, cod caught inshore during the summer and held over winter also exhibited patterns of antifreeze production elevated over those of the 1980s (Fig. 8*b*). Of the 67 fish sampled during March and April between 1992 and 1995, 40 fish (60%) developed TH levels >0.6°C; 19.4% of these fish had TH levels higher than any that had been recorded between 1980 (when these studies began) and 1991 (Table 2).

The mean value of all TH data for March of all years collected prior to the shift in 1992 was compared with all the postshift March data using Student's *t* test. Values for April were treated in the same manner. Preshift March mean TH ± 1 SE was 0.38 ± 0.011°C (*n* = 107). Postshift March TH was 0.63 ± 0.022°C (*n* = 42). Preshift April TH was 0.32 ± 0.01°C (*n* = 111). Postshift April TH was 0.70 ± 0.043°C (*n* = 25). The March postshift mean TH was 64.5% higher than its preshift counterpart, while the April postshift mean was more than double that of the mean of April measurements taken prior to 1992. The differences between the pre- and post-shift values were highly significant for both months (*P* < 0.001)

Water temperatures in the holding tanks were monitored several times a week from 1986 onwards during these studies (Fig. 8*c*). Since AFGP production in adult cod is triggered primarily by low water temperature (Fletcher et al. 1987), it was important to have a clear picture of the thermal conditions to which the cod were exposed during the course of these experiments. The two coldest winters (1988–1989 and 1990–1991) fell prior to the antifreeze shift. Ambient temperatures and antifreeze production capacity were not correlated either before or after 1991 (*P* > 0.05).

Vertebral numbers for the 1990 year-class did not differ among four discrete cod aggregations located in the Hawke Channel, the St. Anthony Basin, the Notre Dame Channel, and the north cape of the Grand Bank in June 1994 (Fig. 1;

Fig. 8. Plasma TH levels (mean ± 1 SE) for cod captured on the east coast of Newfoundland (Avalon Peninsula) during summer (except 1989), held over the winter subsequent to capture, and monitored for antifreeze production. (*a*) 1980–1990, with 1980–1981 (solid circles), 1981–1982 (open circles), 1982–1983 (solid inverted triangles), 1983–1984 (open inverted triangles), 1984–1985 (solid squares), 1985–1986 (open squares), 1986–1987 (solid diamonds), 1987–1988 (open diamonds), 1988–1989 (solid triangles), 1990–1991 (open triangles), and the curve representing a least squares best-fit model (four terms: $R^2 = 0.8$, $n = 631$); (*b*) 1991–1994 inclusive ($n = 272$), with 1991–1992 (solid circles), 1992–1993 (open circles), 1993–1994 (solid inverted triangles), 1994–1995 (open inverted triangles), and the model from Fig. 8*a*); (*c*) seawater temperatures in tanks where antifreeze experiments were conducted from 1986 to 1995, with 1986–1987 (open circles), 1987–1988 (open squares), 1988–1989 (open triangles), 1989–1990 (open diamonds), 1990–1991 (open hexagons), 1991–1992 (solid circles), 1992–1993 (solid squares), 1993–1994 (solid triangles), and 1994–1995 (solid diamonds). Temperatures are given as monthly means calculated from measurements taken at least four times per week throughout the study period.
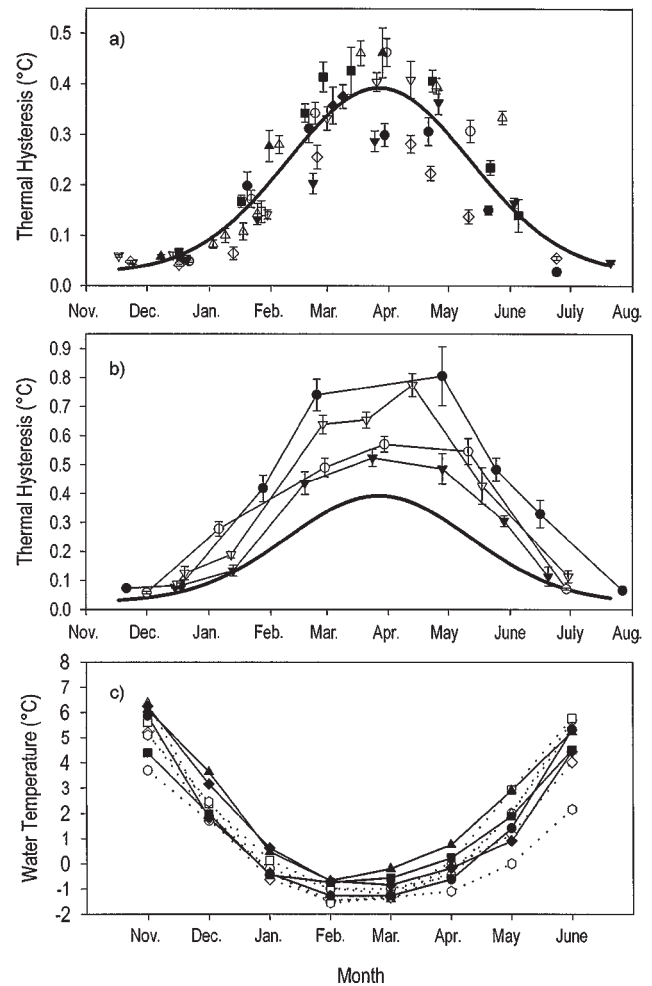

Table 3). The mean for each group did not differ significantly from vertebral numbers reported by Templeman (1981) for the northeast Newfoundland and Labrador Shelf in the years 1947–1971 or from historical Russian data from

Table 2. Distribution (%) of TH values (°C, midpoints of ranges) in adult cod (>45 cm) during the months of peak antifreeze levels (March and April) in years prior to (1981–1991) and after (1992–1995) the shift in antifreeze production capacity.

	TH						
	<0.45	0.55	0.65	0.75	0.85	0.95	>1
1981–1991							
March (n = 107)	84	13	2	1			
April (n = 111)	95	5					
1992–1995							
March (n = 42)	17	26	41	7	5	2	2
April (n = 25)	24	12	4	24	20	8	8

Table 3. Mean vertebral counts (SE in parentheses) from cod from four regions on the northeast Newfoundland and Labrador Shelf (Hawke Channel, St. Anthony Basin, and the Notre Dame Channel) and from the north cape of the Grand Bank).

	1994		1961–1971		1947–1960		1960–1961	
	n	Mean	n	Mean	n	Mean	n	Mean
Hawke Channel	41	55.15 (0.16)	613	55.19 (0.09)	300	55.40 (0.08)	298	55.31 (0.06)
St. Anthony Basin	46	55.04 (0.16)	480	55.30 (0.08)	325	55.34 (0.09)		
Notre Dame Channel	40	55.02 (0.12)	105	55.24 (0.11)	226	55.38 (0.08)		
North cape	62	55.02 (0.12)	1180	54.80 (0.03)	590	54.75 (0.10)	258	54.40 (0.07)

Note: Data from 1994 are from fish of total length <35 cm (aged as 1990 year-class). A random selection of commercial and research vessel captured cod were sampled in 1961–1971 and 1947–1960 (data from Templeman 1981). The 1960–1961 data are from Postolakii (1963). Duncan's multiple range test indicated that the historical data from the north cape formed one group and the rest of the data, including the 1994 north cape fish, formed another ($P < 0.05$).

the same area. However, the mean number of vertebrae from the north cape site was significantly higher than reported historically for that area and was similar to that of more northerly located cod (Table 3).

Weight-at-age of cod aged 5–7 years, which comprised over 90% of the migrating fish during the late 1980s and early 1990s, declined in the southern area (3L and 3K) in the early 1990s to levels similar to that of cod from the northern area (2J) in the 1980s (Fig. 9). Cod of age 8 in 3L also declined in weight but not to the levels in 2J. Cod of ages 5 and 6 in 2J declined in weight in the early 1990s, but cod of ages 7 and 8 did not.

What happened in the environment during these changes?

The period of decline of the northern cod beginning in the 1960s has been accompanied by substantial changes and variability in the environment of the Northwest Atlantic (Fig. 10). Vertically averaged temperature, from a station on the inner shelf, shows a decline of greater than 1°C from the late 1960s to the early 1990s (Fig. 10c). The period from the mid-1980s to mid-1990s was particularly cold, with the early 1990s the coldest in the 60-year series. The early 1990s featured heavy and prolonged ice cover and low salinities (Figs. 10b and 10d). Most of the variance associated with the intraannual changes in temperature, wind stress, and sea ice cover can be related to large-scale pressure differences over the North Atlantic. The North Atlantic Oscillation index (NAO) (Fig. 10a), which is the pressure difference between the Azores and Iceland, strongly influences interannual variability in the ocean and the atmosphere over the entire North Atlantic (Dickson et al. 1996). It is also likely that there is a feedback between the ocean and the atmosphere that regulates, or at least influences, the peri-
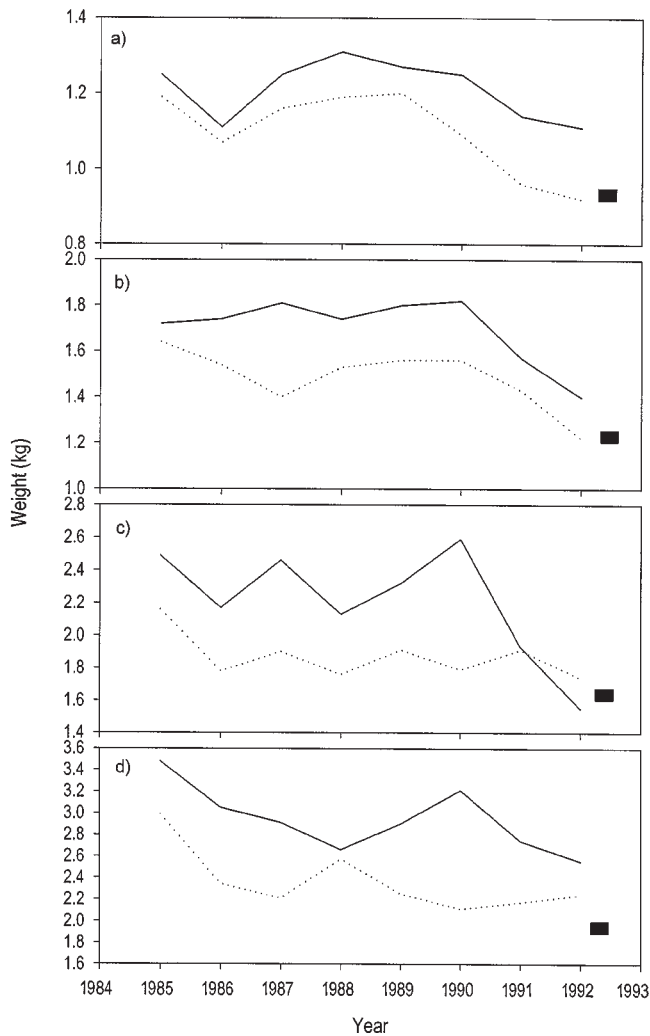
odicity of the NAO, since longer time scale atmospheric phenomena are typically connected to the longer "memory" of the ocean. The NAO reached its highest peak in the 60-year time series in 1989 and 1990 and remained high until 1996.

Discussion

Our work supports the predictions of the shift hypothesis and indicates that cod moved southward on the northeast Newfoundland Shelf in the late 1980s and early 1990s. Cod became aggregated within a small area on the north cape of the Grand Bank and in the Bonavista corridor by the early 1990s. While many of these fish likely came from the north (deYoung and Rose 1993), as evidenced by their smaller size-at-age, enhanced antifreeze production capacity, and higher vertebral count, some may have originated from northern areas of the Grand Bank. These findings are contrary to the hypothesis that no important large-scale changes in distribution or movement patterns occurred in the late 1980s and early 1990s, other than those caused by local overfishing (Hutchings and Myers 1994; Hutchings 1996; Myers et al. 1996). *These conclusions do not discount the importance of overfishing to stock decline.* In contrast, our findings tend to highlight how overfishing could have occurred in such a highly studied, regulated, and managed fishery and how the best-intended management can go awry if ecosystem considerations are not taken into account. Southerly shifting concentrations led to increased vulnerability to overfishing, both legal and illegal, both Canadian and foreign, and resulted in a rapid decline of this stock (Rose and Kulka 1999).
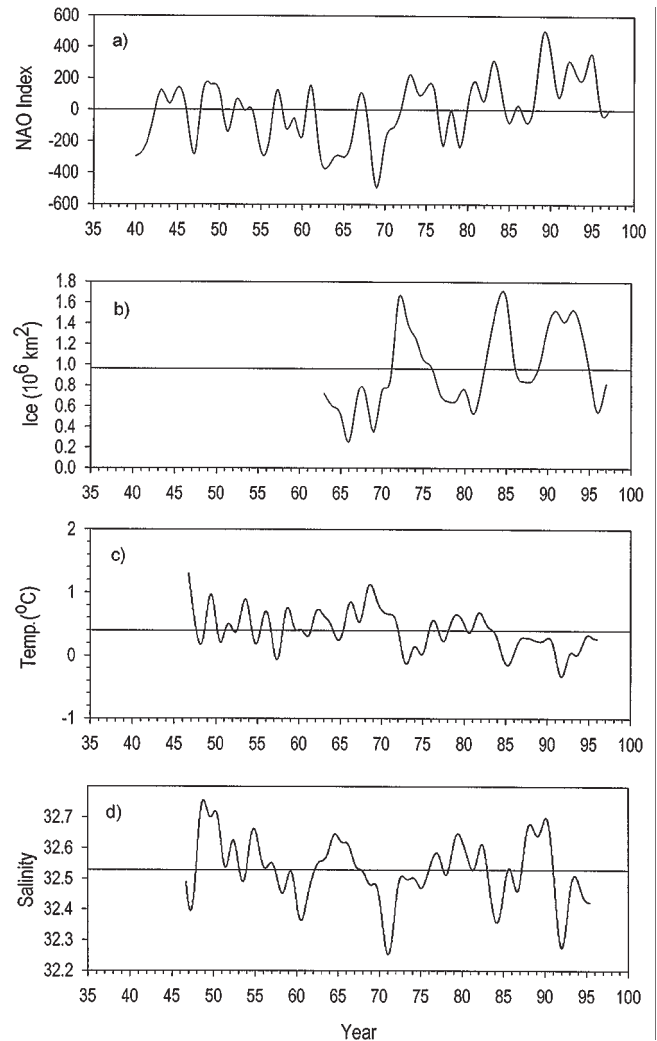
Our data show at least two large-scale changes in cod distribution during the late 1980s and 1990s that were not

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Fig. 9. Mean size-at-age of northern cod of ages 5–8 (*a*–*d*, respectively) for 1985–1992 from the DFO fall survey in 3L (solid line) and 3K (dotted line), and mean size-at-age during the 1980s in 2J (square) (data from Bishop et al. 1993).

Fig. 10. (*a*) Annual average NAO, (*b*) ice cover averaged annually for the Newfoundland and Labrador Shelf, (*c*) temperature, and (*d*) salinity for 1940–1997 from the inner Newfoundland Shelf averaged over the water column and filtered to remove the seasonal signal. The horizontal reference lines in Figs. 10*b*–10*d* are means.

caused directly by the fishery (the first prediction of the shift hypothesis). In the fall of 1990, cod were relatively abundant in northern 3K and 2J on the Hamilton Bank, as was evident from the fall survey. However, cod aggregations could not be located in the same region a few months later at the onset of the winter fishery (very low CPUE) but were readily located further south. It might be argued that declining effort in the north in 1991 disallows the conclusion that few fish were there. However, fishers argue that effort in 2J was sufficient to locate any major aggregations (J. Kelly, former trawler captain, Little Bay, Placentia Bay, personal communication), and evidence shows that by the late-1980s, this fleet had extraordinary knowledge of fish movements and locations, in fact targeting the remaining aggregations with great acuity (Rose and Kulka 1999). Moreover, the very high CPUE in 3K and northern 3L in winter 1991 is consistent with cod having shifted south by this time. Southern shifts have been previously reported. Travin and Pechenik (1963) reported that "under definite conditions the cod inhabiting the Labrador area spawn considerably farther

southward (3K and 3L)." Wroblewski et al. (1995) reported southerly movements along the edge of the continental shelf in early winter. Consistent with such a shift, in the spring of 1991, cod were abundant in the south (3K and 3L). Seasonal movements southward are also consistent with the spatial and temporal returns of fish tagged in the southern range in 1990 and 1991 (Rose 1993). However, seasonal migrations ceased by the fall of 1992 and cannot account for the continued reduction of fish in the north. Higher mortality rates in the northern than in the southern populations fished in the south during the early 1990s could account for the quicker decline in the north. However, selection of northern fish by these fisheries seems unlikely, especially as the northern fish are smaller at age.

Large-scale distribution changes are also evident between 1992 and 1994, when there was no fishery (the offshore fishery ceased in February 1992, and a full moratorium on fishing within the Canadian EEZ was implemented July 2,

1992). Despite the moratorium, the biomass of cod utilizing the Bonavista corridor declined from approximately 100 000 to a few thousand tonnes from 1992 to 1994. Cod were observed moving further eastward from the corridor along the north cape of the Grand Bank in May of 1991. Following that observation, relatively large numbers of cod, indistinguishable from those monitored in 1992 in terms of age and size, were located approximately 100 km to the east in the winter and spring of 1993 (outside the EEZ) at the same time that fish disappeared in the Bonavista corridor. The most likely explanation for these facts is that the fish remaining in the Bonavista corridor in 1992 migrated from that region by the spring of 1993 and that a substantial portion of them moved further to the east and outside the EEZ. An alternative explanation is a local and natural mass mortality for which we have no evidence.

Our data also indicate that cod densities and abundance increased in the early 1990s in the southern range, even though stock levels were declining (the second prediction of the shift hypothesis). All available data sources exhibited this trend, including the DFO fall survey, the winter fishery, the spring acoustic/trawl research, and the inshore summer fishery. The strength of this conclusion is to be drawn not from any single survey or data source, as all have their biases, but from the consistency of the conglomerate of evidence from such diverse sources. The concentration of cod that occurred in the early 1990s has been termed "hyper-aggregation," in which local density not only remains stable but increases as biomass declines (Rose and Kulka 1999). These findings are consistent with the existence in the Bonavista corridor of a dense aggregation of cod measuring approximately 37 by 56 km by 20–100 m deep in June 1990 (Rose 1993) that reformed, albeit in declining volume, each winter–spring from 1990 to 1992. Although the historic record indicates that the Bonavista corridor formed part of the annual cod migration route, the aggregation of such a large number of fish in 1990 (approximately 500 000 000) was unique, at least for the period 1983–1994. Examination of the acoustic record (comparable echograms from 1983 to 1994) indicated that nothing comparable with the 1990 aggregation had been observed previously. There is additional evidence that such a southerly concentration was atypical of earlier periods. Foreign fisheries enjoyed their highest catches and CPUE in the north in the 1950s and 1960s (Travin and Pechenik 1963), and the Canadian fisheries in the late 1970s and early 1980s also had higher CPUE in the north. Why would unrestricted and profit-driven fisheries, with little or no competition among vessels (these were cooperative fleets and there is little indication of a relationship between effort and CPUE in 3L), steam over large and dense aggregations to reach more distant grounds? And why would CPUE be lower in the south than in the north historically and then increase to record levels in the south in the early 1990s, at a time of concentration of effort and a major stock decline? Finally, had there been no distribution shift, the higher fishing effort in the south would have been expected to reduce the southern fish first, not last, as is evident in all available data.

Patterns in the coastal fisheries are also consistent with a distribution shift beginning in the mid- to late 1980s. Relative availability to the southern fisheries increased by an or-der of magnitude while decreasing in the north, at a time when overall abundance was declining. Of note, trap catches in the south (3L) in 1990 were the highest since statistics were available (1975), while in the more northerly zones, trap catches were very low and declining. Again in 1991, trap catches were relatively high in the southern region and virtually nil to the north. Substantial increases in effort in the trap fisheries almost certainly occurred during this period (e.g., Hutchings and Myers 1994), which may tend to confound the relationship between trap catch and abundance (Rose 1992). However, the order of magnitude increase in availability within a few years is unlikely to be solely an artifact of increases in effort. The record catches in the early 1990s in the south are more likely attributable to changes in distribution and migration patterns.

The offshore fisheries showed patterns similar to those of the inshore fisheries. During the early 1990s, the southern offshore fisheries, both Canadian and foreign, maintained and even increased their CPUE and catches. For the Canadian fisheries, CPUE was maintained because increasing densities of fish were aggregating on southern fishing grounds (Rose and Kulka 1999). The Canadian fleet still attempted to fish in the northern areas in the late 1980s and early 1990s, largely as a result of government regulations, but CPUE was very low. Of note, the Spanish trawler fleet arrived on the nose of the Grand Bank in 1990. This fleet and the rest of the foreign fishery reported record catches of cod in 1991 (>50 000 t reported). It is difficult to conceive how such catches could have occurred without southern movements of cod to this fishing area, as has been demonstrated for the better studied fishing grounds within the Canadian EEZ (Rose and Kulka 1999).

We also found more direct evidence of real changes in cod distribution in the early 1990s (the third prediction of the shift hypothesis). The winter pattern of antifreeze production in cod captured in the south was consistent for over a decade until 1990. However, cod captured in the same region in 1991 had a much greater capacity to produce antifreeze than any group previously studied. This shift was abrupt and unexpected, and the observed elevation in cold hardiness continued through 1994. Overwintering temperatures were no more severe in the years of exceptional antifreeze production than in the preceding 10 years and thus cannot be invoked to explain these observations.

Population differences in antifreeze production capacity have been found in several northern teleost species that have a wide geographic distribution and a greater need for cold protection at high latitudes. Both winter flounder (*Pleuronectes americanus*) and ocean pout (*Macrozoarces americanus*) from the Newfoundland region are capable of developing significantly higher antifreeze levels than fish of the same species from further south (Fletcher et al. 1985*a*, 1985*b*). This phenomenon has recently been described in the Atlantic cod. Juvenile Atlantic cod collected from a northerly site (the tip of Newfoundland's Great Northern Peninsula) developed TH values approximately 50% higher than juvenile cod collected from three bays along the north coast of Newfoundland when held under identical conditions over a winter period (Goddard et al. 1999). TH values between adults and juveniles cannot be directly compared, since juvenile cod are known to have a greater antifreeze production

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capacity than adults (Kao and Fletcher 1988; Goddard et al. 1992). However, the postshift adult cod collected in the southerly region between 1991 and 1994 developed TH levels considerably more than 60% higher than the adults collected from the same area between 1980 and 1990. Thus, the elevation of antifreeze production capacity of the postshift adults over that of the preshift adults more than equals the elevation of antifreeze production capacity of northern juveniles over juvenile cod from more southerly areas.

These data lead us to conclude that the abrupt upward shift (1991–1992) in the antifreeze production capacity of cod sampled in the southern region between 1980 and 1995 was due to an influx into the area of cod originating further north from an area demanding even greater freeze protection for survival. Since the shift was first reported in the winter of 1991–1992, this suggests that some northern fish had moved into southern waters by the summer of 1991.

Meristic evidence is also consistent with the hypothesis that northern fish were present in their southern range in the early 1990s. The vertebral count is formed during early development and is temperature dependent. Slower growing northern fish have a higher count. Postolakii (1963) and Templeman (1981) demonstrated a difference between northern and southern fish in this stock. However, in 1994, there was no difference among the northern and southern areas, and southern fish had vertebral counts identical to those of northern fish in historical data. Although this change might also be explained by environmental changes between historical and recent times, the vertebral data are consistent with fish movement from north to south.

The rather abrupt decline in mean weight-at-age of cod in the south (3L) in 1991 also supports the prediction that northern fish shifted to southern waters. The mean weight of southern fish of ages 5–7, which formed the bulk (>80%) of the extant migrating biomass (cod of the northern stock begin large scale migrations at ages 4–5 (Rose 1993)), declined to near the level of northern fish of the same age by 1992. It is important to note that the decline in weight-at-age was not a consequence of declining condition in southern fish. Condition of 3L fish remained stable from 1981 to 1992 (Taggart et al. 1994). We can think of no alternative explanation for the decline in weight-at-age other than an incursion of smaller fish in equal condition. The condition of fish that remained in 2J declined after 1989 (Taggart et al. 1994), which suggests that environmental conditions worsened in the north.

Recent studies suggest that there may be genetic differences between cod resident from the Bonavista corridor northward and those on the Grand Bank (Bentzen et al. 1996; Ruzzante et al. 1996, 1998). Unfortunately, the data used in these studies were mostly from juvenile cod and not from adults of separate spawning groups. It is noteworthy that Bentzen et al. (1996) concluded that their results indicated a different stock structure than suggested by deYoung and Rose (1993). However, we interpret the results of Bentzen et al. (1996) and Ruzzante et al. (1996, 1999) as broadly supportive of deYoung and Rose (1993), who hypothesized the existence of a geographic cline of populations from Labrador to the northern area of the Grand Bank. Of note, the known migration routes of the northern cod do not cross onto the Grand Bank except at the southern margins of

the Bonavista corridor in the north cape region (Rose 1993; Colbourne et al. 1997b). Hence, movements from southern Labrador to the north cape of the Grand Bank are within the stock range of northern cod, and no major genetic differences are to be expected. However, we suggest that the north cape may be a seasonal or episodic mixing area for northern and Grand Bank cod, which differs somewhat from Ruzzante et al. (1999). It is noteworthy that cod collected on the nose of the Grand Bank in the winter of 1993 differed from other southern cod in allele frequencies at one locus but did not differ from fish sampled further north (Bentzen et al. 1996). These fish were subsequently removed from analyses conducted by Bentzen et al. (1996) because they did not resemble other Grand Bank cod. The location of genetically northern-type fish on the northeast corner of the Grand Bank is consistent with the hypothesis that northern cod were present in the southern ranges, and to the nose of the Grand Bank, in the early 1990s.

Following our interpretation of observations from the 1980s and early 1990s, the arguments put forth by Hutchings (1996) that no large-scale changes in distribution or migration patterns occurred during the early 1990s require examination. Tagging studies cited by Hutchings (1996) that purport not to support movement (Myers and Cadigan 1995) cannot resolve the shift hypothesis. Unfortunately, no tagging was conducted in the northern area (2J) immediately before or during the years when movement is thought to have occurred (see Taggart et al. (1995) for a synopsis of most of the tagging data). Moreover, the use of fish tagged in 3K as "northern" in opposition to northern 3L as "southern" (Myers and Cadigan 1995) is unwarranted because the main migration route of the northeast shelf component of the stock crosses the 3K–3L boundary (Rose 1993; Wroblewski et al. 1995; Colbourne et al. 1997b). Hutchings (1996) also argued that the presence of northern cod in the north during the fall of 1990 and 1991 (e.g., Fig. 4) is evidence against the shift hypothesis (as did Lilly 1994). However, their interpretations are based entirely on fall data. Seasonal data show that a transient northern presence in fall was likely a residual of the migration cycle. The seminal point is that these fish did not stay in the north for the critical period of overwintering and spawning, as once they may have. Moreover, by 1992, even a transient presence in the north was not evident.

Hutchings (1996) also argued, as we have, that size-at-age of older migratory fish in the south would be expected to have declined somewhat in the early 1990s if northern fish had shifted south. However, Hutchings (1996) used only 2 years of data from the DFO fall survey to conclude that size-at-age did not decline in the southern zone (3L) in 1989 or 1990. A more complete analysis indicated that weight-at-age declined by approximately 25% in the south, to levels nearer those of northern fish, in 1991 and 1992. Hence, these results are fully consistent with a shift of lesser weight-at-age fish from the northern to the southern region in the early 1990s. It is noteworthy that the decline was not apparent until after 1990, although the shift may have begun a year or two earlier. However, up until 1991, the component of the fall migration that includes a northern route back to the wintering grounds was still much in evidence. Hence, although a winter shift may have begun in the late 1980s, its full impact

was not to be observed in the fall survey, or the spring surveys, until the early 1990s. For similar reasons, the abrupt change in antifreeze production may not have been evident until 1991 in the southern zone.

Some of the criticisms of Hutchings (1996) address uncertainties about the cause of the shift, in particular related to environmental hypotheses. Rose et al. (1994), employing both survey and fishery data, showed that on average, cod were located further north in warm years and south in cold years. Hutchings (1996) claimed that these findings were dependent on the inclusion of fish from the northern Grand Bank, which may or may not be a component of the northern stock (we agree that this is uncertain). However, re-analyses of subsets of the same data from which were excised an increasing proportion of the southerly range up to 47.5°N, well to the north of the contested fish, did not change the overall interannual distribution pattern (Fig. 11). Moreover, the offshore fishery data mirror these survey data (Rose et al. 1994). There is also confirmatory evidence from the inshore fisheries, as southern trap catches have been invariably high when the cold intermediate layer anomaly (Colbourne et al. 1997a) is positive. Hence, survey and fishery data consistently suggest that cod are more southerly distributed in colder years and more northerly distributed in warmer years. We believe analyses of mean latitudes to be meaningful and to support the shift hypothesis, in contradiction of Hutchings and Myers (1994) and Hutchings (1996).

What caused the shift?

A first hypothesis is that the shift was caused by abiotic environmental change. Latitudinal shifts do correlate with sea temperatures (Rose et al. 1994). Moreover, the NAO reached its peak value in the 60-year series in 1989, the year that the recent major shift began in earnest. In the cold years of the early 1990s that followed, cod were located in the warmest waters available during the winter and spring. For example, mean water temperatures where cod aggregated in the outer Bonavista corridor in June 1991, the coldest year on record, were above 3.5°C (0.5°C above the historical average for that area). Nevertheless, there are difficulties in concluding that cod simply moved either to avoid cold conditions (Lilly 1994) or to seek out warmer conditions. Warm waters (2–4°C) exist at depths >300 m in all Newfoundland regions even in the coldest years (although the distribution of these temperatures may be contracted). It is also uncertain as to what temperatures cod actually experience over a year and how they might react to differing seasonal temperature regimes. Seasonal temperature variability is much greater than interannual variability, except near the bottom (Petrie et al. 1991). Hence, cod migrating near bottom may be most influenced by the annual signal. In perhaps the best attempt thus far to resolve these complexities, Colbourne et al. (1997b) showed that during a single migration cycle, cod may experience temperatures that average a full degree colder in cold than in warm years. The effects that such differences may have on cod distribution are uncertain. deYoung and Rose (1993) hypothesized that cod might integrate thermal conditions over the seasons, and hence respond to the annual signal. If true, broad-scale measures of the thermal state of the ecosystem, or broad-scale indices of ocean climate such as the NAO, may be more valid than sin-

Fig. 11. Mean latitude of northern cod distribution (weighted by standardized CPUE) for 1981–1992 under various southern boundary conditions: >46°N (solid circles), >47°N (open circles), >47.5°N (inverted triangles).
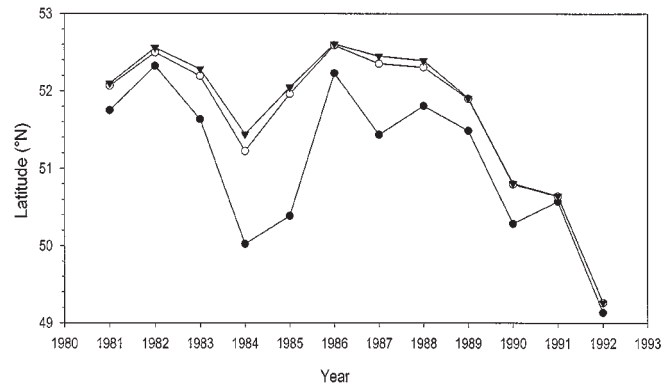
gle measures of where cod are at a particular time (during a survey) as indicators of annual distribution. Such a relationship could explain the "paradox" of a relationship between temperature and cod distribution in this stock (deYoung and Rose 1993) and why north–south distribution correlates with broad-scale thermal indices (Rose et al. 1994). In conclusion, although the mechanism remains opaque, variations in ocean climate almost certainly influence the latitudinal distribution of northern cod.

A second hypothesis is that northern cod shifted their distribution in response to changes in the biotic environment, in particular the distribution of capelin, their chief prey. A major decline of capelin off Labrador occurred in 1989, just before the southerly shift in cod (Lilly 1994; Carscadden and Nakashima 1997). During this period, capelin moved east to the Flemish Cap, well outside the Canadian EEZ, and perhaps south as far as the Scotian Shelf (Frank et al. 1996). Within the known range of the northern cod, capelin concentrated during the early 1990s on the north cape of the Grand Bank and just south of the Bonavista corridor (see Lilly 1994), in areas adjacent to those where cod aggregated. The capelin shift has also been linked to cooling ocean conditions (Carscadden and Nakashima 1997). Hence, a prey shift is a likely mechanism linking a shift in cod to changes in ocean climate.

A third hypothesis is that the fisheries of the past 40 years have influenced distribution patterns in less direct ways than simply fishing down concentrations. There are several possible fishery-related effects on stock dynamics and behavior that could underlie a distribution shift. MacCall (1990) proposed a "basin model" in which density dependence leads to range contraction to "favored" habitat during stock decline. deYoung and Rose (1993) used this model as a basis for their hypothesis on distribution shift but modified it to include environmental change as a cause of range contraction. Cod have been reported to modify their thermal associations as stock abundance changes (Swain and Wade 1993). Hence, because of abundance declines (MacCall 1990), environmental effects (deYoung and Rose 1993), or an interaction between these factors, distribution may contract to favored habitat. However, for migratory stocks such as northern cod that spawn and feed in disparate regions, the identification of

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a single favored habitat is problematic. For example, the Bonavista corridor, the area where northern cod last congregated in the early 1990s, was likely near optimal in terms of thermal conditions (warm) and adjacency to prey (capelin). However, this same area was likely poor habitat in terms of spawning. deYoung and Rose (1993) correctly predicted that southern spawning in 1991 and 1992 would produce poor recruitment. Moreover, if the widespread historical population structure of the northern cod was fundamental to productivity (deYoung and Rose 1993), then the long-term effects of decades of over-fishing may not only have been to directly reduce population levels, but also to increase the latent productivity of this stock by reducing the potential for diversity in spawning distribution and migration patterns.

The fisheries almost certainly resulted in a collapsed age structure. Historically, fish 10–20 years of age were a significant component of the northern cod (see data in Bishop et al. 1993). As late as 1990, there were substantial numbers of age 8+ fish, but by 1992, there were few fish >6 years of age. Such a reduction, combined with the reduction in biomass by a factor of 5 during these years, led Rose (1993) and Rose et al. (1995) to speculate that migration patterns were changing as a consequence of density- and age-dependent effects. In brief, with fewer fish, there would be less impetus to migrate, and with fewer older fish, the social transmission of the routes might cease, and migration might occur imprecisely or not at all (Rose et al. 1995). These predictions are consistent with recent events, as the migration ceased in 1993 and has not been evident since.

The fishery could also have altered habitat. However, we have no data on the northern cod habitat with which to address this hypothesis.

In summary, there is evidence that ocean climate change, shifting prey distributions, and density- and age-dependent population responses resulting from the fishery all played a significant and interactive role in the changes in distribution and migration patterns observed in the northern cod in the late 1980s and early 1990s. This complex situation underscores the need for a more comprehensive "ecosystem" approach to fisheries.

Fishery and the environment: what caused the decline?

Large-scale unsustainable fishing practices began in the 1950s and decimated key northern components of the once abundant Labrador fishery. It is our view that the northern cod never recovered from this over-fishing. Three decades later, there is little doubt that fishing mortality again was unsustainable during the late 1980s and early 1990s and led to more widespread population collapse (Hutchings and Myers 1994; Sinclair and Murawski 1997). The question is whether environmental factors played a role in the collapse and hence may be expected to play a role in the future. We have shown that the decline of the northern cod was not simply a fishing down of concentrations from north to south, as argued by Hutchings and Myers (1994, and several other papers by the same authors). It appears near certain that major environmental changes and several ecological anomalies took place during the period of cod decline (Drinkwater and Mountain 1997; Sinclair and Murawski 1997) and that these contributed substantially to the decline in the northern cod. The southward shift in northern cod led to increased vulner-

ability to fishing (Rose et al. 1994) and to reduced recruitment (deYoung and Rose 1993). The environmental changes affected many species other than cod. Capelin exhibited slow growth and delayed spawning and shifted southwards beginning in the late 1980s (Frank et al. 1996; Carscadden and Nakashima 1997). These changes have been attributed to the cooler waters of the 1990s (Carscadden and Nakashima 1997). Montevecchi and Myers (1997) documented an abrupt change in food for gannets, from Atlantic mackerel (*Scomber scombrus*) to capelin, on Funk Island off the northeast coast of Newfoundland in 1990. Atlantic salmon (*Salmo salar*) exhibited changed migration patterns in the early 1990s (Narayanan et al. 1995). Other species, such as American plaice (*Hippoglossoides platessoides*), declined under low exploitation (Bowering et al. 1997). Species as diverse as marine butterflies (*Oikopleura* spp.) and Arctic cod, whose historical ranges were much more northerly, became widely distributed in the southern areas in the early 1990s (e.g., Drinkwater and Mountain 1997). Pandalid shrimp and snow crab populations have surpassed any previously observed levels. It is difficult to find any aspect of the northern cod ecosystem that did not change in the late 1980s and early 1990s.

In conclusion, we think it unlikely that all of the changes in the northern cod ecosystem, or in the cod populations themselves, can be attributed in total to the fisheries. Large fluctuations in the cod stocks would likely occur with no fisheries at all, as reported from 1710 to 1720 (Innes 1940). Nevertheless, there is little doubt that the catastrophic and sustained declines in cod evident over the past 40 years would not have occurred without the fisheries, and the effects of these fisheries have been manifest not only in the cod populations but throughout the ecosystem. The key question is how persistent these changes will be, and are some, indeed, irreversible.

After the moratorium: did the foreign fishery play a role?

The moratorium on the fishery in the Canadian EEZ halted neither the changes in distribution patterns nor the decline in northern cod abundance. We propose that the two factors are related, as for the earlier period from the late 1980s to 1992. We have presented evidence that southerly movements along the northeast shelf may have been extended along the north cape of the Grand Bank in the early 1990s, especially after 1992. Such movement is consistent with the observed presence of large aggregations of cod outside the EEZ in the winter and spring of 1993. It is noteworthy that beginning in 1990 and continuing after the Canadian moratorium in July 1992, more than 50 trawlers from EU countries fished on the nose of the Grand Bank. This fishery could account for the disappearance of over 2000 tagged fish, and their aggregation, that were present on the north cape of the Grand Bank in the spring of 1991, and moving east toward the boundary of the EEZ, and for the disappearance of the extant aggregations located outside the EEZ in 1993. It is also likely that this fishery contributed to the disappearance of the fish (approximately 100 000 t) present in the Bonavista corridor in 1992, if these fish moved southeastward. Data in Kulka et al. (1995) show a progressive shift in the areas of high catch rates of the Canadian fleet to

the southeast beginning in the late 1980s, such that by 1992, the largest fishing ground was adjacent to the EEZ limit. The reported catch of the foreign fleet was approximately 51 000 t in 1991. The true removals will likely never be known, but it is clear that despite the steep decline in stock abundance, a minimum of 51 000 t was available in the small area of the nose of the Grand Bank (approximately 10 000 km^2). Such availability implies a mean density approaching 0.01 fish·m^{-2} over the full area, if the fishery caught every fish there (and much higher local densities if a more typically heterogenous distribution pattern is assumed (e.g., Rose and Kulka 1999)). Given that such densities are comparable with those measured in the Bonavista corridor in the early 1990s (Rose 1993), it is implausible that they represent anything but an active movement to and concentration of fish on the nose of the Grand Bank. The EU (Spanish) fleet was well positioned for fishing southward-migrating cod. We conclude that distribution shifts led to continued fishing after the moratorium in the Canadian EEZ in 1992 and continued population decline.

The future

Will the northern cod rebuild? How long will it take and how will rebuilding occur? Recruitment of juveniles across the former range is the key to rebuilding. Over the past decade, recruitment has been generally poor. The southern spawning distributions of 1991–1993 generated almost nil recruitment (Anderson and Dalley 1997), and despite a slight improvement in 1994, more recent recruitment has been poor (Lilly et al. 1999). Thus far, the more abundant inshore spawning (Rose 1996, unpublished data) appears not to have repopulated the larger shelf zone (Anderson and Dalley 1997). In contrast, a very limited northern shelf spawning (G.A. Rose, unpublished data) in 1994 resulted in an immediate increase in the numbers of juveniles on the shelf (Anderson and Dalley 1997). Hence, we conclude that rebuilding the northern shelf spawning groups is the key to the rebuilding of the full stock.

Will the northern spawning grounds be recolonized or must all rebuilding occur locally? At present, we cannot definitively answer this question. However, cod off northern Labrador (2GH) have not rebuilt since their decline four decades ago in the 1960s. The reasons for this are not known. But the question arises as to why 2J fish did not recolonize these more northerly areas. There are several possible explanations: (*i*) abiotic or biotic environmental conditions were unfavorable, (*ii*) 2J fish never attained some abundance threshold necessary for emigration (2J was heavily fished during this period, and this fishery spilled over the 2J–2H boundary in the late 1970s, which suggests that 2J fish may have attempted to move north), and (*iii*) genetic or behavioral constraints made recolonization problematic. It may be important that high antifreeze producers, and presumably northern fish, were still present off southern Newfoundland in the summer of 1994 (the last year of sampling). This suggests that, in terms of cold tolerance, the genetic or phenotypic diversity necessary for northern recolonization has not been eliminated.

The rebuilding of the northern cod was predicted to take decades, based on the distributions model of deYoung and Rose (1993). Alternatively, projections of rebuilding sched-

ules based on nonecological population models, formulated on the notion that stocks will simply increase at some fixed rate when fishing stops (e.g., Myers et al. 1997), indicated much faster rebuilding. For example, projections by Roughgarden and Smith (1996) based on such theory indicate that northern cod abundance should be over 1.5×10^6 t by 1997! The reality is closer to an order of magnitude lower (Lilly et al. 1999). Similar projections made by Myers et al. (1997) based on a lower growth rate are more realistic but still overestimate observed population recovery. This disparity suggests that factors other than current population size and parameters internal to populations are important to the rebuilding process and that external "ecosystem" factors play a role in population growth. Behavioral changes at low population sizes may also complicate any simplistic view of stock rebuilding. Based on the present studies, we cannot forecast a timetable for rebuilding, but we can forecast steps thought to be diagnostic of the stage of rebuilding. In stage 1, holding to the theory that northern spawning drives population abundance in the northern stock, abiotic and biotic conditions in the north must revert to favorable states for cod. Of importance are warming conditions and the return and reestablishment of capelin as a major food source. It is noteworthy that oceanic conditions off Labrador have returned to normal since 1996 (Colbourne et al. 1997*a*), and a resurgence of capelin off Labrador has recently been observed (R. O'Driscoll, Fisheries and Marine Institute, St. John's, Nfld., unpublished data). In stage 2, adult cod reverse the southerly shift back to the north and in time reform large (>100 000 t) spawning aggregations. It follows that if rebuilding of the historic stock complex is an objective, both cod and capelin stocks must increase in numbers (and age) so that emigration from southern regions is more likely to occur. Reseeding of juveniles from Greenland waters is also possible, but at present unlikely as a result of low stock levels there (Dickson and Brander 1994). In stage 3, recruitment of juveniles across the shelf will begin. We are currently at stage 1. There is precedent for such staged recoveries of large marine fish stocks. The Norwegian spring-spawning herring, devastated by overfishing in the 1970s, reestablished a full migratory life cycle in stops and starts from a much reduced area inhabited for almost three decades (Dragesund et al. 1977). Hence, the adaptive migratory behavior of the northern cod, which in the early 1990s caused major shifts in distribution and amplified the effects of overfishing on the undoing of this stock, may also be its salvation.

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