Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse[1]

Jeffrey A. Hutchings

Abstract: The collapse of northern cod, *Gadus morhua*, off Newfoundland and Labrador was associated with clearly defined spatial and temporal changes in density and biomass. Between 1981 and 1992, low density research survey tows (<100 kg/tow) increased gradually from 76 to 97% concomitant with a gradual decline in medium density tows (100–500 kg/tow) from 22 to 2%. By contrast, high density tows (>500 kg/tow) remained proportionately constant (~1.5%) until 1992, whereafter they declined to zero. Southward, spatio-temporal changes in stock biomass were unaccompanied by a shift in cod distribution. A simple density composition model provides a biological basis for observed changes in mobile and fixed-gear catch rates, increased catchability of cod with declining stock biomass, and rapid increases in fishing mortality. A nested aggregation model of a small, constant number of dense cod aggregations, each encompassed by, and recruited from, lower density areas, explains how cod vulnerability to fishing can increase with declining stock biomass. A review of recent research identifies excessive fishing mortality as the sole significant cause of northern cod's collapse. Prevention of fishery collapses arguably rests on the dominant question to emerge from this review: what are the effects of fishing on the behaviour, life history, and population biology of exploited fishes?

Résumé : L'effondrement des stocks de morue, *Gadus morhua*, au large de Terre-Neuve et du Labrador est associé à des changements spatio-temporels nets de densité et de biomasse. Entre 1981 et 1992, les traits de dénombrement à faible densité de capture (<100 kg par trait) se sont faits de plus en plus fréquents, passant de 76 à 97%, tandis que les traits à densité moyenne (100–500 kg par trait) sont passés de 22 à 2%. Toutefois, les traits à forte densité de capture (>500 kg par trait) sont restés sensiblement constants (≈1,5%) jusqu'en 1992 avant de tomber à zéro. Vers le sud, les changements spatio-temporels de la biomasse des stocks ne se sont pas accompagnés d'une modification de la répartition de la morue. Un modèle simple de composition par densité offre un fondement biologique aux changements observés relativement aux taux de capture au moyen d'engins mobiles et d'engins fixes, à la capturabilité accrue de la morue à mesure que la biomasse des stocks diminue, et à la mortalité par pêche, qui est en hausse rapide. Un modèle d'agrégation à plusieurs degrés décrivant un petit nombre constant de denses concentrations de morue, chacune circonscrite par des zones de concentration moindre d'où se fait le recrutement dans les concentrations élevées, permet d'expliquer comment la vulnérabilité à la pêche de la morue peut s'intensifier à mesure que la biomasse du stock diminue. Une recherche documentaire montre que la très forte mortalité par pêche est l'unique cause importante de l'effondrement des stocks de morue. Il est logique de penser que pour éviter l'effondrement des pêches, on doit s'attaquer à la question centrale que cette recherche a fait apparaître : quels sont les effets de la pêche sur le comportement, le cycle biologique et la biologie des populations exploitées?
[Traduit par la Rédaction]

Introduction

The collapse of the Atlantic cod, *Gadus morhua*, fisheries off eastern Canada has prompted considerable debate concerning the question of whether excessive fishing pressure or excessive natural mortality was the primary cause of the stock declines (e.g., deYoung and Rose 1993; Lear and Parsons 1993; Atkinson and Bennett 1994; Hutchings and Myers 1994*a*, 1995; Myers and Cadigan 1995*a*, 1995*b*; Myers et al. 1996*a*, 1996*b*). Such debate is healthy and should serve to narrow the range of potential causes to the point that new research initiatives and management strategies that reduce the likelihood of recurrence of these collapses will be identified and implemented.

The northern cod stock, once the world's largest (McGrath 1911), experienced a collapse considerably more severe than that of other Canadian east coast cod stocks. Between 1962 (the first year for which age-specific abundance estimates are available) and 1992, the estimated spawner biomass of northern cod had declined almost two orders of magnitude (by contrast, the mean size of the spawner biomass of other cod stocks at the time of their collapse was 13% of their historical maxima; Myers et al. 1996*b*). The concomitant 94% decrease in recruitment (the abundance of cod aged 3 years, the age at which cod are first vulnerable to commercial fishing gear) is not surprising given the strong stock-recruitment relationship that appears to exist for this stock (Hutchings and Myers 1994*a*). Northern cod spawn throughout the continental shelf from Hamilton Bank south to Grand Bank (Hutchings et al. 1993) with approximately 50% of males and females maturing at 5 and 6 years, respectively (Taggart et al. 1994). Tagging

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J.A. Hutchings. Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

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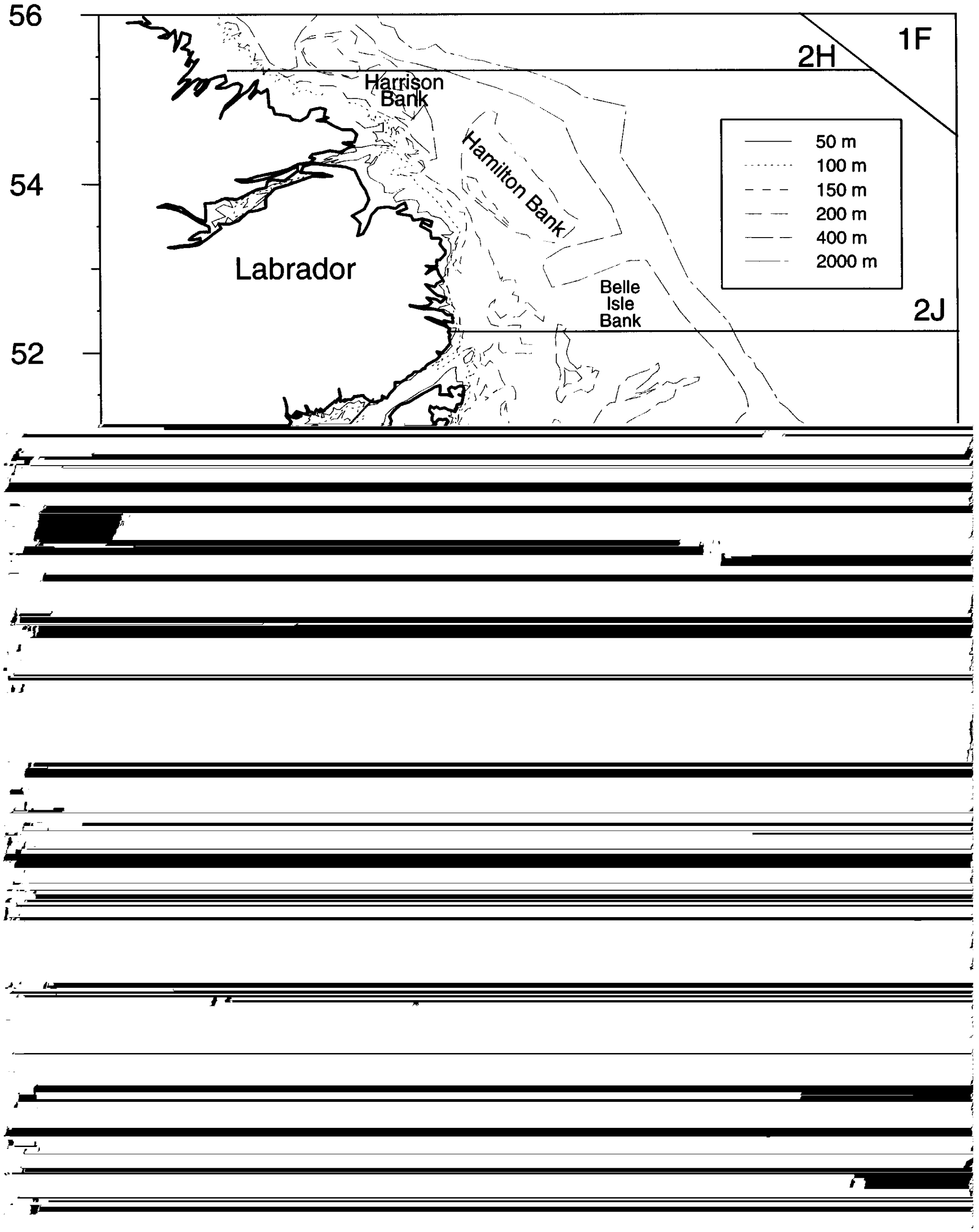
Fig. 1. Map showing the Northwest Atlantic Fishery Organisation (NAFO) management units off Newfoundland and Labrador. The northern cod stock is delineated by NAFO divisions 2J, 3K, and 3L.



studies (Templeman 1965; Lear 1984) indicate that northern cod undergo spring feeding migrations from offshore regions to inshore waters, where they disperse among the headlands and bays and become vulnerable to fixed fishing gear (e.g., gill nets, cod traps, line trawls, hand lines). These cod appear to move offshore again in autumn and remain there during winter when they form prespawning and spawning aggregations that render them highly vulnerable to the mobile fishing fleets that target these aggregations (Hutchings 1995; Kulka et al. 1995). Although the stock is managed as a single unit encompassing Northwest Atlantic Fishery Organisation, or NAFO, divisions 2J, 3K, and 3L (Fig. 1), there is considerable evidence of separate inshore and offshore stocks based on analyses of tagging experiments (Templeman 1965; Lear 1984; Myers et al. 1997), genetic data (Ruzzante et al. 1996), spawning locations (Hutchings et al. 1993), and the local knowledge of fishermen (Hutchings et al. 1996; Neis et al.[2]).

Debate concerning the causes of the decline of northern cod has occurred largely in the absence of a spatio-temporal model of the density distribution of cod. An exception is the work by Warren (1997) who, on the basis of an analysis that separated the autocorrelation in the research survey data into its spatial and temporal components, concluded that the spatial structure

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[2] B. Neis, J.A. Hutchings, R.L Haedrich, D. Schneider, and L. Felt. Scientific debates, disappearing lumpfish and sticky nets: fishers' ecological knowledge and adaptive management. Submitted for publication.

of northern cod had changed from a highly structured stock in 1985 to one possessing little structure in 1992. It has been hypothesized that cod shifted their distribution southward just prior to the stock collapse (deYoung and Rose 1993; Rose et al. 1994) and that cod became increasingly concentrated through the late 1980s and early 1990s (Bishop et al. 1993). If true, such changes in distribution and density composition may have increased the vulnerability of cod to fishing gear and accelerated the stock's rate of decline.

My objectives are to examine research survey data on northern cod to describe spatial and temporal variability in cod density, to demonstrate how such information can be used to assess the relative importance of fishing and the environment to the stock's collapse, and to illustrate how such data can be used to identify criteria upon which the re-opening of collapsed fisheries might be based. I construct simple models to describe the numerical changes in cod density (density composition model) and the temporal changes in the spatial structure of cod (nested aggregation model) that were concurrent with declining abundance of northern cod through the 1980s and early 1990s. To place these models, and their predictions, into a broader context, I review recent research on the causes of the collapse of northern cod. Lastly, I focus upon research initiatives that may serve to increase our understanding of the effects of fishing on exploited populations and identify means of ensuring their long-term persistence.

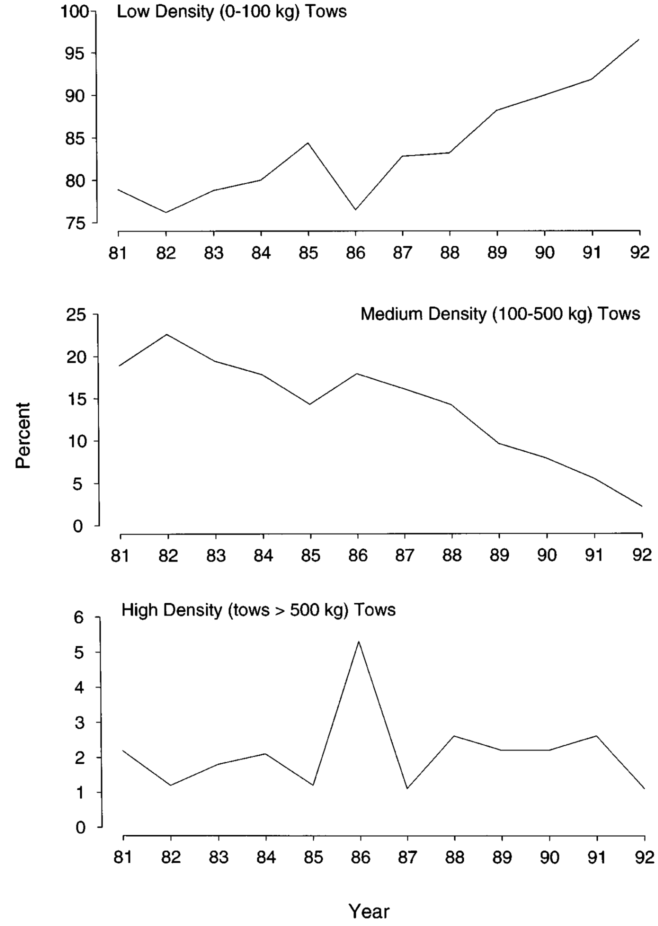
Density composition of northern cod

Research surveys have sampled the entire 2J3KL area over a relatively short period of time (8–10 weeks in most years) every autumn (October through December) since 1981. The survey area is divided into 76 sections called strata, the boundaries of which are delineated primarily by depth. Each stratum is sampled every year, although the within-stratum locations of each half-hour, approx. 0.046-km^2 tow are chosen at random (2–26 tows per stratum between 1981 and 1992). With the exception of the relatively early 1984 3L survey, the timing of the surveys has not changed significantly through time. Given that the annual timing of the peak inshore catches did not change significantly from 1981 to 1990 ($F_{[1,7]} = 1.55$; $p = 0.253$), it would appear that the timing of the autumnal offshore migration by cod changed little over the same period.

I grouped research survey tows conducted between 1981 and 1992 into low (0–100 kg), medium (100–500 kg), and high biomass (greater than 500 kg) tows. Given that each tow samples approximately the same swept area, these groups can be identified as low, medium, and high density tows. These would correspond to 0 to 2.2, 2.2 to 11.0, and greater than 11.0 t/km^2 (to a maximum of 139 t/km^2 in 1986), respectively. The percentage of tows in each density class was calculated for the entire area sampled by the autumn surveys in 2J3KL for each year. Tows in which the trawling gear did not operate properly were excluded from the analysis.

The percentages of tows by density class showed consistent trends over time (Fig. 2). Of all tows conducted annually from 1981 to 1984, roughly 78% were low density tows, 20% were medium density tows, and 2% sampled cod at high densities. Omitting the 1986 datum when sampling conditions resulted in unusually high catchabilities of cod, low density tows in the mid–1980s (1985 to 1988) increased in prevalence and medium density tows decreased while the percentage of high density tows remained largely unchanged. The annual percentage of high density tows remained constant at roughly 2% through 1991 while the percentages of low density tows had increased to 92% and medium density tows had declined to 6%. By 1992, low density tows constituted 97% of all tows with medium and high density tows constituting approximately 2% and 1% of all tows, respectively. There have been no high density research tows of northern cod since 1992 (Department of Fisheries and Oceans, unpublished data).

Fig. 2. Temporal changes in the proportional representation of low (<100 kg), medium (100–500 kg), and high (>500 kg) biomass tows in the autumn research survey data for northern cod from 1981 to 1992.



Density composition model

The temporal pattern in density composition of tows may reflect predictable responses by cod to declining stock biomass. I constructed simple models to describe observed changes in the proportions of low, medium, and high density tows of cod over time:

$$(1a)\quad \alpha_{L(t)} = \alpha_{L(t=0)} + \beta_{L1}(t), \text{ when } \alpha_M > \alpha_{M*}$$

$$(1b)\quad \alpha_{L(t)} = \alpha_{L(t=t^*)} + \beta_{L2}(t-t^*), \text{ when } \alpha_M \le \alpha_{M*}$$

$$(2a)\quad \alpha_{M(t)} = \alpha_{M(t=0)} - \beta_{M1}(t), \text{ when } \alpha_M > \alpha_{M*}$$

$$(2b)\quad \alpha_{M(t)} = \alpha_{M(t=t^*)} - \beta_{M2}(t-t^*), \text{ when } \alpha_M \le \alpha_{M*}$$

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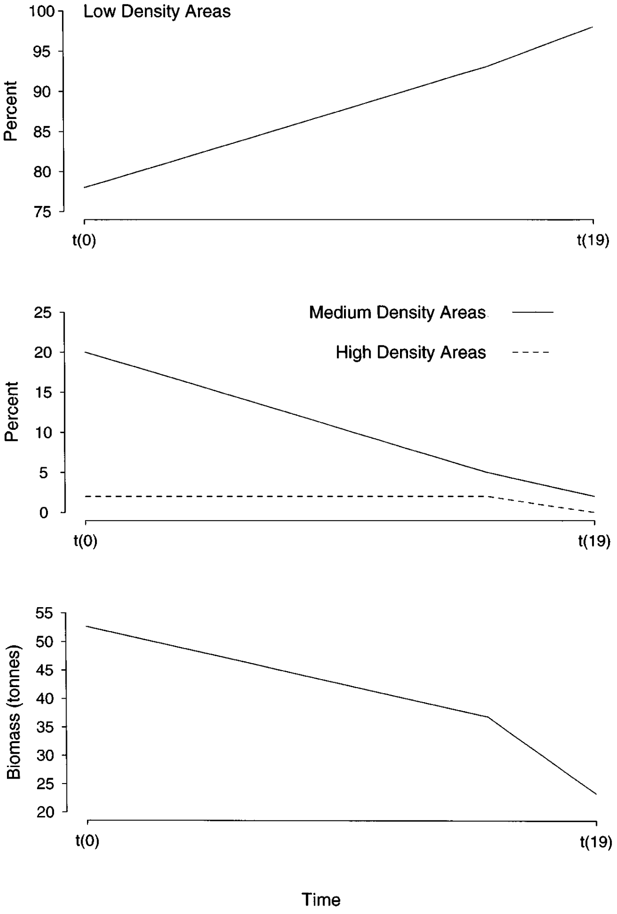
Fig. 3. Temporal changes in the proportional representation of low, medium, and high density areas of northern cod corresponding to tthe density composition model described by eqs. 1–3 in the text. Changes in total stock biomass associated with this model (cf. eq. 4) are presented in the bottom panel. Time is in arbitrary units.



(3*a*) $\alpha_{H(t)} = \alpha_{H(t=0)}$, when $\alpha_M > \alpha_{M*}$

(3*b*) $\alpha_{H(t)} = \alpha_{H(t=t^*)} - \beta_H(t-t^*)$, when $\alpha_M \leq \alpha_{M*}$

From initial values at time $t = 0$ (i.e., $\alpha_{L(t=0)}$ and $\alpha_{M(t=0)}$), the proportion of low and medium density tows increases and decreases, respectively, at a constant rate ($\beta_{L1} = \beta_{M1} = 0.01\ t^{-1}$) until time = t^*, when the percentage of medium tows reaches a threshold, whereafter the rates of change decline ($\beta_{L2} = 0.0075\ t^{-1}$; $\beta_{M2} = 0.0050\ t^{-1}$). The proportion of high density tows is modelled to remain constant at its initial value, $\alpha_{H(t=0)}$, until t^*, whereafter the proportion of high density tows declines at a constant rate of $\beta_H = 0.005\ t^{-1}$. (Values of β for each density class were chosen to be consistent with empirical data; Fig. 2.)

Concomitant with changes in density composition are changes in stock biomass, $N_{(t)}$, where

(4) $N_{(t)} = \mu_L T\alpha_{L(t)} + \mu_M T\alpha_{M(t)} + \mu_H T\alpha_{H(t)}$

The total number of tows per year, T, equalled the 1981–1992 average of 424. The mean biomasses of cod in low, medium, and high density tows were $\mu_L = 50$ kg, $\mu_M = 300$ kg, and $\mu_H = 1260$ kg, respectively. These values represent the mid-range biomass values for the low and medium density tows and the 1981–1992 average of high density tows.

The temporal trends described by the density composition model (eqs. 1–3; Fig. 3) are similar to, albeit less variable than, those observed in the research survey data (Fig. 2). Changes in model stock biomass with changes in density (Fig. 3, lower panel) can be used to predict temporal changes in biomass and mortality indices often quantified in stock assessments. I examine three such indices: (*i*) catch rates of mobile and fixed gear, (*ii*) catch rate as a predictor of stock biomass, and (*iii*) fishing mortality.

As stock biomass declines, the density composition model predicts different trends in the catch rates of cod in high and in medium–low density areas. Catch rates in high density areas are predicted to remain relatively stable before declining sharply when the percentage of medium density tows falls below a threshold level (5% in the present model, as observed in the northern cod research surveys). Catch rates in medium and low density areas, however, are predicted to decrease continuously with declining stock biomass (Fig. 4A). These predicted catch rate trends in high and medium–low density areas correspond to those observed in the trawler and gill-net sectors of the northern cod fishery, respectively (Fig. 5A). (Trawler and gill-net catch rate data are expressed as proportions of their respective maxima.) Trawler catch rates changed relatively little from 1982 to 1989, declining at a rate of about 2% per year, before declining 16% per annum thereafter. In constrast, gill-net catch rates in the inshore (from 1985, the first year for which data are available) and offshore fisheries (from its initiation in 1986) declined at the considerably faster rates of 13 and 14%, respectively (data from Hutchings and Myers 1994*a*).

Until 1988, the catch rate of commercial trawlers was assumed to be proportional to the size of the northern cod stock (Baird et al. 1991). The density composition model predicts that catch rates in high density areas should remain constant, despite declining stock biomass, until stock size falls to a sufficiently low level whereafter catch rate declines proportionately with stock biomass (Fig. 4B). This predicted relationship between catch rate in high density areas and stock biomass corresponds with that observed between commercial trawler catch rate and harvestable northern cod biomass from 1982 to 1991 (Fig. 5B). Thus, the density composition model provides an explanation for the negative relationship between catchability and northern cod biomass documented by Hutchings and Myers (1994*a*).

The density composition model predicts that the instantaneous rate of fishing mortality, F, associated with the decline in stock biomass increases relatively slowly prior to a comparatively short period in which F increases rapidly (Fig. 4C). Here, fishing mortality in year t was determined from the equation $\mathrm{HR}_{(t)} = 1 - e^{(-F(t))}$, where harvest rate (HR) in year t is

(5) $$\mathrm{HR}_{(t)} = \frac{\theta}{N_{L(t)} + N_{M(t)} + N_{H(t)}}$$

and where the value of θ, analogous to a constant total allowable catch (TAC), was such that F in year $t = 0$ equalled the value of F estimated for the northern cod fishery in 1982 ($F_{1982} = 0.44$; Bishop et al. 1994). Coincident with declining stock biomass, the density composition model predicted that

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Fig. 4. Temporal changes in metrics of cod biomass and stock health predicted by the density composition model (eqs. 1–3 in the text). (A) Predicted temporal changes in catch rate in high and medium–low density areas. (B) Predicted relationship between catch rate in high density areas and stock biomass. (C) Predicted changes in instantaneous fishing mortality with time. Time is given in arbitrary units.

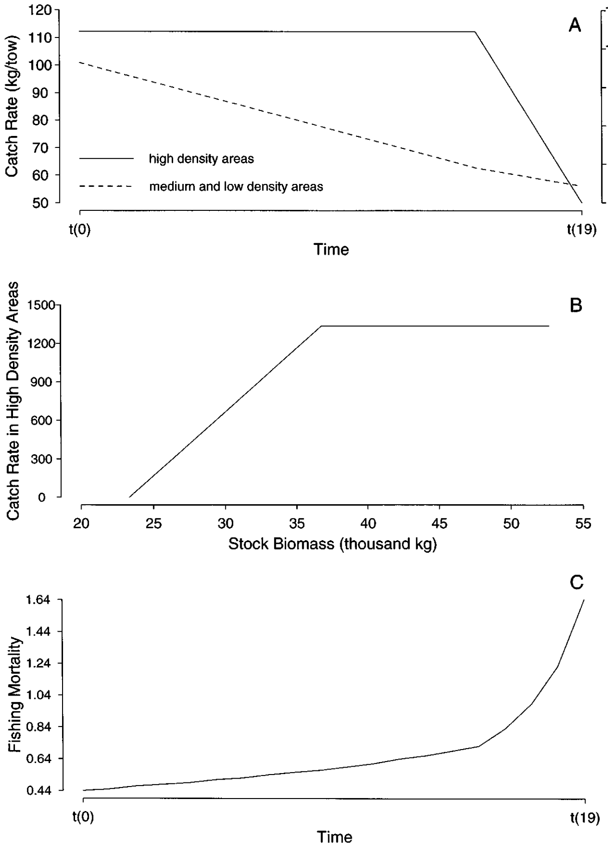
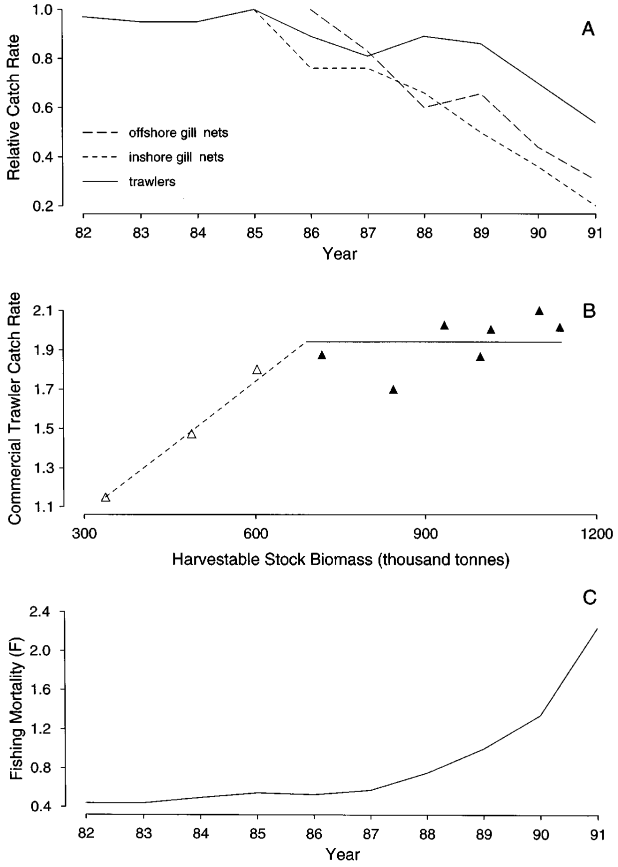


Fig. 5. Observed changes in metrics of cod biomass and stock health. (A) Temporal changes in catch rates of cod by trawlers and gill nets. (B) Relationship between trawler catch rate and harvestable biomass of northern cod (cod aged 3 years and older), as estimated by virtual population analysis (VPA). (C) Changes in instantaneous fishing mortality of northern cod, estimated by VPA, from 1982 to 1991.



F should increase slowly from 0.44 to 0.72 between *t*(0) and *t*(15) before rising rapidly to 1.64 by *t*(19) (Fig. 4C). This pattern in fishing mortality predicted by the density composition model is consistent with the changes in *F* of northern cod fully recruited to the trawling gear (ages 7 to 9 years) estimated by virtual population analysis, or VPA (Bishop et al. 1994); between 1982 and 1988, *F* increased from 0.44 to 0.75 before increasing rapidly to 1.34 in 1991 and 2.23 in 1992 (Fig. 5C).

General agreement between the abundance metrics predicted by the density composition model (Fig. 4) and those observed in the northern cod fishery (Fig. 5) suggest that an understanding of the factors that contributed to the stock's collapse is incomplete in the absence of a model of the spatial structure of the northern cod stock.

How should trends in abundance and biomass be estimated from research surveys?

The similarity between predicted and observed patterns of stock abundance metrics (Figs. 4, 5), coupled with observed changes in the density composition of research tows between 1981 and 1992 (Fig. 2), indicates that northern cod were increasingly at risk of collapse from the mid-1980s. If true, why did the research survey trend in stock biomass fail to detect a decline in stock biomass until 1991 (Fig. 6A)? Either northern cod did not, in fact, begin to decline until 1991, leading to the conclusion that the stock declined rapidly between 1990 and 1991, or the means of describing trends in stock biomass was not robust to annual changes in the variance of abundance estimates and (or) changes in the stock's density composition.

Survey biomass, sometimes referred to as minimum trawlable biomass, for the 76 strata sampled during autumn in year t, $N_{(t)}$, is estimated as

$$N_{(t)} = \sum_{i=1}^{76} \mu_{i(t)}\omega_i \tag{6}$$

where

$$\omega_i = a_i / \sum_{i=1}^{76} a_i$$

Total biomass equals the sum of the mean biomass estimates for individual strata i, μ_i, each of which is weighted by its stratum area, a_i. Annual frequency distributions of biomass per tow resemble extended Poisson distributions (i.e., long positive

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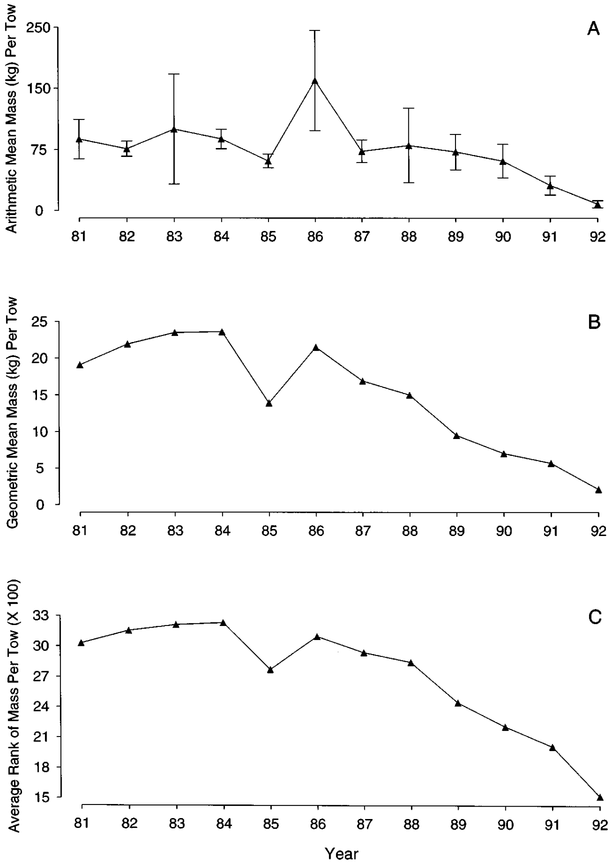
Fig. 6. Changes in (A) arithmetic mean (±SE; estimated from Bishop et al. (1994)) mass per tow, (B) geometric mean mass per tow, and (C) average rank of mass per tow of northern cod calculated from research surveys between 1981 and 1992.



skew; J.A. Hutchings, unpublished data). The justification for calculating the arithmetic mean is that it provides an unbiased estimate of biomass. However, there is concern that μ_i may not possess zero design bias, i.e., the average over all possible samples may not be the population average because of the way in which samples are taken within strata (Noel Cadigan, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, NF A1C 5X1, personal communication). In addition, the standard errors of biomass estimates, often as high as 30–40%, vary considerably among years (Bishop et al. 1994).

Thus, temporal trends in stock survey biomass have been described by an estimator presumed to have no bias but high, and annually changing, variance (Fig. 6A). However, it is not clear that the criterion of zero bias necessarily warrants the use of the arithmetic mean as an estimator of abundance to the exclusion of other estimators. For example, the criterion that an abundance estimator minimize the mean squared error (MSE = bias^2 + variance) may favour the use of estimators other than the mean (Cochran 1977). A biased estimator with small variance can have a smaller MSE than an unbiased estimator with large variance.

The goal of minimizing MSE, or some other criterion that reduces variance, would seem to be justified when the objective is to examine trends in abundance as opposed to providing abundance estimates on a yearly basis. This is an important distinction. Plotting annual mean biomass estimates and using such a plot to detect abundance changes through time would only be justified if the myriad factors that influence cod abundance and their availability to the survey gear do not vary from year to year. Yearly changes in catchability of northern cod are well illustrated by the extremely high, and biologically unreasonable, 1986 biomass estimate. The assumption of constant interannual catchability has also been questioned for the southern Gulf of St. Lawrence groundfish research surveys (Swain et al. 1994).

Changes in density composition also contributed to interannual differences in the variance in biomass estimates. The proportional decline in medium density tows coupled with a stable representation of high density tows (the mean annual biomass of high density tows did not change with time; $F_{[11,109]} = 0.75$, $p = 0.69$) resulted in the mean being increasingly dependent on proportionately fewer tows. Annually, from 1981 to 1985, one half of the estimated survey biomass could be attributed to the highest 10% of the tows; by the late 1980s, 50% of the survey biomass was attributable to fewer than 2% of the tows (J.A. Hutchings, unpublished data). For example, the stock size estimated from the 1989 research surveys would have been reduced by half if it were not for 8 of the 450 tows conducted that autumn (the highest of which was sampled on the very last tow of that year's survey).

The temporal trend in arithmetic mean weight per tow suggests that northern cod biomass changed little, perhaps declining slightly, from 1981 to 1990 (Fig. 6A). The large decline between 1990 and 1991, which continued through 1992, prompted the view that the stock had declined suddenly, and unexpectedly, in 1991 (spring being the favoured time; Lear and Parsons 1993; Atkinson and Bennett 1994). However, as argued previously, interannual changes in the variance about the mean may render the plotting of annual arithmetic means to describe temporal trends problematic. To reduce the effects that a few large tows have on the mean and to reduce the effects of other sources of variability in the mean, I log-transformed the biomass per tow data (logarithmic transformations of zeroes was accommodated by adding 1 to each biomass datum), calculated the means of the log-transformed data (weighted by stratum area), and then untransformed the means to express the data in kilograms per tow (Fig. 6B).

The trend in geometric mean biomass (Fig. 6B) differs significantly from that generated by the time series of arithmetic mean biomass (Fig. 6A). The trend in geometric mean suggests that northern cod biomass peaked in 1984 and declined thereafter. This pattern of northern cod stock size is consistent with VPA-based trends in harvestable biomass (Bishop et al. 1994), catch rate data from fixed gear fisheries (Hutchings and Myers 1994*a*), and the personal experience of inshore fishermen (Neis et al., see footnote 2). Interestingly, the geometric mean significantly reduces the influence of the 1986 datum on the overall temporal trend.

A rank-based trend estimator provides another means of describing trends in stock biomass that is robust to unusually large survey catches. Here one ranks all mass per tow data for all years (the largest tow receiving the highest rank), computes an average rank of mass per tow for each year, and then plots the average ranks through time. The rank-based trend in northern cod biomass yields a pattern similar to that produced by the geometric mean (Fig. 6C); northern cod biomass peaked in

1984 and declined thereafter. A comparison of adjacent years indicates a significant difference in rank between 1988 and 1989 (contrast test; $F_{[1,12]} = 16.97$, $p = 0.0001$) and between adjacent years thereafter (F ranging from 4.27 to 31.34, p ranging from 0.0001 to 0.0388). Contrast tests also identified a significant difference between ranks for 1984 and 1987 ($F_{[1,12]} = 9.84$, $p = 0.0017$), suggesting that 1987 was the earliest year in which a rank-based trend estimator would have detected the decline that was occurring in northern cod biomass.

The concordance between the latter trends (geometric mean and ranked mass per tow) and other indices of northern cod biomass, coupled with the lack of agreement between the trend in arithmetic means and any other metric, suggests that trends based on arithmetic means of research survey data have inaccurately reflected trends in actual stock abundance. One possible reason for this discrepancy is a violation of the assumption of randomness in survey design that resulted in an over-representation of high biomass tows in the surveys in the late 1980s (e.g., a change in the protocol for selecting alternative sampling locations because of unsuitability of original locations, increased movement of fish during the survey period). Temporal trends in biomass based on estimators other than the arithmetic mean (e.g., geometric mean, ranked mass per tow, median) may have considerable merit. One potential risk in using estimators such as the geometric mean, however, is that they may be overly sensitive to changes in fish distribution. Nonetheless, it would be prudent for stock assessments to include a comparison of biomass trends from more than one survey-based estimator of stock size. Similarity among trends would provide assurance that estimated trends reflect actual trends; disparity among trends would justify uncertainty in stock status and warrant a cautious management strategy.

Recent changes in the distribution of northern cod: real or illusory?

Previous analyses of research survey data have suggested that a dramatic change in the spatial distribution of northern cod occurred just prior to the stock collapse in 1992. The evidence for a southern shift in 1989 or 1990 has been considered strong enough that the hypothesis is now routinely accepted (e.g., Department of Fisheries and Oceans 1995; Kulka et al. 1995; Wroblewski et al. 1995). The southward shift has been thought to have been effected by a changing environment, e.g., colder water temperatures (deYoung and Rose 1993; Rose et al. 1994) and (or) ecosystem-driven shifts in prey abundance (Rose et al. 1994; Warren 1997), and is, therefore, attractive to those who assert that the collapse of northern cod was environmentally driven (see Atkinson and Bennett 1994). It has also been suggested that northern cod became increasingly concentrated (i.e., increased biomass per unit area) through the late 1980s (Bishop et al. 1993), possibly increasing the vulnerability of northern cod to commercial fishing and contributing to the rapidity of the stock decline (Rose et al. 1994). These hypotheses warrant re-examination in light of the trends in cod density revealed by the research survey data.

Spatial distribution of high and medium density aggregations of northern cod

The location of high density research tows in autumn indicates that the most dense aggregations of cod are more likely to be located near the edge of the continental shelf than they are to coastal Newfoundland and Labrador (Fig. 7). With few exceptions, high density groups are situated at depths greater than 200 m. The only area in which high concentrations of cod were consistently found at depths less than 200 m was the southern half of 3L on the northern and central portions of the Grand Bank. These Grand Bank groups were evident from 1984 through 1987 and in 1990. The central location of these groups, near the border of 3L with 3NO (see Fig. 1 for division locations), suggests either that these fish moved north from the southern half of the Grand Bank in 1984–1987 and 1990 or, perhaps more likely, that this group represents a substock of cod whose offshore and inshore movements are restricted to the Grand Bank (Templeman 1962; Lear 1984). These observations, coupled with the absence of high density aggregations south of Funk Island Bank in 1989, argue against the hypothesis that cod experienced southerly shifts in their distribution in 1984 and 1985 and in the years after 1988 as proposed by deYoung and Rose (1993) and Rose et al. (1994). Additional inconsistencies with the southern shift hypothesis are the observations that large groups of cod were located throughout the northernmost NAFO division (2J) in 1984, 1985, 1989, and 1991. If an unfavourable environment precipitated a southerly shift in cod distribution, one would have expected cod in the northernmost, and presumably least favourable, part of the range to have moved south. The spatial plots of high density aggregations indicate that this did not occur.

Temporal changes in the distribution of medium density tows appear to be less variable than those of high density tows (Fig. 8). The location of medium density aggregations on the Grand Bank provides additional support for the hypothesis that these fish are part of a substock whose movements are restricted to Grand Bank. There is evidence of medium density groups of cod on north–central Grand Bank every year from 1981 to 1992 (with the exception of 1991). There are few, if any, differences in the spatial distribution of medium density aggregations on north–central Grand Bank in the years 1983 through 1990.

Rather than reflecting dramatic temporal changes in location, the spatial distribution plots of high and medium density tows are indicative of stability rather than variability. Rose (1993) predicted that northern cod migration routes coincide with deep (greater than 300 m), warm water (2–3°C) trenches in the northeast Newfoundland Shelf. Depending on the sampling time in autumn, cod aggregations would be expected to be found either along or at the end of these migration routes. The three routes proposed by Rose (1993) would lead to cod aggregating on or near (*i*) Hamilton Bank, (*ii*) Funk Island and Belle Isle Banks, and (*iii*) at the terminus of the channel running east from the Bonavista Peninsula. The spatial plots of high, and to a lesser degree medium, density tows from 1981 to 1992 tend to support Rose's (1993) prediction. Cod were highly aggregated on or near Hamilton Bank every year from 1981 to 1989 and in 1991, on Belle Isle and Funk Island Banks every year except 1985 and 1992, and at the eastern terminus of the Bonavista channel in 1981, 1984–1986, 1988, and 1990–1992 (Fig. 7). To these three areas can be added a fourth, north–central Grand Bank, where cod were densely aggregated between 1984 and 1987 and in 1990.

The spatial distribution of medium density aggregations is

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Fig. 7. Locations of high biomass (>500 kg) research survey tows of northern cod between 1981 and 1992. Note that in 1991 and 1992 sampling effort in the south was almost three times that elsewhere in the survey area (see text for details). Depth contours are 200 m (broken line) and 400 m (solid line).

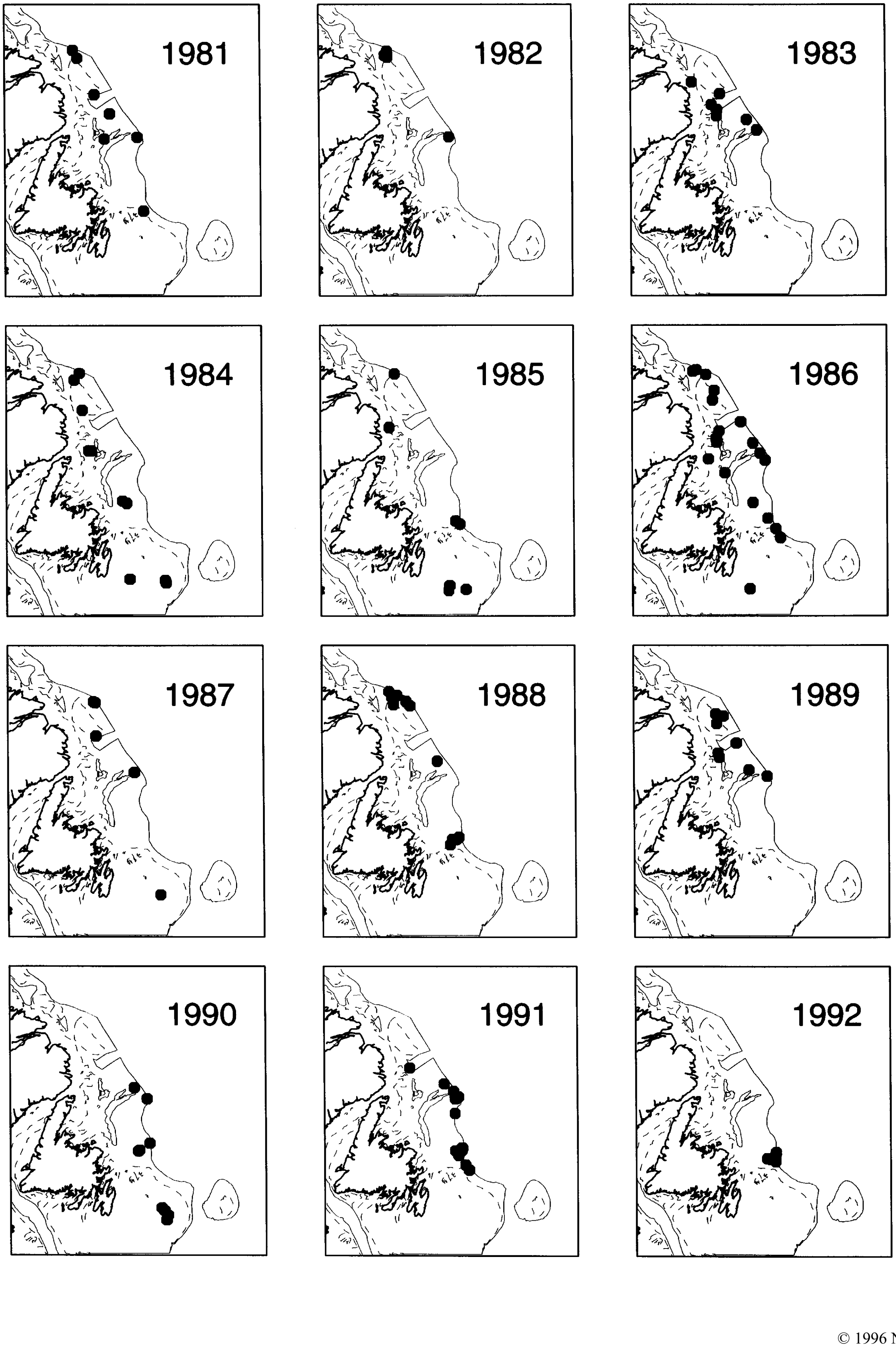

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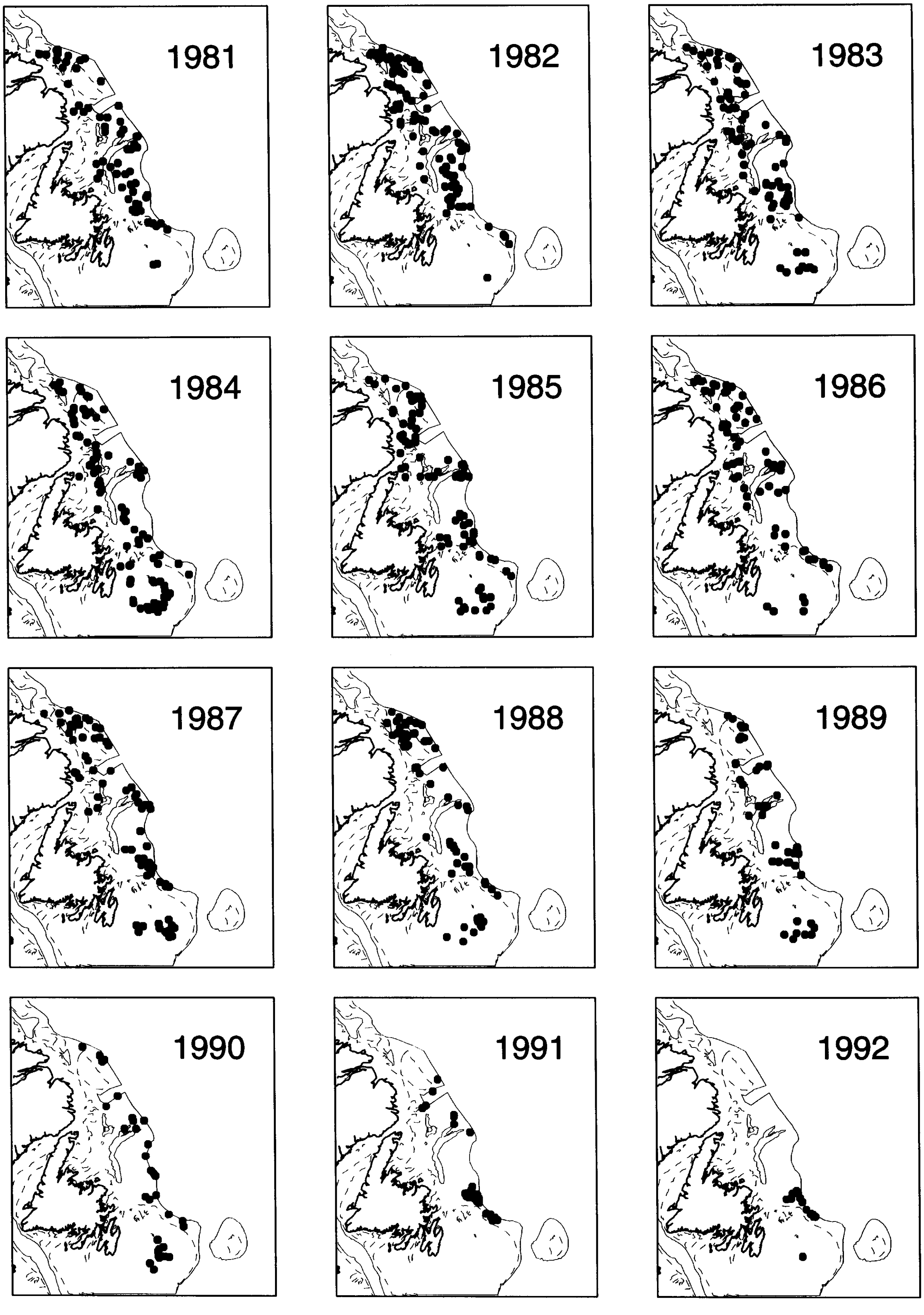
Fig. 8. Locations of medium biomass (100–500 kg) research survey tows of northern cod between 1981 and 1992. Note that in 1991 and 1992 sampling effort in the south was almost three times that elsewhere in the survey area (see text for details). Depth contours are 200 m (broken line) and 400 m (solid line).



consistent with that of high density aggregations (Fig. 8). Medium density tows were sampled in each of the four offshore regions until 1991 when none were observed on north–central Grand Bank and in 1992 when the Bonavista and north–central Grand Bank concentrations were the only ones observed. Temporal changes in the distribution of medium density tows are not consistent with the hypothesis that cod shifted their distribution southward in 1989 and 1990. Rather, the spatial changes in the late 1980s and early 1990s are consistent with a gradual reduction in cod beginning in the north.

When evaluating the temporal trends in the location of high and medium density tows in Figs. 7–8, note that significant increases in survey sampling effort (number of tows per stratum) occurred in 3L in 1991 and 1992 relative to the remainder of the survey area. The increase was largely restricted to the eastern edge of the boundary between 3K and 3L, near the end of a channel that extends westward to the Bonavista Peninsula, and included strata 346, 366, 368, and 369 in 3L and 638 in 3K. These strata correspond roughly to the six southernmost high density tow locations in 1991 and all such locations in 1992 in Fig. 7. Compared with the average number of tows per stratum from 1981 to 1990, sampling effort in 1991 and 1992 for all but these five strata increased by an average 25%. For the five strata on the eastern edge of the 3K–3L boundary, the number of tows per stratum in 1991 and 1992 more than trebled. Thus, the relatively high number of medium and high density tows near the eastern edge of the 3K–3L boundary in 1991 and 1992, i.e., the southernmost high and medium density tows north of the Grand Banks in 1991 and 1992 (Figs. 7–8), reflects sampling effort rather than a southward movement of individuals. Given the increase in sampling effort that occurred in these areas relative to the remainder of the survey area, the number of tows in this area should be reduced by a factor of 3.17.

Confounding latitudinal changes in distribution with latitudinal changes in abundance

There is neither direct nor indirect evidence that cod shifted their distribution southward in 1989 or in 1990. (By a distributional shift, I am referring to spatial changes in abundance caused by active movement of fish.) The purported southward shift reported by previous authors appears, in part, to be an artifact of using changes in the arithmetic means biomass among NAFO divisions (2J, 3K, and 3L). Some of the reasons against the use of trends based on arithmetic means were discussed earlier. There are additional biases that need to be recognized. The main evidence for a southward change in distribution is the observation that the mean latitude of research survey biomass in 1989 and in later years is less than it was in previous years, with the exception of 1984 and 1985 (Rose et al. 1994). Uncritical use of mean latitudinal data overlooks the large influence that relatively small changes in density can have on such data. For example, as indicated by the spatial plots of high and medium density tows, cod are always located in abundance on north–central Grand Bank. There is no suggestion from Figs. 7 and 8 that cod in this region had moved from any other region. However, spurious latitudinal changes can be obtained in years in which these Grand Bank cod aggregated closer together or in years in which the research tows happened to sample the relatively few dense aggregations that exist there. The mean latitude of survey biomass in such years will appear to have declined despite the lack of latitudinal movement by cod.

The primary reason for not using changes in mean latitude of survey biomass or mean survey biomass per NAFO division as metrics of distributional change is that spatial changes in biomass can be confounded by numerical changes in abundance. It is just as valid, for example, to argue that declining mean latitude in biomass is indicative of a depletion of fish from high latitudes as it is indicative of a southward movement of fish. One means of accounting for changes in abundance when assessing possible changes in distribution is to examine spatio-temporal changes in the density composition of cod by NAFO division. The southward shift hypothesis proposes that cod shifted their distribution southward in 1989 and (or) 1990 (deYoung and Rose 1993; Rose et al. 1994). The conditions that prompt such a hypothesis are

$$n_{\mathrm{N}(1989)} < n_{\mathrm{N}(1988)} \text{ and } n_{\mathrm{S}(1989)} > n_{\mathrm{S}(1988)}$$

or

$$n_{\mathrm{N}(1990)} < n_{\mathrm{N}(1989)} \text{ and } n_{\mathrm{S}(1990)} > n_{\mathrm{S}(1989)}$$

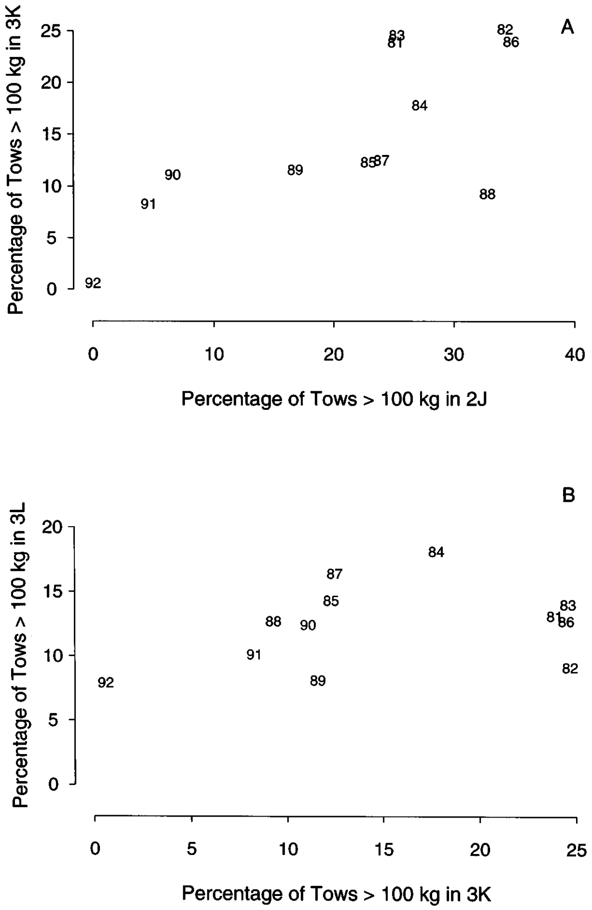
where $n_{\mathrm{N}(t)}$ and $n_{\mathrm{S}(t)}$ represent abundance in the northern and southern of two adjacent NAFO divisions in year t. Bivariate plots of tows in adjacent divisions indicate that declines in the percentage of tows greater than 100 kg in 2J in 1989 and 1990 were accompanied by little change in the percentages in 3K in those years (Fig. 9A); this is also true of tows in 3K and 3L (Fig. 9B). For example, a southern shift of cod from 2J to 3K between 1989 and 1990 would have placed the 1990 datum in the upper left portion of Fig. 9A.

The lack of divisional shifts in the percentage of tows indicated in Fig. 9 argues against the southward shift hypothesis. The strong association between cod biomass in 2J and that in 3K suggests that a common factor influences fish abundance in these divisions (Fig. 9). The independence of cod biomass in 3K with that in 3L may indicate that the factors influencing abundance in these regions are dissimilar. This is consistent with the hypothesis, evident from tagging data (Templeman 1962; Lear 1984) and genetic analyses (Bentzen et al. 1997), that cod in 3L are of a different stock than those in 2J and 3K.

Latitudinal differences in growth rate and fishing mortality

Divisional comparisons of weight-at-age data for northern cod do not support the southward shift hypothesis. If cod had moved south in large numbers in 1989 or in 1990, such a massive distributional change should have been evident in the age-specific weights of cod sampled during the surveys. Cod in 2J have lower weights at age than do cod in 3K, which correspondingly have lower weights at age than cod in 3L (Templeman 1965). Combining age-specific weights for cod aged 6 through 9 years (the dominant ages in the surveys) from 1981 to 1988 (Bishop et al. 1994), the average size of cod in 2J is 83% that of cod in 3K, which are 88% that of cod in 3L (Table 1). If 2J cod had moved south into 3K, or 3K cod south into 3L, in either 1989 or 1990, this should have resulted in a reduction in the difference in age-specific weights among divisions (unless one assumes that only the fastest growing individuals moved south in each year). That is, the ratio of age-specific weights for cod in 2J to those for cod in 3K, and similarly for cod in 3K compared with cod in 3L, should have

Fig. 9. Scatter plots of the percentage of research survey tows sampling more than 100 kg of northern cod from adjacent north–south NAFO divisions. Each datum is represented by the survey year. (A) Tows in 3K (south) versus tows in 2J (north). (B) Tows in 3L (south) versus tows in 3K (north).



approached unity in 1989 and 1990. Instead, the relative difference in age-specific weights for cod in 2J and 3K in 1989 and 1990 was unchanged from the 1981–1988 average whereas the ratio of age-specific weights in 3K to cod in 3L declined rather than increased (Table 1).

It has been argued that the declining abundance in the northern part of the northern cod's range cannot be attributed to fishing (deYoung and Rose 1993; Rose et al. 1994). This argument is based on the observation that fishing effort (number of trawling hours) is typically higher in 3L than it is in 2J and 3K. The assumption that number of trawling hours in a given NAFO division is directly proportional to the fishing mortality experienced by cod that are located in that division in late autumn is unwarranted because of cod movement among divisions and because of the exposure of cod to fishing mortality from gear other than otter trawls. For example, on the basis of tagging studies, it is clear that cod that reside in 2J during late autumn and early winter migrate across the northeast Newfoundland Shelf to inshore waters in 2J, 3K, and 3L (Lear 1984). Tagging studies also indicate that extremely high fishing mortality can be exerted by the inshore fishery (Myers et al. 1997).

Table 1. Average mass (kg) for cod aged 6–9 years sampled in the autumn research surveys conducted in NAFO divisions 2J, 3K, and 3L in selected years from 1981 to 1990.

NAFO division	1981–1988	1989	1990
2J	2.10	1.71	1.65
3K	2.52	2.12	1.98
3L	2.87	2.67	2.88
2J/3K	0.83	0.81	0.83
3K/3L	0.88	0.79	0.69

Additional evidence that the southward decline in cod abundance represents depletion owing to fishing rather than a shift in abundance has been forthcoming from analyses of tagging experiments and from genetic analyses. Myers et al. (1995*a*) reported that fishing mortalities were higher in the north than they were in the south. This is consistent with the hypothesis that the decline of cod in 2J prior to their disappearance in 3K and 3L was due to fishing. Temporal changes in the proportion of tag recoveries from cod tagged in 3K that occurred on offshore banks south of 3K do not support the southward shift hypothesis. Of cod tagged in 3K between 1985 and 1989, a smaller percentage was recovered south of 3K (median 3.9%) compared with cod tagged in 3K between 1979 and 1984 (median 6.9%) (Myers et al. 1995*a*). Consistent with the hypothesis that northern cod have not significantly shifted their distribution since the late 1980s is the observation from microsatellite DNA analyses that the spatial distribution of cod genotypes in the 1960s, 1970s, 1980s, and 1990s has remained constant through time (R. Doyle, Department of Biology, Dalhousie University, Halifax, N.S., unpublished data).

Nested aggregation model for the spatial decline of northern cod

The density composition data (Fig. 2) and the spatial distribution of medium and high density research survey tows (Figs. 7–8) suggest that the distribution of northern cod in late autumn and winter can be characterized by a small but temporally constant number of high density aggregations (Fig. 10; the time scale associated with this nested aggregation model and the percentage of space occupied by high, medium, and low densities of cod correspond with those of the density composition model given in Fig. 3). I have assumed here that aggregations can be modelled as circles, a shape consistent with field observations based on hydroacoustic data (Rose 1993). I have assumed further that high density aggregations are encircled by medium density aggregations. One alternative model is that high and medium density aggregations are spatially distinct entities. However, the general, albeit coarse, correspondence between the distribution of high and medium density tows (Figs. 7–8) suggests that the model of nested aggregations is not unreasonable. Implicit in the nested aggregation model is the assumption that there are fitness advantages to being members of large groups (e.g., protection from predators, increased probability of locating prey; Pitcher and Parrish 1993). All individuals may be prevented from being members of high density aggregations because of aggressive interactions (these can be very intense under certain conditions, e.g., spawning; Brawn 1961; J. Hutchings and T. Bishop, unpublished data). Alternatively, the proportion of the cod

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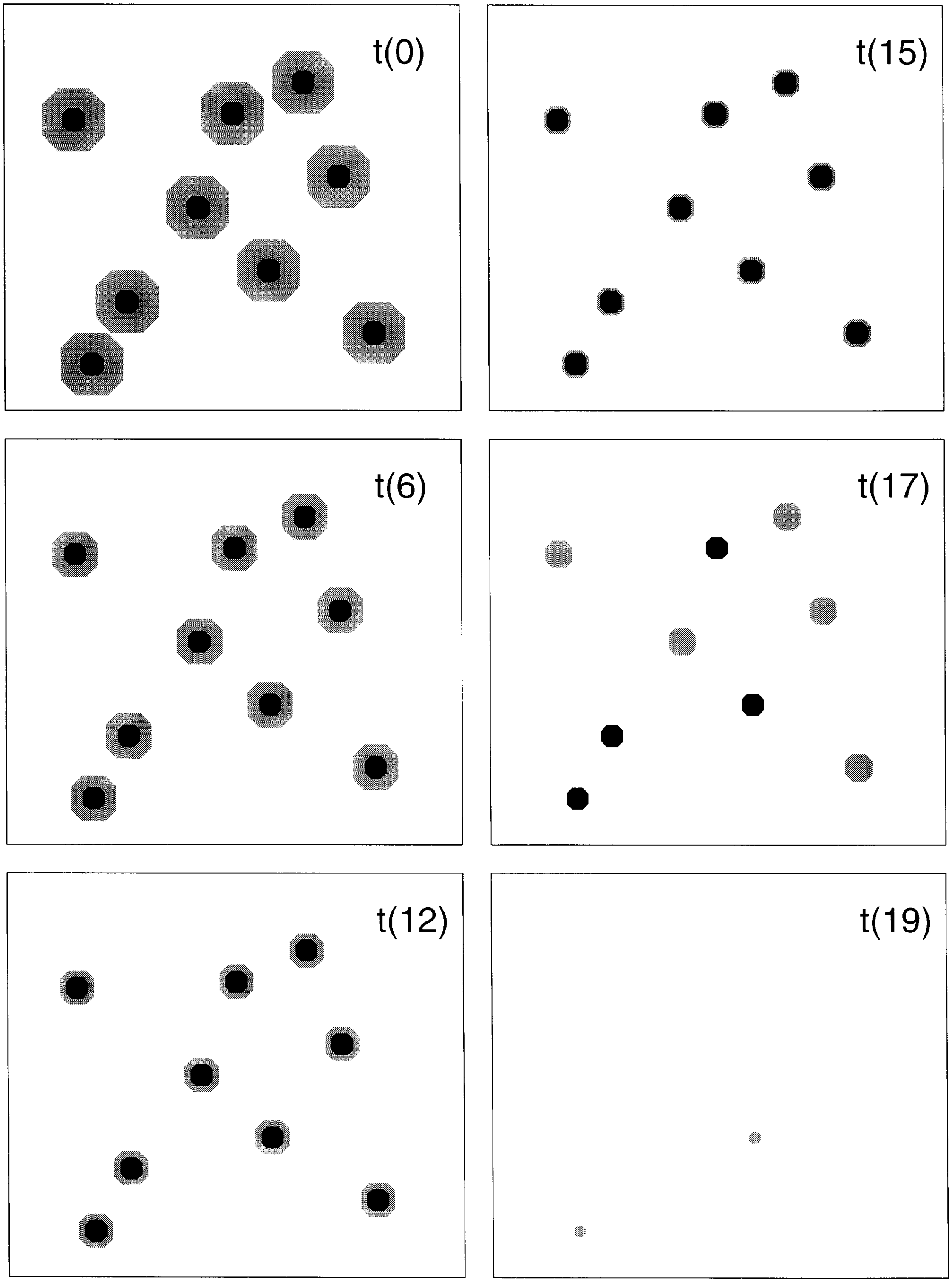
Fig. 10. Nested composition model describing changes in the density composition of the northern cod stock with declining stock biomass. High (>500 kg/tow), medium (100–500 kg/tow), and low (<100 kg/tow) densities of cod are distinguished by black, grey, and white areas, respectively. The percentage of area in each time square corresponding to each density category corresponds to those described in the density composition model (see Fig. 3).



stock occupying aggregations of different density may follow an ideal free distribution (Fretwell and Lucas 1970).

Fishing strategies exploit the spatial aggregations of cod by concentrating effort where catch rates are highest. Thus, mobile trawlers fishing for northern cod concentrate their effort during winter on the high density aggregations (Warner 1977;

Hutchings and Myers 1994*a*; Kulka et al. 1995). Fishers using fixed gear such as gill nets and cod traps are presumably exploiting cod at medium and low densities after they have dispersed along the coast following their spring inshore migration.

Research survey data indicate that the percentage of high density tows remains constant over time. This suggests that despite being "fished down" by trawlers, high density aggregations may be able to maintain their numerical integrity by recruiting cod from medium density areas. Again this is predicated on the reasonable assumption that there are fitness advantages to being part of a high density aggregation and that this is always the preferred behavioural strategy of cod. Temporal patterns in trawler and fixed-gear catch rates can be explained by this model. As stock biomass declines, trawler catch rates will remain constant as long as biomass is sufficiently high to allow cod to form high density aggregations. In contrast, as trawlers fish down high density aggregations, there will be fewer fish migrating inshore and dispersing along the coast, resulting in a steady decline in fixed-gear catch rates (Fig. 5A; Hutchings and Myers 1994*a*). This would lead to a time lag of 1 year between the fishing down of the high density aggregations and recruitment from medium density aggregations. Thus, as cod abundance declines, the areal extent of high density groups remains unchanged, whereas that of the medium and low density areas would be expected to decline and increase, respectively. Somewhat similar observations have been made for southern Gulf of St. Lawrence cod for which the area containing 50% of the population remained constant despite declines in stock abundance (Swain and Sinclair 1994).

When cod abundance has declined to a level at which the recruitment of cod from medium density areas is unable to replace those fished from high density aggregations (this would correspond to time t^* in eqs. 1–3 at which the threshold percentage of medium density areas had been reached), the high density aggregations begin to disappear and catch rates in high density areas begin to decline. Prior to time t^*, as stock biomass declines, fixed-gear fisheries exploiting cod at medium and low densities would be predicted to experience declining catch rates while trawler catch rates remained high. Perhaps most importantly, after several years of declining fish abundance in medium density areas, the nested aggregation model predicts that the areal extent of cod will become limited to a few, highly dense aggregations. Again, this is consistent with empirical data. Between 1989 and 1991, 50–60% of the estimated survey biomass of northern cod was located in these few highly dense groups (i.e., >500 kg/tow) compared with an average 21% from 1981 to 1985, rendering the stock increasingly vulnerable to mobile fishing gear. At constant catches (the TAC for northern cod increased from 1981 to 1988 before declining slightly from 1989 to 1991), the density composition model predicted that after several years of increasing fishing mortality, F would increase rapidly. This temporal pattern in F has also been estimated by VPA (Bishop et al. 1994) and by tagging data (Myers et al. 1995*a*).

The spatial model of northern cod aggregations presented here (*i*) provides a framework for explaining changes in the density composition of cod in the 1980s and early 1990s, (*ii*) provides an explanation for the observed divergence in fixed-gear and mobile-gear catch rates that began in the mid 1980s (Hutchings and Myers 1994*a*), (*iii*) accounts for the curvilinear relationship between trawler catch rate and harvestable biomass of northern cod (Hutchings and Myers 1994*a*), and (*iv*) suggests that the behaviour of forming high density aggregations increases the vulnerability of northern cod to fishing gear as stock size declines, thus providing one reason why fishing mortality increased so rapidly in the late 1980s and early 1990s. The nested aggregation model represents one possible framework for the changes in stock density composition documented in the research survey data. It may be possible to use the survey data to estimate the probability with which alternative spatial models of cod aggregation are consistent with these data.

Review of alternative hypotheses for the collapse of northern cod

From the time that a moratorium was imposed on the commercial fishery for northern cod in July 1992, there has been considerable debate over the relative importance of environmental factors and fishing to the stock's collapse. Alternative hypotheses characterize the increase in mortality of cod throughout the 1980s and early 1990s as being largely a function of increasing natural mortality, increasing fishing mortality, or some combination thereof. Many of these hypotheses have been subjected to statistical analysis, others have not. These will be reviewed briefly to place the previously described density composition and nested aggregation models, and the insights they provide about the collapse of northern cod, in a broad context.

Decline of noncommercial species

The concomitant decline of some fish species not directly targeted by fishing has frequently been cited as evidence that ecosystem change contributed significantly to the stock's collapse (Atkinson 1993; Atkinson and Bennett 1994; Department of Fisheries and Oceans 1995; Fisheries Resource Conservation Council 1995). These declines have been described from trends in arithmetic mean biomass (Atkinson 1993; Gomes et al. 1995). As discussed earlier, there can be strong limitations to the extent to which trends based upon arithmetic means reflect actual changes in stock abundance. Some researchers examining changes in fish community structure on the northeast Newfoundland Shelf have identified bycatch fishing mortality as a dominant influence of abundance changes in noncommercial species on the northeast Newfoundland Shelf (Gomes et al. 1995; Haedrich 1995). Others disagree with this interpretation, particularly with regard to the decline of American plaice, *Hippoglossoides platessoides*, in division 2J. Brodie et al. (1995), for example, argue that fishing cannot account for the decline of 2J plaice because reported catches of plaice have been low and have never reached their TAC of 10 000 t in the 1980s. One implication of this conclusion is that changes in the environment caused the natural mortality of plaice to increase dramatically in the 1980s.

Data from research surveys and commercial catches suggest that the mortality of American plaice caught as bycatch in the northern cod fishery have been considerable. For example, research survey data collected throughout 2J from 1981 to 1992 indicate that, on average, 95.1% of all tows that caught cod also caught American plaice. This suggests that the habitats of cod and plaice overlap considerably and that the

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Table 2. Associations between the incidence of American plaice, *Hippoglossoides platessoides*, and Atlantic cod, *Gadus morhua*, in research survey tows in NAFO division 2J from 1981 to 1992.

Year	Tows of cod containing plaice (%)	Regression between plaice (y) and cod (x) biomass	p	Catches of 2J plaice (t)	
				Reported	Predicted
1981	100	$y = 0.055x - 1.10$	<0.001	96	1479
1982	92	$y = 0.076x + 0.63$	0.002	204	5115
1983	77	$y = 0.181x - 0.05$	<0.001	168	7500
1984	93	$y = 0.589x + 17.1$	<0.001	92	7076
1985	82	$y = -0.040x + 2.74$	0.70	34	0
1986	92	$y = 0.075x + 2.76$	0.003	100	901
1987	71	$y = 0.172x + 2.72$	0.44	239	7196
1988	83	$y = 0.025x + 0.35$	0.003	106	1037
1989	94	$y = 0.022x + 3.42$	0.20	3225	761
1990	83	$y = 0.070x + 1.04$	<0.001	991	1295
1991	100	$y = -0.011x + 5.15$	0.47	69	0
1992	90	$y = -0.533x + 2.22$	0.19	5	0

Note: Reported catches of plaice in 2J from Brodie et al. (1995). Predicted catches of plaice in 2J were calculated from the reported catches of 2J cod by trawlers (data in Bishop et al. 1994), using the regressions between plaice and cod for strata 222 through 233, inclusive, and stratum 236 (x and y are in kilograms).

probability of catching both species together in trawl gear is very high.

Annual regressions between plaice and cod biomass can be used to estimate the biomass of plaice caught as bycatch in the fishery for cod in 2J (the value for cod biomass being the reported catch of trawlers in 2J; Bishop et al. 1994). For this analysis, the tows on which the plaice–cod regressions were based were restricted to the area encompassed by the winter trawler fishery for northern cod (Wroblewski et al. 1995), i.e., strata 222 through 233, inclusive, and stratum 236 (Table 2). From 1981 to 1992, an annual average of 88.1% of all tows that caught cod in these strata also captured American plaice.

The predicted catches of American plaice in 2J exceed the reported catches every year between 1981 and 1990 except 1985 and 1989 (Table 2). Annually from 1981 to 1984, actual catches are predicted to have been more than one order of magnitude greater than reported catches; the discrepancies were lower between 1986 and 1990. The smaller differences between predicted and reported plaice catches in the late 1980s may be attributable to the increase in observer coverage of Canadian trawlers fishing for northern cod from 20% before 1987 to 100% thereafter (Wroblewski et al. 1995). Predicted plaice catches have been underestimated in this analysis because of discarding of northern cod and because of the omittance of other 2J groundfish fisheries. Elsewhere in the northwest Atlantic, high bycatches of American plaice in the cod fishery, a problem long recognized in the Gulf of St. Lawrence (e.g., Chouinard and Metuzals 1984), have prompted the industry to request that stricter regulatory measures be imposed to reduce this nontargeted fishing mortality (e.g., Atlantic Groundfish Advisory Committee 1992).

On the basis of the survey data, then, it is logical to assume that the catching of American plaice in commercial trawls fishing for cod would have been unavoidable and that the amount of plaice captured as bycatch would have increased with increasing catches of cod. The argument that fishing cannot explain the decline of 2J plaice because of low annual ratios of (reported catch)/(survey biomass), a proxy for exploitation rate (Brodie et al. 1995), needs to be re-evaluated in light of the differences in reported and actual plaice catches predicted from research survey data.

Poor recruitment to the fishery

Northern cod, and other northwest Atlantic cod stocks, were closed because of a scarcity of individuals of reproductive age, i.e., low spawner biomass. It has been proposed that a primary reason for this relative absence of spawners was an increase in the natural mortality of cod aged 1–3 years in the 1980s (deYoung and Rose 1993; Atkinson and Bennett 1994; Mann and Drinkwater 1994). This “poor recruitment” hypothesis has recently been examined for the six Canadian cod stocks for which fishing moratoria currently exist. Using research survey data, Myers et al. (1996*a*) tested the null hypothesis that recruitment of those year-classes that would have dominated the spawner biomass at the time of the moratoria (collapse recruitment) was not significantly different from the average annual recruitment preceding those year-classes (precollapse recruitment). This hypothesis could not be rejected for five of the six stocks examined. The only stock for which the precollapse recruitment exceeded the collapse recruitment was the southern Grand Bank stock (divisions 3N–3O), much of which exists outside Canada’s 200-mile limit. Declining recruitment in southern Grand Bank cod in the late 1980s would appear to be the result of the fishing gear used by foreign trawlers that caught disproportionately high numbers of 2- and 3-year-old cod (Walsh et al. 1995). The conclusion that poor recruitment did not contribute to the collapse of cod has also been reached for the southern Gulf of St. Lawrence stock (Sinclair et al. 1995). Analyses that previously linked poor recruitment to environmental factors such as cold water temperature (deYoung and Rose 1993) and low salinity (Myers et al. 1993) have not been supported on re-examination of the data (Hutchings and Myers 1994*a*).

Increased predation by marine mammals

The influence of seal predation on the collapse of northwest Atlantic cod stocks is one area in which there is general agreement. Harp seals, *Phoca groenlandica*, which eat primarily 1- and 2-year-old Atlantic cod (Stenson et al. 1995), increased in

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abundance throughout the northwest Atlantic in the 1980s (Shelton et al. 1995). Increased predation of cod by seals should have resulted in reduced numbers of 3 year olds, i.e., recruits to the fishery in the 1980s. However, the lack of significant changes in mean recruitment between precollapse and collapse periods (see above) suggests that seals did not have a significant effect on the collapse of east coast cod stocks (Myers et al. 1996*a*). The hypothesis that seal predation was a major factor contributing to the decline of Atlantic cod has also been rejected for southern Gulf of St. Lawrence cod (divisions 4T–4Vn; Sinclair et al. 1995) and eastern Scotian Shelf cod (divisions 4Vs–4W; Mohn and Bowen 1994).

It is not clear whether predation of 1- and 2-year-old cod by seals is retarding the rate of recovery of the collapsed stocks. The only independent source of abundance data on cod aged 1 and 2 years, the research survey data, provides no evidence that mortality at these ages has changed significantly since the early 1980s (A. Sinclair, R. Myers, and J. Hutchings, unpublished data). Using a deterministic, age-structured population dynamics model, Mohn and Bowen (1994) estimated that the mortality of juvenile cod on the eastern Scotian Shelf caused by predation by grey seals, *Halichoerus grypus*, may have increased fourfold between the early 1980s and the early 1990s. The statistical power of both analyses is relatively low. Because of the paucity of abundance and mortality data on juvenile cod, there are no empirical data to support the hypothesis that the influence of seal predation on the recovery of northern cod is disproportionately greater than the influence on recruitment of other predators of juvenile cod, historically low levels of cod spawner biomass, competitors of cod for food and space (e.g., possibly Arctic cod, *Boreogadus saida*), and natural environmental variability in recruitment.

Reported and unreported catches of young cod

Recent work suggests that increased discarding of prereproductive individuals contributed to the rapidity with which the northwest Atlantic cod stocks collapsed. Myers et al. (1996*a*) noted that VPA estimates of recruitment declined with time at a significantly greater rate than did recruitment estimated from research surveys. Given that VPA abundance data are based on reported catches, Myers et al. (1996*a*) hypothesized that the negatively biased VPA estimates of recruitment could be explained by temporally increasing levels of discarding and catch misreporting of pre-reproductive cod. Their hypothesis was supported by the observation that the rate of increase in mortality of 3-year-old cod, as estimated from research surveys, with VPA-based fishing mortality of cod fully recruited to the fishery was significantly greater than the rate of increase in 3-year-old cod mortality estimated by VPA. The hypothesis is based on the premise that as stock abundance declines, it becomes increasingly difficult to catch large fish. The increased effort required to maintain catch levels would result in increased catches of undersized fish, which cannot be sold, that are then discarded and then excluded from the catch data upon which VPA data are based, leading to negatively biased estimates of past abundance. A limited number of interviews with trawlermen and fishery observers (Eco-Research Programme, Memorial University of Newfoundland, unpublished data) indicate that discard estimates for trawlers in the northern cod, purportedly less than 2% by weight in the late 1980s (Kulka 1989), have been seriously underestimated. Reports from Department of Fisheries and Oceans port technicians provide additional evidence that official trawler discard data for northern cod are negatively biased. One such report, dated 24 December 1990, noted that trawlers fishing northern cod in 2J were "having to catch 500K [thousand], discarding 300K undersize, to get 200K legal size 2J cod" (Angel et al. 1994, p. 102). Widespread catch misreporting and discarding have been reported for the trawler fisheries for the northern (Palmer and Sinclair 1996) and southern Gulf of St. Lawrence cod (Sinclair et al. 1995) and the eastern Scotian Shelf (Angel et al. 1994) cod fisheries.

The inshore trap fishery was another source of high fishing mortality on pre-reproductive cod. Trap selectivity studies indicate that the percentage of trap catches (by number) that comprised undersized cod (cod less than 41 cm, approximately 3–4 years old, are generally not marketable in Newfoundland) can range from as little as 25% (e.g., Cape Broyle in 1990) to as much as 87% (e.g., Torbay in 1991) (Brothers and Hollett 1991; Brothers and Peddle 1991). Estimates of discarding in the trap fishery have been obtained from interviews with 45 fishermen south of St. John's (Cape Broyle) west to Fogo, Notre Dame Bay (J.A. Hutchings and M. Ferguson, unpublished data). All fishermen interviewed indicated that they discarded undersized cod from their traps. By weight, the average estimated discarding rate per trap haul averaged 17% and ranged from 10 to 50%. Comparing discarding rates between the early and late 1980s, inshore fishermen in some areas indicated that discarding may have more than doubled during this period because of the decline in abundance of larger, older cod.

The decline in availability of larger cod in the late 1980s and early 1990s is evident from the reported catch statistics for the northern cod fishery in 1990 and 1991 (Bishop et al. 1993). Until 1990, the decline of northern cod was partially masked in the commercial catch statistics by the extremely strong 1981 year-class (this cohort produced the highest absolute recruitment since 1968). This is evident from the observation that the catches produced by this year-class in the late 1980s were the highest since the early and mid-1970s. For example, the numerical catch of 5-year-old cod in 1986 was the highest since 1973, the 1987 and 1988 catches of 6 and 7 year olds were the highest since 1974, and the 1989 catch of 8 year olds was the highest since 1975. By contrast, the 1990 and 1991 commercial landings were dominated by cod aged 3–5 years. The 1986 year-class produced the largest catches of 4 and 5 year olds since 1977 and 1973, respectively; in 1991, the 1987 year-class contributed the highest catches of 3 year olds since 1976. One direct consequence of this overexploitation of 3, 4, and 5 year olds in 1990, 1991, and 1992 is that northern cod spawner biomass has remained at historically low levels into the mid-1990s despite the fishing moratorium.

Environmental–ecosystem changes and the role of fishing in the collapse of northern cod

Hypotheses linking the collapse of northern cod to environmental or ecosystem change bear the implicit assumption that environmental conditions in the late 1980s and early 1990s were temporally anomalous, given that collapses of the magnitude documented in 1992 have never been previously recorded. A comparison of various environmental indices on a decadal and on a century time scale indicate that the environ-

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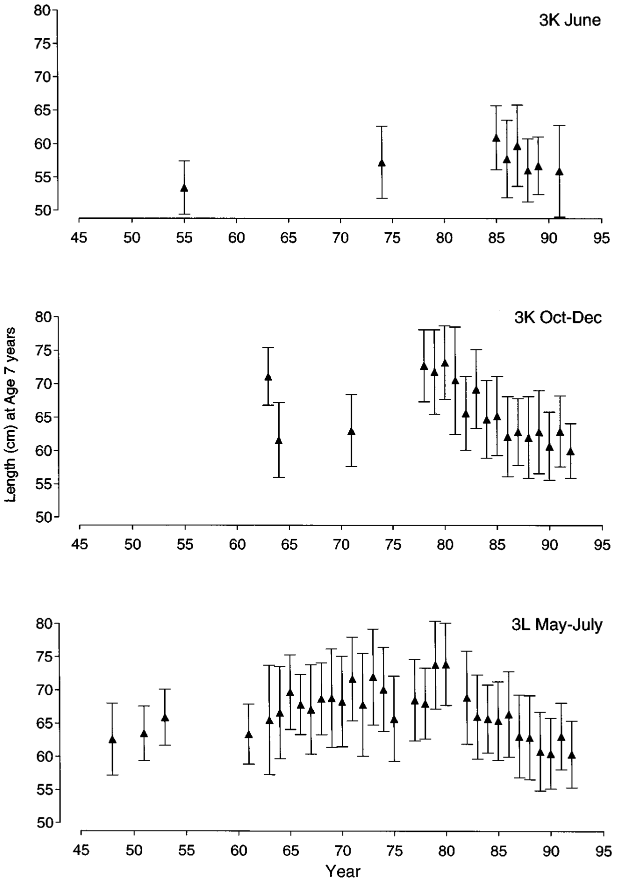
Fig. 11. Long-term temporal changes in mean length-at-age for northern cod aged 7 years. Data are for research cruises conducted in June in 3K (1955 to 1991), between October and December in 3K (1963 to 1992), and from May through July in 3L (1948 to 1992). Error bars represent one standard deviation.



mental conditions experienced by northern cod since the late 1980s have clearly been experienced by the stock in the past. For example, water temperatures recorded on the northeast Newfoundland Shelf were not temporally anomalous in the early 1990s. The same is true of water temperatures in the Gulf of St. Lawrence (Sinclair et al. 1995), Cabot Strait, and the Scotian Shelf (Drinkwater et al. 1995). Although low, the depth-averaged water temperatures recorded at a hydrographic station east of St. John's (station 27) in 1991 did not differ statistically from those in 1972–1974 and 1984–1985; bottom and near-bottom temperatures at this station were, in fact, lower in these two previous time periods (Hutchings and Myers 1994*a*). In addition, the volume of water less than 0°C (the cold intermediate layer or CIL) in 1990 and 1991 off southern Labrador was actually lower than it was in 1972 and in 1985; the 1990–1991 CIL volume further south off Cape Bonavista was also less than the CIL volume in 1985 and comparable with that recorded in this area in 1972 (Colbourne 1995).

Data available over a considerably longer time scale (e.g., water temperatures on Grand Bank since 1910, ice clearance data from Labrador since 1800, air temperature data from St. John's since 1874, the latter two of which are significantly associated with water temperature at station 27) indicate that northern cod catches of the size that were not sustainable in the 1980s were sustainable in the 19th and early 20th centuries in an environment that was, on average, considerably colder (Hutchings and Myers 1994*a*). In addition to its rejection on statistical grounds (Hutchings and Myers 1994*a*), the hypothesis that cold water temperatures cause poor recruitment does not bear up well under the observation that recruitment of St. Pierre Bank cod (division 3Ps) in the 1980s was not affected by a massive 2°C decline in water temperatures, from an average of 1 to –1°C, in 1985 (January through June average temperature at 50 m; Hutchings and Myers 1994*b*); there is no evidence of a similar decline in temperature in 2J3KL (Hutchings and Myers 1994*a*; Colbourne 1995). The description of oceanographic conditions in the early 1990s as temporally anomalous is unjustified on the basis of time series of several water temperature data.

There is, to date, no direct evidence linking the decline of northern cod to changes in the environment or ecosystem. Any effect of temperature or salinity on recruitment can be rejected on statistical grounds (Hutchings and Myers 1994*a*). The null hypothesis that cod did not shift their distribution southward in 1989 or 1990 (one purported response to environmental–ecosystem change; deYoung and Rose 1993; Rose et al. 1994) cannot be rejected by empirical data. As discussed earlier, neither the research survey data, age-specific growth data, tagging experiments, or spatial-temporal analyses of DNA indicate that cod shifted their distribution southward in the late 1980s or early 1990s. Lilly (1995) reported that there is no evidence that average stomach fullness of cod declined before or in parallel with the decline of northern cod. This argues against the hypothesis that a severe decline in prey abundance contributed to the cod collapse (Atkinson and Bennett 1994).

The argument that the collapse of northern cod can be attributed to an interaction between overfishing and a deteriorating environment (reflected by declining age-specific body sizes) has suffered from Pauly's (1995) "shifting baseline syndrome of fisheries." Time series of weights at age used in such analyses almost always begin in the late 1970s or early 1980s (e.g., Bishop et al. 1994; Taggart et al. 1994); however, if the time series is extended to include age-specific body sizes over all years for which such data are available, it is apparent that it is the large age-specific body sizes of the late 1970s and early 1980s that are anomalous (Fig. 11). (The similarity in temporal trends within 3K and between 3K and 3L suggests that these data are not unduly biased by small-scale spatial differences in sampling.) The decline in weight at age observed through the 1980s may be attributable to the increased rate of harvesting of the fastest growers within each cohort. Consistent with this hypothesis are the observations that the high age-specific body sizes measured in the late 1970s and early 1980s coincided with the time period during which cod experienced the lowest offshore fishing mortality since the early 1960s (Bishop et al. 1994; Myers et al. 1995*a*). In addition, the physical oceanographic environment of the late 1970s and early 1980s (e.g., water temperature; Hutchings and Myers 1994*a*) was not notably favourable for growth. The inability to detect an environmental influence on cod mortality does not mean, of course, that the environment has no effect on cod production. It would seem reasonable, however, on the basis of available data for northern cod and its environment, to conclude that such an

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effect has been small relative to the influence of fishing mortality.

It has been suggested that the collapse of northern cod occurred suddenly over a single year, the spring of 1991 being the favoured time (Lear and Parsons 1993; Atkinson and Bennett 1994). As discussed earlier, there is good reason to believe that this perception can be partly attributed to the use of trends in arithmetic mean biomass as a primary indicator of stock abundance. Other metrics, such as the geometric mean biomass, the rank-based biomass trend, and the spatial distribution of cod biomass through 2J3KL (Figs. 6–8), indicate that the decline of northern cod was gradual rather than abrupt. The decline in the percentage composition of medium density research survey tows also clearly indicates a decline in cod abundance throughout the 1980s (Fig. 2). The decline in fixed-gear catch rates, evident since the mid–1980s, suggests that the stock had been decreasing since at least 1985 (Hutchings and Myers 1994*a*). The dramatic spatial shift in the gill-net fishery in the mid–1980s from inshore to offshore waters in response to declining catch rates is further evidence of a decline prior to the 1990s (Hutchings and Myers 1994*a*, 1995).

There is considerable evidence, then, to support the hypothesis that overfishing was the primary, if not sole, cause of the collapse of the northern cod. The northern cod decline occurred gradually throughout the mid-1980s (Hutchings and Myers 1994*a*; present paper) at the same time that offshore (Hutchings and Myers 1994*a*) and inshore (Neis et al., see footnote 2) fishing effort was increasing (a description of temporal changes in gear technology in the northern cod fishery is provided by Hutchings and Myers 1995). Northern cod were not sustainable at the age-specific rates of survival and fecundity experienced between 1985 and 1992 (Hutchings and Myers 1994*a*). Statistical analyses of catch-at-age data for northern cod provide no evidence of an increase in natural mortality of northern cod in 1991 (Myers and Cadigan 1995*a*, 1995*b*). One of the strongest sources of evidence that fishing mortality was excessive are the estimates of fishing mortality derived from tagging studies, which indicate that F on northern cod had exceeded 1.0 by the late 1980s (Myers et al. 1995*a*; 1997). The primary role of overfishing has also been accepted as an explanation for the collapse of southern Gulf of St. Lawrence cod for which trends in environmental factors and seal abundance were inconsistent with trends in cod mortality (Sinclair et al. 1995). The absence of depensation in stock-recruitment data from 125 commercially fished stocks is generally consistent with the hypothesis that stock collapses worldwide can be attributed primarily to fishing, rather than nonfishing, sources of mortality (Myers et al. 1995*b*).

Conclusions

The observation that over 90% of the world's fish stocks have been overexploited (Alverson et al. 1994) suggests either that the effects of fishing on exploited populations are constantly and consistently underestimated (i.e., poorly understood) or that their effects are well known but management agencies lack sufficient authority to control harvesting levels. In the case of Canadian cod stocks, the former condition would appear to hold true.

The inability to control fishing mortality that led to the collapse of Canada's groundfish stocks underscores a general lack of knowledge of the effects of different gear on the fishing mortality of targeted and nontargeted fish species. There is a need for a research initiative the objectives of which would be to quantify the size and age selectivities of all species caught by (*i*) gear type (e.g., otter trawl, gill net, trap, hook and line); (*ii*) gear characteristics (e.g., time period of gear usage, mesh size, trap and trawl design, type of hook and bait); (*iii*) time of day; (*iv*) time of year; and (*v*) geographical characteristics of the fishing grounds (e.g., proximity to land (inshore vs. offshore), bottom substrate (sand, boulder), water depth).

These data would allow one to assess a priori the risk of fishing mortality for nontargeted species by factors such as gear and region. For example, total allowable catches for species *a*, based on factors such as gear, vessel size, and season, could include bycatch probability estimates for species *b, c, d,* etc. From a conservation perspective, inclusion of such bycatch estimates in the quota would reduce the threat imposed on fish stocks by practises such as misreporting and dumping of catches. Comprehensive knowledge of the age- and size-specific vulnerabilities of targeted and nontargeted species to various gears (by mesh size, by season, by bottom substrate) would enable managers to select gear types, fishing seasons, and fishing areas in such a way as to minimize the capture of immature and (or) undersized, unmarketable individuals.

Failure to recognize the decline in northern cod biomass from the mid–1980s can be partly attributed to the use of catch rates by commercial trawlers as a metric of stock abundance (Baird et al. 1991). Although the research survey biomass index suggested that the stock had changed little in size between the early and late 1980s, the density composition data provided by the research surveys indicate that the survey biomass index was positively biased. I suggested earlier that this could be attributed to the use of annual arithmetic means to interpret temporal trends in biomass or to an overrepresentation of high density tows attributable to survey design bias. To increase the probability of detecting true changes in stock biomass, the use of alternative abundance estimators from the research survey data (e.g., geometric mean, rank-based means, median) should be encouraged.

It is also evident, for the northern cod fishery, that declining abundance was reflected by decreasing fixed-gear catch rates (Hutchings and Myers 1994*a*). These data clearly have the potential to provide an abundance metric for northern cod. The use of fixed-gear catch rates would also involve considerably closer interactions between fishers and the Department of Fisheries and Oceans than have existed in the past. One consequence of such stronger communications would be recognition of the scientific value of fishers' local knowledge (Neis 1992; Neis et al., see footnote 2). For example, local knowledge of the dates when fish are caught in fixed-gear locations can provide data on seasonal and directional movements of cod (and other fishes) in inshore waters, information for which there presently are no biological data. With respect to stock identification, fishers can provide information on temporal and spatial isolation of cod populations through identification of overwintering grounds (capture of cod through ice), spawning areas (presence of females and males in ripe and running condition), juvenile habitat (bycatch of young cod in caplin traps), morphological characteristics, and seasonal migrations. Thus, in addition to serving as partners in management strategies, inshore fishers can provide a wealth of information upon which hypotheses concerning the biology of cod can be formulated and tested and upon which juvenile and spawning areas (possible candidates for future protection) can be identified.

Seasonal or permanent closure of marine habitat (marine protected areas or MPAs; Shackell and Willison 1995) may increase the likelihood that commercially exploited fish populations can be maintained at sustainable levels. Seasonal fishery closures, particularly during periods of high catch rates, can act as a conservation measure by reducing overall fishing mortality. This was the basis for implementing seasonal spawning area closures for haddock, *Melanogrammus aeglefinus*, on Browns and Georges Banks southwest of Nova Scotia (Halliday 1987). Hutchings (1995) explored the usefulness of seasonal fishing closures on the northern cod fishery. He suggested that an offshore fishing ban on northern cod from January through May, the months coinciding with the highest catch rates associated with the fishing of spawning and prespawning aggregations, would conform to historical fishing patterns in this fishery and would re-establish the temporal and spatial refuges experienced by this stock prior to the 1950s.

Seasonal MPAs may have considerable merit when assessed against the effectiveness of other forms of regulatory control such as bycatch limitations and catch quotas. Enforcement of areal closures would be more cost effective and certainly easier to enforce than quota restrictions, compliance being determined by an absence of vessels fishing for cod. Although it has not been demonstrated that the prohibition of trawling of spawning northern cod is of intrinsic biological benefit, such a benefit cannot be justifiably discounted. If trawling disrupts the complex behavioural dominance hierarchies evident during spawning (Brawn 1961; J.A. Hutchings and T. Bishop, unpublished data), such fishing activity may reduce the number of matings per individual and deleteriously influence recruitment. It may be noteworthy, for example, that the exceptionally strong year-classes of northern cod between 1978 and 1981, the highest recruitment since the late 1960s (Bishop et al. 1994), coincided with the lowest level of trawling effort observed since the late 1950s (Hutchings and Myers 1994*a*, 1995). Despite its clear management implications, research on the effects of trawling on cod reproductive behaviour and fertilization success has yet to be undertaken.

The changes in density composition of northern cod documented here may provide useful and unambiguous criteria for re-opening the fishery. These data suggest that the re-opening of the fishery should not be considered until the percentage of high density autumn research survey tows (i.e., tows catching more than 500 kg of cod) reaches 2% of the total (Fig. 2). Once this criterion has been attained, the percentage of medium density tows (tows catching between 100 and 500 kg) should be allowed to increase to at least 20%. This density composition of northern cod would correspond roughly to the size of the stock in the early 1980s (Fig. 2) and should safely permit an annual harvest of northern cod of 100 000 to 150 000 t. One implicit assumption in using this criterion is that the density-dependent changes in the distribution of cod during stock recovery will mirror those observed during the stock decline. Density criteria could then be used in conjunction with a criterion stipulating that the fishery remain closed until the age-frequency distribution of cod sampled in the research surveys matched those observed during a period of comparatively high cod abundance.

There may be considerable merit in examining research survey data sets from other Atlantic cod stocks to model density-dependent changes in spatial structure (e.g., Myers and Stokes 1989; Swain and Wade 1993; Swain and Sinclair 1994), to assess the extent to which cod spatial structure can influence vulnerability to overexploitation, and to determine whether the density composition data for other stocks suggest criteria for re-opening these fisheries similar to those proposed for the northern cod fishery.

When will northern cod recover? This depends on one's definition of what constitutes a recovery. Population biologists would argue that a recovery would constitute a return of northern cod to its historical level of abundance. On the basis of the earliest available data from the early 1960s, such a recovery can be said to have occurred when spawner biomass exceeds 1.5 million t (it was probably less than 50 000 t in 1994) and recruitment exceeds 1 billion 3-year-old cod (Hutchings and Myers 1994*a*). However, the time scale for such a recovery unquestionably numbers in the decades and socioeconomic and political pressures (notwithstanding potentially important biological changes in the relative abundance of other species) will not permit such a period of time to elapse before the fishery is re-opened.

In the interim, it is critical that every effort be made to answer the dominant question that emerges from the review presented herein and on which future fisheries research, and the prevention of future fishery collapses, arguably hinges: What are the effects of fishing on the behaviour, life history, and population biology of exploited fishes?

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