# Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined

G.A. Rose and D.W. Kulka

**Abstract**: Misinterpretations of elevated catch-per-unit-effort (CPUE) in the northern cod (*Gadus morhua*) fishery contributed to overestimations of stock size, inflated quotas, and unsustainable fishing mortality in the 1980s and early 1990s. We hypothesize that concentration of the fish and fishery led to extreme hyperstability in the CPUE–abundance relationship. In the late 1980s, migrant cod began to concentrate within the Bonavista corridor, their most southerly cross-shelf migration route. By the spring of 1990, approximately 450 000 t was concentrated within 7000 km$^2$ at densities quadruple those of the 1980s. Densities remained high through 1992, while abundance declined fivefold. During this period, cod hyperaggregated (local densities increased with decreasing biomass) in the Bonavista corridor and CPUE increased. To the north, no hyperaggregation occurred, and densities and CPUE declined with biomass. In the Bonavista corridor from 1990 to 1993, CPUE was hyperstable with local cod density. Areas of high cod densities (>0.1 fish·m$^{-2}$) shrunk as regional estimates of cod biomass declined. The spatial extent of the fishery contracted proportional to the shrinkage in area occupied by the fish. Hence, CPUE was related to abundance at the local scales of a fishing set (local acoustic density) but not to abundance at regional or stock scales.

**Résumé** : En raison d'interprétations erronées de l'indice élevé des captures par unité d'effort (CPUE) qui était observé dans la pêche à la morue franche (*Gadus morhua*) du Nord, on a surestimé la taille du stock, fixé des quotas exagérés et enregistré une mortalité par pêche non durable dans les années 80 et au début des années 90. Nous posons que la concentration des poissons et de la pêche a entraîné une hyperstabilité extrême du rapport CPUE–abondance. À la fin des années 80, la morue migrante a commencé à se concentrer dans le corridor de Bonavista, sa voie migratoire la plus méridionale en travers de la plate-forme continentale. Dès le printemps 1990, environ 450 000 t de morue étaient concentrées sur une superficie de 7000 km$^2$, avec des densités quatre fois supérieures à celles relevées dans les années 80. Les densités sont demeurées élevées jusqu'en 1992, tandis que l'abondance était cinq fois plus faible. Pendant cette période, on a noté une hyperagrégation de la morue (les densités augmentaient localement avec la baisse de la biomasse) dans le corridor de Bonavista, et l'indice CPUE a augmenté. Vers le nord, il n'y avait pas d'hyperconcentrations de morue, et les densités et l'indice CPUE diminuaient avec la biomasse. Dans la corrider de Bonavista, de 1990 à 1993, l'indice CPUE était hyperstable par rapport à la densité locale de la morue. Les aires à densité élevée (>0,1 poisson·m$^{-2}$) se sont resserrées à mesure que les estimations de la biomasse régionale de morue diminuaient. L'étendue spatiale de la pêche a diminué de façon proportionnelle au rétrécissement de l'aire occupée par les poissons. Donc, l'indice CPUE était lié à l'abondance à l'échelle locale d'un trait de pêche (densité acoustique locale) mais pas à l'échelle de la région ou du stock.

[Traduit par la Rédaction]

## Introduction

The decline of the northern cod (*Gadus morhua*) stock off Newfoundland and Labrador was almost certainly precipitated by overfishing (deYoung and Rose 1993; Rose et al. 1994). However, the conclusion that overfishing acted in isolation from ecological factors, and without major changes in cod distribution (Hutchings and Myers 1994; Hutchings 1996), is questioned in this paper. We propose that changes in the spatial distribution of cod not only contributed to the overfishing but also to inappropriate interpretations of catch-per-unit-effort (CPUE) from the offshore trawler fishery.

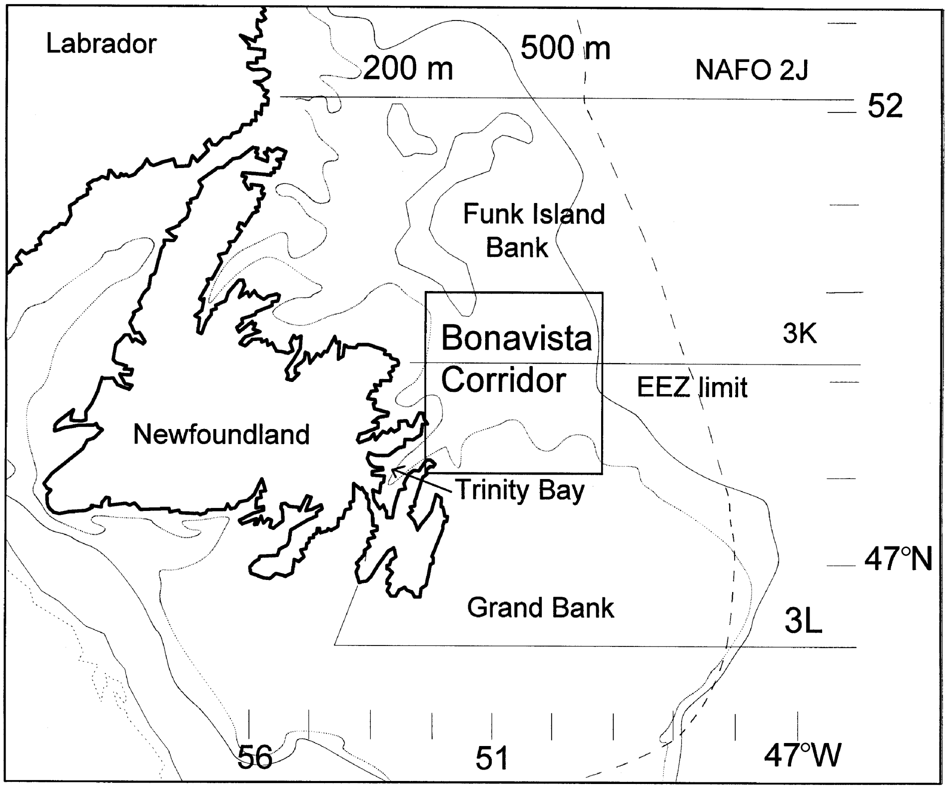
Analytical assessments of the northern cod in the 1980s employed CPUE of the mobile winter trawler fisheries under the assumption that this index would be linearly related to stock size at the scale of the full stock. However, the assumption of linearity between catch rates and stock size has been questioned for over 30 years (Paloheimo and Dickie 1964). For pelagic shoaling fishes such as the clupeids, it is widely acknowledged that CPUE is unlikely to reflect abundance because local densities are behaviorally determined (reviewed by Winters and Wheeler 1985). Early in the development of the winter trawler fishery for cod in Newfoundland waters, which targeted prespawning and spawning

Received October 17, 1997. Accepted September 8, 1998.
J14262

**G.A. Rose.**[1] Fisheries and Marine Institute, Memorial University of Newfoundland, St. John's, NF A1C 5R3, Canada.
**D.W. Kulka.** Department of Fisheries and Oceans, Science Branch, St. John's, NF A1C 5X1, Canada.

[1] Author to whom all correspondence should be addressed. e-mail: grose@caribou.mi.mun.ca

**Fig. 1.** Newfoundland region and Bonavista corridor study area.



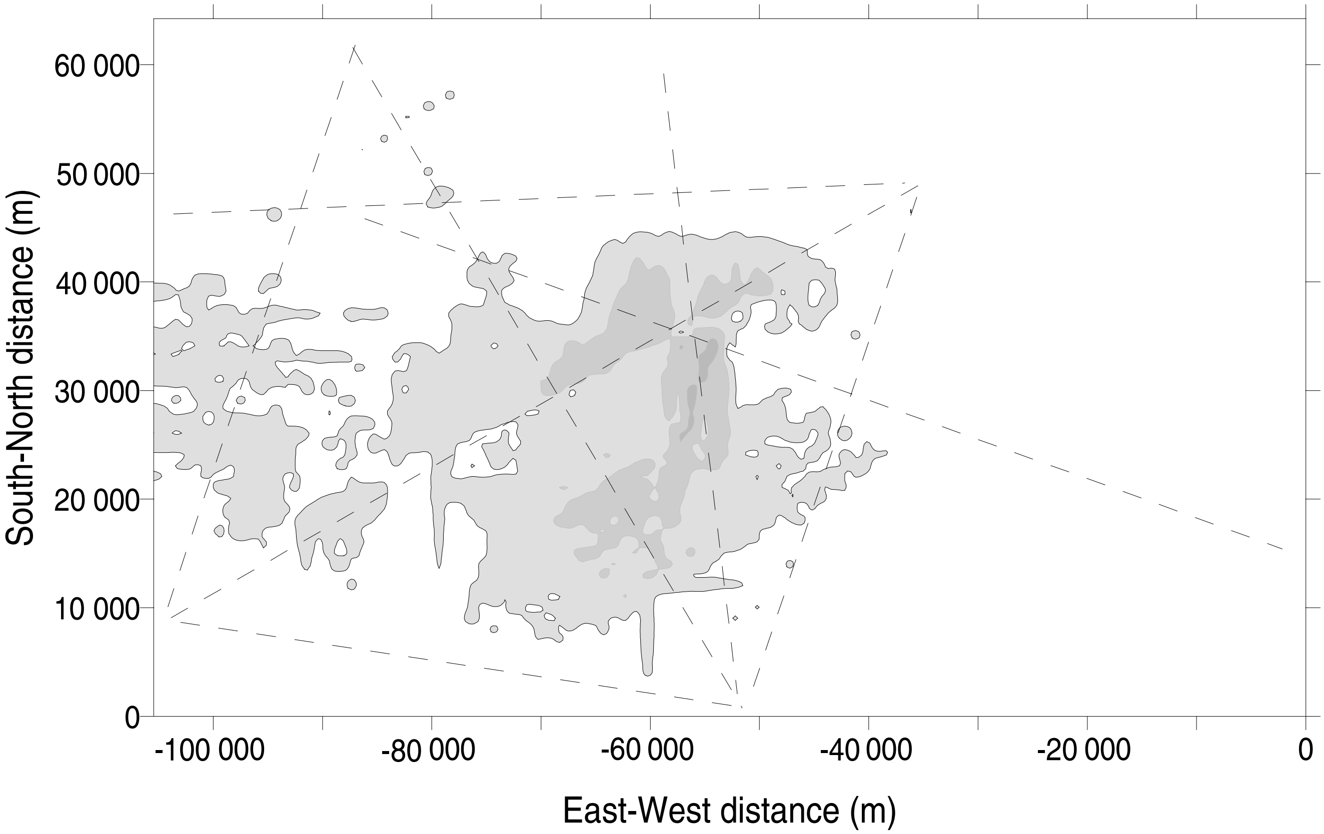
aggregations, Templeman (1966) recognized that CPUE was unlikely to track abundance changes for similar reasons. Two decades later, the lack of linearity between CPUE of cod fisheries employing moveable gear (gillnet) and fish abundance was demonstrated in experimental work by Rose and Leggett (1989, 1991). Nevertheless, attempts to use CPUE as a stock abundance index in analytical assessments continued well into the 1990s (e.g., Bishop et al. 1993).

We hypothesize that changes in spatial patterns of abundance of demersal fish can bring about changes in CPUE and catchability (ratio of CPUE to abundance). Catchability must be constant for CPUE to form a useful index of abundance. Changes in the spatial distribution of the northern cod have occurred since the late 1980s, coincident with the period of steepest stock decline (deYoung and Rose 1993; Kulka et al. 1995; Warren 1997). Rose et al. (1994) argued that these distribution changes may have played a role in the rate of decline of this stock. According to this argument, southward movements of cod increased their vulnerability to the inshore and offshore Canadian fisheries in the early 1990s (until the moratorium on fishing within the Canadian zone) and to the Spanish trawler fleet that began fishing adjacent waters outside the Canadian Exclusive Economic Zone in 1990 (Rose et al. 1994). Atkinson et al. (1997) concluded that beginning in the late 1980s, the extant stock may have aggregated in their southern range at densities well above historic norms. Accordingly, increased vulnerability to contemporary fishing practices (both legal and illegal, Canadian and foreign) could have brought about an abrupt decline of the stock both before and after the moratorium in Canadian waters (Rose et al. 1994). Alternatively, several workers have discounted the importance of widespread spatial change to the overfishing of the northern cod (Hutchings and Myers 1994; Hutchings 1996), and others have taken no account of it (Hilborn and Walters 1992; Walters and Maguire 1996).

The decline of the northern cod since the 1960s occurred progressively from north to south (Taggart et al. 1994). In the early 1990s, the last observed concentration on the northeast Newfoundland shelf was located in the "Bonavista corridor," which is the most southerly cross-shelf migration route for this stock (Rose 1993) (Fig. 1). Both inshore and offshore fisheries were concentrated in the Bonavista corridor and in the adjacent areas during this period of cod decline. Although the corridor was undoubtedly used by cod in their historic onshore migrations, as evidenced by a concentration of inshore fisheries at its shoreward reach (e.g., Lear et al. 1986), the corridor was utilized heavily from 1990 to 1992 (Rose 1993; Rose et al. 1995; Colbourne et al. 1997). However, by 1993, no migrating fish were located in this area (Rose 1996).

In the present paper, we use acoustic and trawl survey data and observer records from the offshore fishery to examine the changing spatial patterns of the northern cod from 1983 to 1993 and their relationship to CPUE from the offshore fishery. We test for hyperstability of CPUE (sensu Hilborn and Walters 1992) relative to biomass at several scales and to local density and also for hyperaggregation, defined as an inverse relationship between local densities and stock abundance. For the period 1990–1993, for which more detailed data are available for the Bonavista corridor, we investigate how biomass, densities, and range changed in

**Fig. 2.** Acoustic densities of the northern cod in the Bonavista corridor study area, 1990. Acoustic transects are shown as broken lines. Densities are shaded in three tones from light to dark (0.1–0.5, 0.5–2.5, and 2.5–5 fish·m$^{-2}$).



a rapidly declining cod population and how fishing patterns and CPUE were influenced by fish spatial distribution dynamics.

## Methods

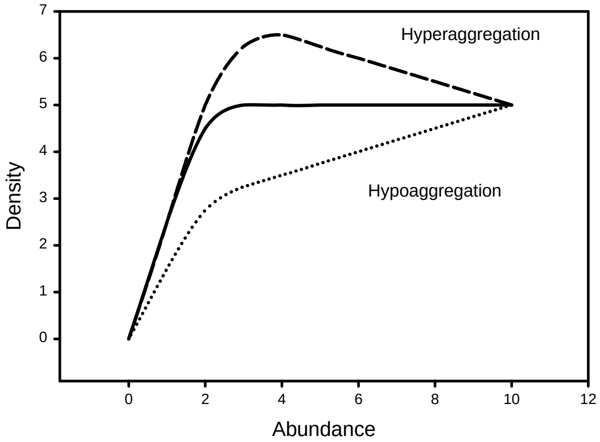
Acoustic searches for cod were conducted in springtime (May–July) annually from 1983 to 1994 in the area bounded by 48°00.0′–50°00.0′ N and 050°00.0′–053°00.0′ W (this region approximates the Bonavista corridor) (Fig. 1). The area comprises a deep (300–400 m) basin between the northern edge of the Grand Bank and the Funk Island Bank, which funnels into the deep waters off Trinity Bay. The Bonavista corridor forms part of Northwest Atlantic Fisheries Organization (NAFO) division 3L, which is the southernmost part of the range of this stock. The full stock range includes NAFO divisions 2J, 3K, and 3L, hereafter 2J3KL, commonly referred to, and managed, as the singular "northern" stock (there is ample evidence to suggest that several populations comprise the northern stock; see review in deYoung and Rose 1993). In all years, the acoustic searches were conducted from the 80-m RV *Gadus Atlantica* by staff of the Northwest Atlantic Fisheries Centre, St. John's, Nfld. Scientific echosounders (Simrad EK400 or BioSonics 102 with 49- or 38-kHz transducers deployed from a towed body) and an Engels high-rise bottom trawl were used. Although until 1990, acoustic search patterns did not cover the full study area each year, in all years, large cod aggregations were located, measured acoustically, and sampled with the bottom trawl in short-duration sets (5–15 min). From 1983 until 1989, the chief purpose of the work was to tag cod, whereas from 1990 until 1992, quantitative acoustic surveying and tagging were undertaken together, and in 1993 and 1994, only quantitative acoustics were undertaken because there was no fishery from which tags would be returned. The fisheries-independent research vessel data reported here are catch rates by weight standardized to a 30-min fishing duration.

The Bonavista corridor study area was surveyed comprehensively using scientific echosounders (BioSonics, Inc., model 102 dual-beam, 38 kHz) each June from 1990 to 1994 (Fig. 1). Echosounders were calibrated using tungsten carbide standard reference spheres (MacLennan and Simmonds 1992). Surveys were conducted from two vessels, the *Gadus Atlantica* and the 60-m *Petrel V.* Acoustic sampling was similar in all years. A randomized grid was run over the area. Located cod aggregations were crisscrossed (producing one plane of density data) as many times as possible before the aggregation shifted position. The number of transects varied as a consequence of migration behaviors (Rose et al. 1995). However, a minimum of four transects across the aggregation, and several others adjacent to it, were used to create a density map (e.g., Fig. 2). Note that very high densities of cod attributable to spawning behavior, especially the case in 1992, have not been included in this paper. In all years, cod were in their migratory phase and demonstrating similar behavior (e.g., Rose 1993). All acoustic work was supported by bottom and midwater trawling for species identification, size, reproductive condition, and other biological information (e.g., Rose and Porter 1996).

Data were integrated at 100- or 1000-m intervals and scaled to absolute biomass (fish per square metre) using the target strength model TS (decibels) = 20 log total length (centimetres) – 66 (Rose and Porter 1996). Density maps were created using the normal kriging algorithm of Surfer (Golden Software) and density centroids calculated. To produce biomass to area data from the density maps, biomass was calculated within increasing areas surrounding the density centroid.

Fishery data have been collected in an observer program on Canadian fishing vessels since 1981 (Kulka and Firth 1987). Prior to 1987, approximately 20% of vessel-days were monitored. Since

**Fig. 3.** Descriptive model of hyper- and hypo-aggregation. Density is measured within fish aggregations or at some scale small compared with the full range of the stock. Units are relative.



1987, there has been 90–100% coverage. The full data set used here includes a total of 275 488 otter trawl sets made during the winter–spring fishery (January–July 1981–1992) in NAFO 2J3KL (Fig. 1). The subset of the data for the Bonavista corridor comprises a total of 65 702 sets made from January to July 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, and duration prior to analyses and are presented as catch rates per hour of fishing time (for full details, see Kulka et al. 1996). No search or other time is included in effort.

### Models of spatial decline

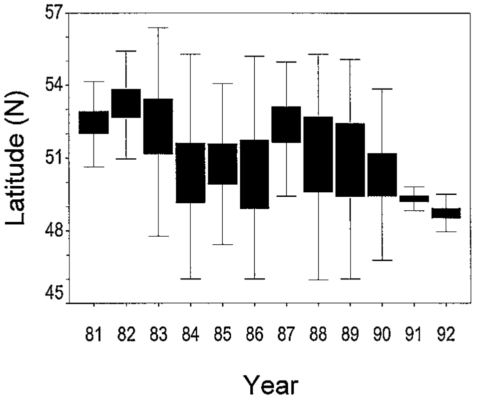
The behavior of nonsedentary fishes leads to two extremes in spatial distribution pattern dynamics (Hilborn and Walters 1992). One extreme is constant-density behavior, where range contracts and expands as abundance changes but local densities remain constant. This type of behavior is characteristic of shoaling species such as the herrings (e.g., Winters and Wheeler 1985). The other extreme exhibits relatively constant overall range but densities that increase and decrease proportional to abundance. Species that do not form shoals or show any type of aggregation behavior might display this type of behavior. These behavior types influence the likely relationship between CPUE and stock size. For example, the relationship between CPUE and abundance is said to be hyperstable if local densities tend to remain constant at the scale of the fishing (in the case of commercial otter trawls, approximately 0.1 km$^2$ or 2–3 linear nautical miles). Hyperstability is associated with constant-density behavior. At the other extreme, the CPUE – stock size relationship is hypostable if densities decline faster than abundance (associated with constant-range behavior). Stability can be tested for with the model CPUE = $a$ biomass$^b$, where $b < 1$ indicates hyperstability and $b > 1$ indicates hypostability (Hilborn and Walters 1992). It follows that density can also be termed to be hyper- or hypo-stable and similarly tested.

We introduce the concept of hyperaggregation, which we define as a negative relationship between local density and stock abundance (fish aggregate with decreasing abundance) (Fig. 3). The opposite effect, hypoaggregation, would lead to local densities declining more rapidly than stock abundance (fish disperse when fewer). Hence, as stocks decline, a hyperaggregation response would be for local densities to increase.

## Results

A full account of the shift in the spatial distribution of the northern cod in the early 1990s is beyond the scope of the present paper. However, it is important to note the southward changes in the fishery beginning in the late 1980s and the reduction in the range fished, especially after 1989 (Fig. 4). Until 1989, mean CPUE for the January–July fishing season generally increased in all zones within the historic range of the northern cod (NAFO 2J3KL) (Fig. 5). However, after 1989, CPUE within the Bonavista corridor continued to increase (Fig. 5*a*), while CPUE declined in areas to the north and south of the corridor (Figs. 5*b* and 5*c*).

**Fig. 4.** Boxplot of mean latitude of sites fished by the commercial otter trawl fleet, weighted by standardized CPUE, for the years 1981–1992 within the area inhabited by the northern cod (NAFO 2J3KL). The box encompasses the interquartile range containing 50% of the values. Whiskers extend from the highest to lowest values excluding outliers.



Fisheries-independent measures of cod densities in the Bonavista corridor (research trawl CPUE) were relatively stable from their inception in the spring of 1982 until 1989 (Fig. 6). However, in 1990, densities increased abruptly to levels fourfold those recorded in the previous decade. Elevated densities continued through 1991 and 1992, but in 1993 the CPUE index suddenly declined to its lowest point in over a decade.

At the scale of the full stock (NAFO 2J3KL), commercial CPUE was weakly and negatively correlated with stock biomass as estimated from the Department of Fisheries and Oceans fall bottom trawl surveys ($r = -0.45$, $P < 0.05$) (Fig. 7). However, at the smaller scales of the NAFO divisions, spatial differences were apparent. CPUE and biomass were positively correlated in the northern area (2J) ($r = 0.58$, $P < 0.05$), not correlated in the middle area (3K) ($P > 0.05$), and negatively correlated in the southern area (3L) ($r = -0.52$, $P < 0.05$). However, trends of biomass and CPUE over time may confound these relationships. Hence, year and biomass were entered as independent variables in multiple regressions with CPUE as the dependent variable for each NAFO division. A selection criterion of $P < 0.05$ was used to exclude variables from the model. Similar to the single-factor correlations, the results differed by area. For the northern area (2J), biomass had a significant and positive effect on CPUE, but year did not (Table 1). In area 3K, time had a significant and positive effect on CPUE (CPUE increased over the years). In the southern zone (3L), both time and biomass were significant determinants of CPUE, with biomass having a negative effect on CPUE.

**Fig. 5.** Standardized mean CPUE and SE from the northern cod otter trawl fishery in NAFO 2J3KL, 1981–1992, (*a*) within the Bonavista corridor study area, (*b*) to the north of the study area, and (*c*) to the south of the study area.

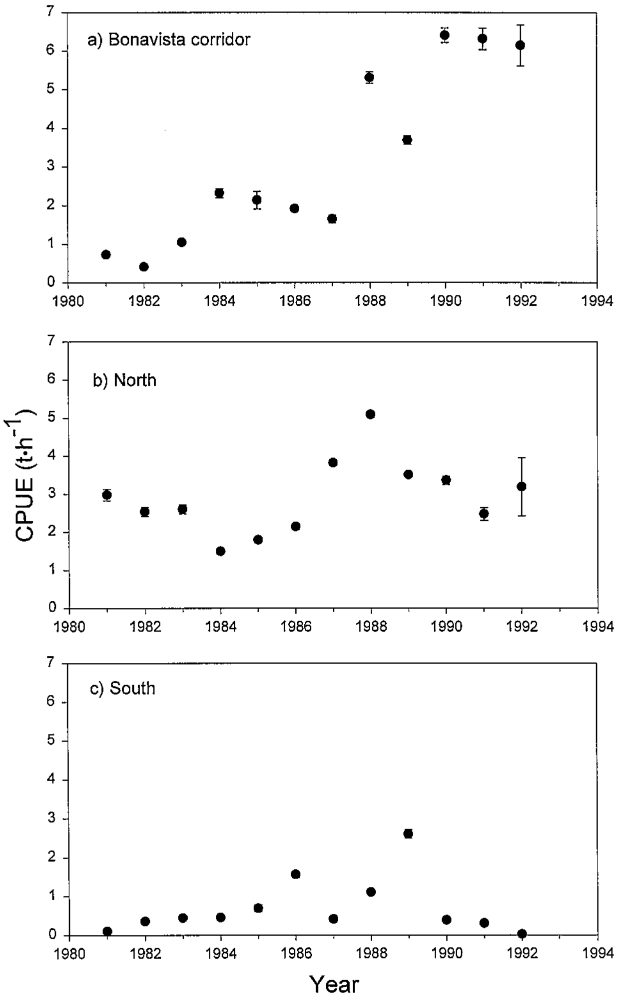


**Fig. 6.** Mean CPUE and SE, representing local northern cod density, from research trawls directed by echosoundings within the Bonavista corridor study area, 1983–1993.

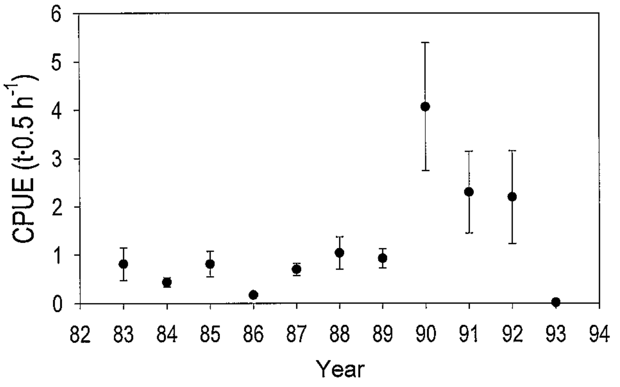
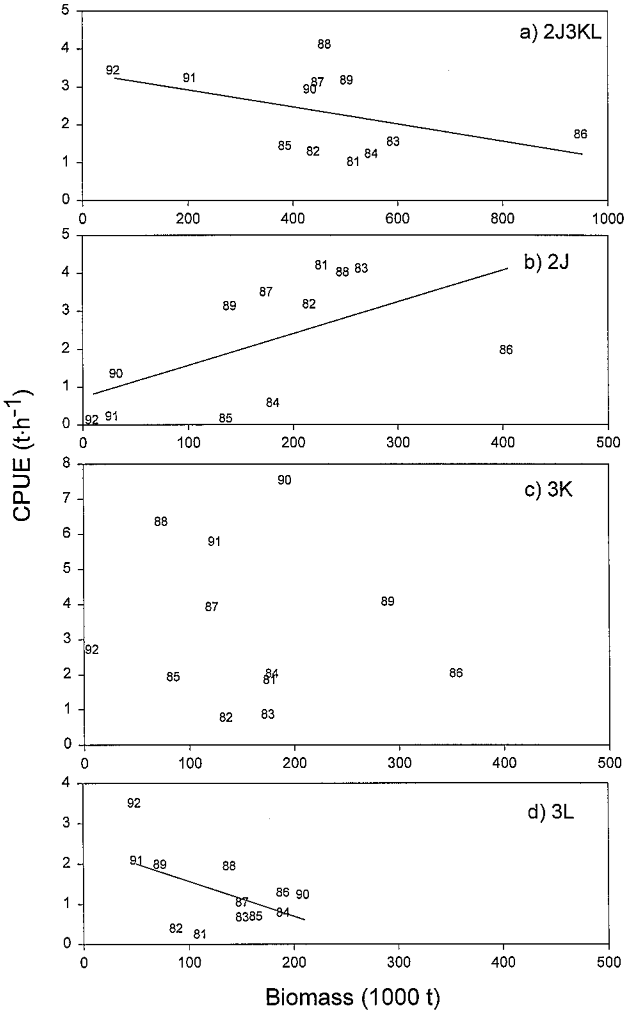


**Fig. 7.** Mean CPUE and SE for the commercial otter trawl fishery against total trawlable biomass of the northern cod stock as determined from the Department of Fisheries and Oceans fall survey, 1981–1992. (*a*) Data for the full stock (NAFO 2J3K3L); (*b*–*d*) contain data for the smaller scales of the individual NAFO divisions.



CPUE was hyperstable with respect to local cod density (not biomass) within the Bonavista corridor from 1983 to 1991 (Fig. 8). Under the model CPUE (tonnes per hour) = 0.13 × density$^{0.53}$ ($R^2$ = 0.89), *b* was significantly less than 1 ($P < 0.05$). The 1992 data were not included in this analysis because the fishery was under a full moratorium prior to the acoustic survey in that year from which the density data were derived.

Biomass and area occupied in the corridor, as determined from volumetric analyses of kriged acoustic data, declined rapidly from 1990 to 1993 (Fig. 9). In June 1990, more than 450 000 t of cod was concentrated within 7000 km$^2$. The biomass–area curve suggests a high degree of aggregation, with 225 000 t (half of the biomass) located within 1500 km$^2$ (20% of the area). By 1991, total abundance had been reduced to less than 300 000 t, half of which was located within 3500 km$^2$ (40% of the area). By 1992, abundance had declined further to approximately 125 000 t, half of which occupied 30% of the range. By 1993, abundance had declined sharply to less than 25 000 t that was evenly

**Table 1.** Summary of backward selection regression of commercial fishery CPUE with independent variables time (year) and research vessel biomass for NAFO 2J3K3L for the years 1981–1992.

| Area | Effect | Coefficient | Significance | Model $R^2$ |
|---|---|---|---|---|
| 2J | Year | | | 0.34 |
| | Biomass | 0.0084 | 0.37 | |
| | Constant | 0.72 | 0.05 | |
| 3K | Year | 0.44 | 0.01 | 0.72 |
| | Biomass | | | |
| | Constant | –35.0 | 0.01 | |
| 3L | Year | 0.21 | 0.01 | 0.85 |
| | Biomass | –0.0047 | 0.05 | |
| | Constant | –15.8 | 0.01 | |

**Note**: Empty cells indicate that the variable was deselected from the model ($P > 0.05$).

**Fig. 8.** Mean CPUE and SE for the commercial otter trawl fishery against relative acoustic density in the Bonavista corridor, 1982–1991. The best-fit power model is CPUE = 0.13 × density$^{0.53}$ ($R^2$ = 0.89).

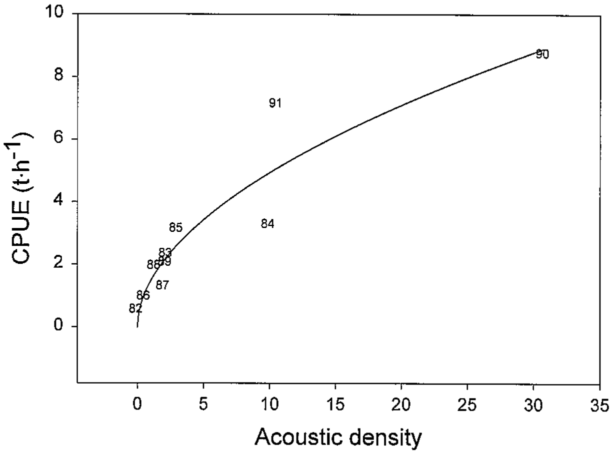
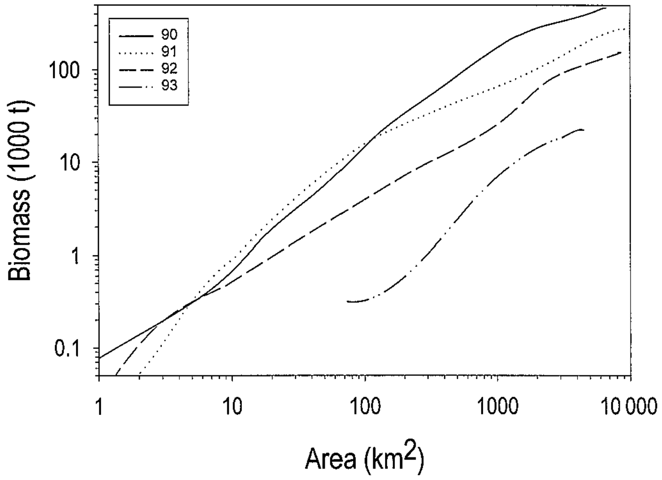


**Fig. 9.** Cumulative density (biomass versus area) profiles for the northern cod in the Bonavista corridor study area, 1990–1993. Statistical analyses are given in Table 2.



dispersed over 4500 km$^2$ (half the fish occupied 50% of the range). The high densities recorded in 1990 were sustained in 1991, but over a much reduced area (Fig. 9). For densities above 0.1 fish·m$^{-2}$ (of interest to the commercial fisheries and present over an extended area only in 1990 and 1991), the cumulative biomass profiles did not differ between 1990 and 1991 (Table 2). However, considering all densities, there were declines each year from 1990 to 1993.

Total area holding high densities above 0.1 fish·m$^{-2}$ was reduced from 1250 to 500 km$^2$ from 1990 to 1991 and to somewhat less than 100 km$^2$ by 1992 (the fishery terminated prior to these measures in 1992) (Fig. 10). At these densities, approximately 3–6 t of fish would have been available to a typical fishing set of the commercial fleet, assuming a swept area of 20 × 5600 m per commercial bottom trawl set (Kulka et al. 1996) and a range of distributions of cod up to 10–25 m from bottom (Rose 1993). The area fished was proportional to the area holding high densities of cod (>0.1 fish·m$^{-2}$) in each year by a constant factor of approximately 20 (Fig. 11).

## Discussion

The historical otter trawl fisheries for northern cod were designed to exploit cod at their highest densities and during their least migratory phase, which occurs in the winter–spring (January–June) period and spans the spawning season (Kulka et al. 1996). During winter the northern cod formed large aggregations that moved within a confined zone along the outer shelf (Kulka et al. 1995; Wroblewski et al. 1995). These aggregations persisted through the springtime spawning period and until some proportion of the fish approached coastal waters during the onshore migration in late June or early July (Rose 1993). CPUE from this fishery was used in attempts to “tune” population assessment models until the early 1990s (Bishop et al. 1993), under an assumption of linearity between CPUE and abundance.

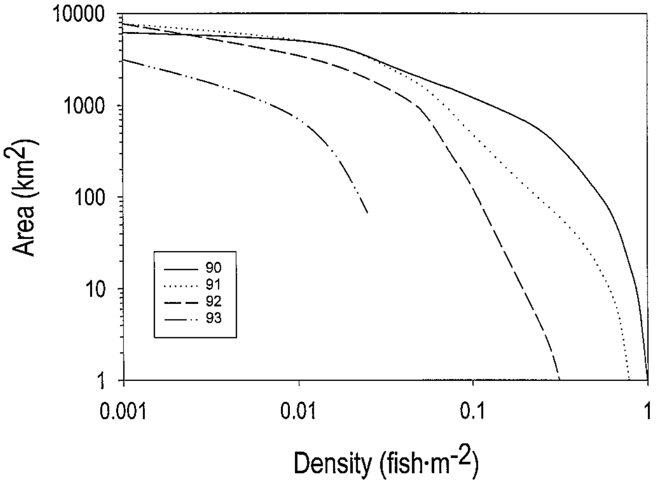
The relationship between CPUE and abundance or biomass has long been debated (e.g., Baranov 1918, cited in Ricker 1975; Garrod 1964; Paloheimo and Dickie 1964). Our data indicate that CPUE did not closely reflect abundance (biomass) at any scale measured (full stock, NAFO divisions, study area). However, at smaller scales, some significant relationships were evident. In the northern zone (2J), CPUE was positively related to biomass. In the southern zone (3L), there was a negative relationship between CPUE and biomass, independent of the time trend in these data. Hence, the hyperaggregation hypothesis is supported for the southern region, but not for the middle (3K) or north region. Our data are insufficient to address the cause of such spatial variation. However, the spatial difference suggests that cod may aggregate differently with respect to abundance over their range. deYoung and Rose (1993) proposed a modified basin model for the northern cod (MacCall 1990) wherein the Bonavista corridor was the basin trough wherein fish aggregated at times of low abundance. Such a model could explain the differing relationship between CPUE and biomass between the northern and southern ranges. For example, densities may only increase with declines in biomass in the trough, but decrease elsewhere. However, by the

**Table 2.** Summary of statistics based on the model log(biomass) = *B* log (area) + *K* applied to acoustic data on biomass and distribution of cod in the Bonavista corridor study area in the springs of 1990–1993.

| | 1990 | | 1991 | | 1992 | | 1993 | |
|---|---|---|---|---|---|---|---|---|
| | *K* | *B* | *K* | *B* | *K* | *B* | *K* | *B* |
| All data | –1.69* (0.24) | 1.09 (0.03) | –0.61* (0.04) | 0.93 (0.05) | –0.32* (0.19) | 0.86 (0.02) | –2.46* (0.38) | 1.02 (0.04) |
| High density | –2.29 (0.14) | 1.18 (0.02) | –2.54 (0.52) | 1.21 (0.07) | | | | |

**Note**: High density is >0.1 fish·m$^2$. SE is given in parentheses. Comparisons are made horizontally between parameters. *Difference ($P < 0.05$).

**Fig. 10.** Cumulative area occupied by the northern cod over the full density range encountered in the Bonavista corridor study area, determined using acoustic estimates, 1990–1993. Areas of commercial interest are >0.1 fish·m$^{-2}$.



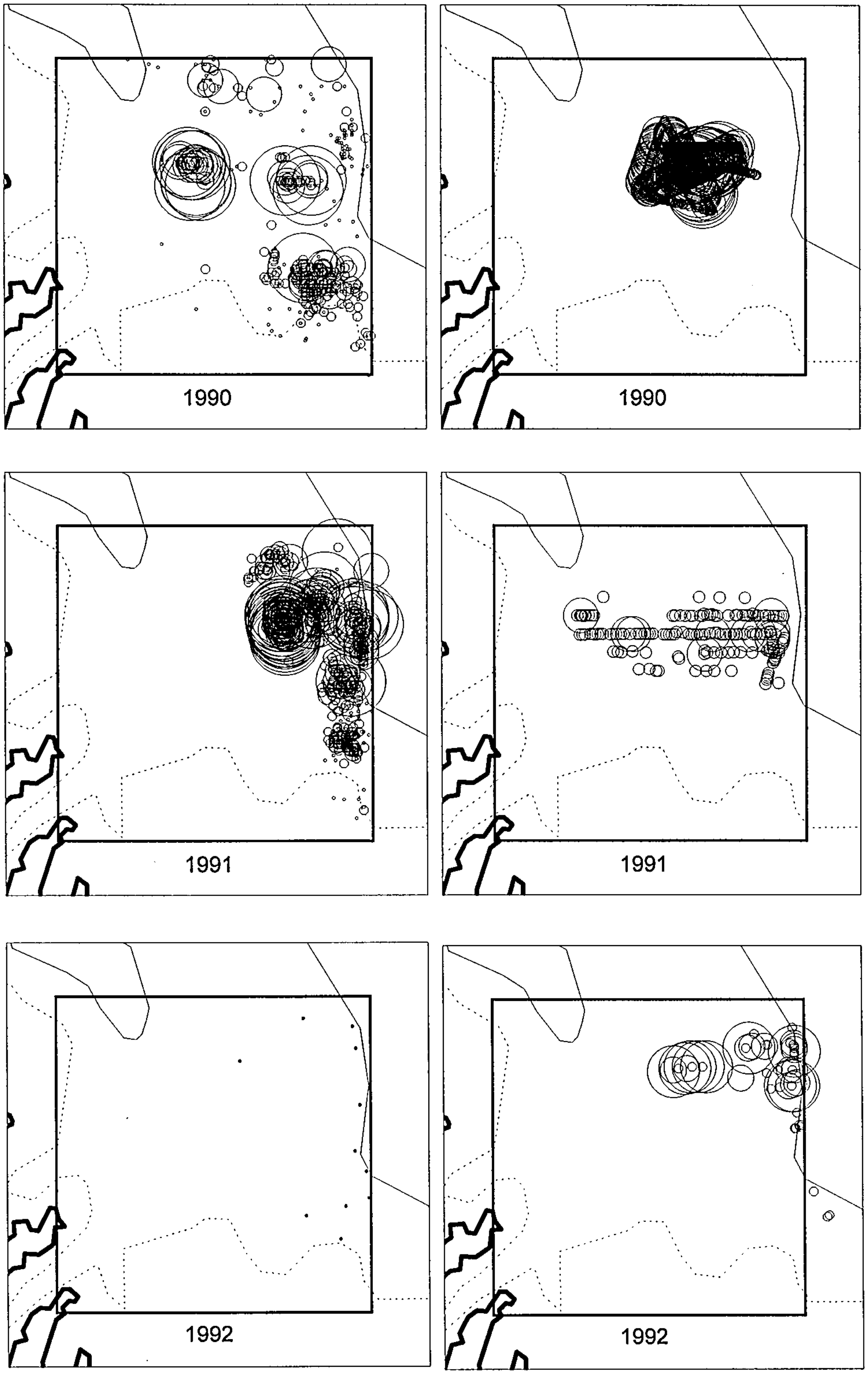
spring of 1993, the approximately 100 000 t of cod present in 1992 was not to be found in the Bonavista corridor or adjacent waters. Hence, the model does not fully account for the spatial demise of the northern cod.

Further evidence supporting hyperaggregation can be garnered from the fishery. The fishery moved southward quickly in the late 1980s to exploit the shifting cod concentrations, despite a management initiative that attempted to spread out the fishing effort (J. Kelly, commercial trawler fisherman, Marystown, Nfld., personal communication). Not only did vessels congregate to the south, but fishing set duration was shortened to reduce increasingly large catches, which in the opinion of fishers and observers were caused by increasing densities of cod (Kulka 1997). There is little doubt that the high cod densities in the Bonavista corridor led to the high catch rates in the late 1980s and until the moratorium on fishing in 1992. However, CPUE was hyperstable with respect to density and not to biomass (Hilborn and Walters 1992). Unfortunately, high cod densities were interpreted as indicative of high abundance in the late 1980s. In 1989, otter trawler skippers and their company stated “our captains are convinced that northern cod are as plentiful as ever offshore and our vessels have few problems catching their trip allotments throughout the year” (memorandum to the Department of Fisheries and Oceans from National Sea Products, Lunenburg, N.S.). Two years later, this fishery had collapsed.

The spatial decline of the northern cod appears to be complex, and as yet only partially understood. As the north to south shift in distribution was occurring, local densities of the extant aggregations were being maintained or even increasing. This situation continued until the spring of 1992, after the imposition of a moratorium on all fishing in Canadian waters (Rose et al. 1995). After 1992, the distribution pattern of the northern cod shifted again (there can be no argument that these fish were simply fished out because there was no fishery at all in the Canadian zone at this time). By 1993, few fish remained in the Bonavista corridor, the area in which the last large aggregations were observed. These findings are inconsistent with the notion that the spatial decline of the northern cod was a simple fishing-down from north to south, as suggested by Hutchings and Myers (1994) and Hutchings (1996). However, the data are consistent with the alternative hypothesis that distribution and aggregation changes increased the availability of the fish to the fisheries. Increased availability to the fisheries could have greatly hastened the decline of this stock and may help explain its quick demise (Rose et al. 1994). We cannot rule out other potential sources of mortality. Nevertheless, distribution changes also offer an explanation of how the foreign fishery, located in the relatively small area of the Grand Bank outside the Canadian Exclusive Economic Zone, continued to increase their catches of cod until 1991 (approximately 50 000 t reported) and why the fishable stock continued to decline after 1992 and a full moratorium on fishing within the Canadian zone. It is important for future interpretations of stock status that the spatial aspects of this stock and its fisheries be explicitly addressed.

We believe that our results may be applicable to other gadoid fisheries. Our analyses indicate that local densities can not only remain relatively stable as biomass changes (resulting in hyperstability in the CPUE–biomass relationship), but can increase as biomass declines. We have termed such behavior “hyperaggregation.” Hyperaggregation may be viewed as an extreme form of hyperstability that resulted from the coincidence of distribution changes and severe overfishing. However, less severe forms of hyperstability may be commonplace. There is a growing literature suggesting that CPUE from mobile fisheries for groundfish does not relate linearly to abundance (e.g., Houghton and Flatman 1981; Rose and Leggett 1989, 1991; Crecco and Overholtz 1990; Gordoa and Hightower 1991; Swain and Wade 1993; Swain et al. 1994). Moreover, most gadoids are shoaling fishes whose local densities are behaviorally determined (e.g., Rose 1993). Hence, a linear and constant catchability (the relationship between CPUE and biomass) should not be expected (O.R. Godo, Institute of Marine Research, Bergen, Norway, personal communication). We suggest that CPUE

**Fig. 11.** Fishing by the commercial otter trawler fleet (left panels) and the distribution of the northern cod from acoustic surveys (right panels), May–July 1990–1992, within the Bonavista corridor study area. Commercial CPUE is shown in five categories representing 0–0.5, 0.5–2.5, 2.5–5, 5–10, and >10 t·h$^{-1}$. Acoustic survey densities are shown in three categories representing 0.01–0.1, 0.1–1, and >1 fish·m$^{-2}$. The total areas fished were approximately 24 740 km$^2$ (1990), 10 840 km$^2$ (1991), and 3450 km$^2$ (1992). Areas occupied by densities of >0.1 fish·m$^{-2}$ were approximately 1250, 500, and 100 km$^2$ for 1990, 1991, and 1992, respectively.



should not be used as an index of abundance for groundfish species without careful examination of the spatial characteristics of both the fish and the fisheries.

In conclusion, we have shown how CPUE of the mobile fishery became elevated during a major decline of the northern cod. Increased CPUE can be attributed to hyperaggregation in the southern extremeties of the stock's range. As a direct consequence, CPUE did not reflect stock abundance (but did reflect local densities). Hyperaggregation resulted in the fish being more vulnerable to contemporary fishing practices (legal and illegal with attendant highgrading and discarding) and led many in industry, science, and management to believe that the stock was still healthy whereas in reality, it was being overfished and declining rapidly.

## Acknowledgments

We thank the crews of the RV *Gadus Atlantica* and *Petrel V* and groundfish and acoustics staff from the Northwest Atlantic Fisheries Centre, in particular D. Porter, C. Lang, and C. Stevens, for assistance at sea and the many fisheries observers. Funding was provided by the Natural Sciences and Engineering Research Council of Canada Fisheries Conservation Chair at Memorial University, the Northern Cod Science Program (Department of Fisheries and Oceans), and the Ocean Production Enhancement Network (a Natural Sciences and Engineering Research Council of Canada Network Centre of Excellence).

## References

Atkinson, B.A., Rose, G.A., Murphy, E., and Bishop, C.A. 1997. Distribution changes and abundance of northern cod (*Gadus morhua*): 1981–1993. Can. J. Fish. Aquat. Sci. **54**(Suppl.1): 132–138.

Baranov, F.I. 1918. On the question of the biological basis of fisheries. Nauchn. Issled. Ikhtiol. Inst. Izv. **1**: 81–128.

Bishop, C.A., Murphy, E.F., Davis, M..B., Baird, J.W., and Rose, G.A. 1993. An assessment of the cod stock in NAFO divisions 2J+3KL. NAFO SCR Doc. 93/86.

Colbourne, E.B., deYoung, B., and Rose, G.A. 1997. Environmental analysis of cod (*Gadus morhua*) migration in relation to the seasonal variations on the Northeast Newfoundland Shelf. Can. J. Fish. Aquat. Sci. **54**(Suppl.1): 149–157.

Crecco, V., and Overholtz, W.J. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. **47**: 385–394.

deYoung, B., and Rose, G.A. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. **50**: 2729–2741.

Garrod, D.J. 1964. Effective fishing effort and catchability coefficient. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **155**: 66–70.

Gordoa, A., and Hightower, J.E. 1991. Changes in catchability in a bottom-trawl fishery for cape hake (*Merluccius capensis*). Can. J. Fish. Aquat. Sci. **48**: 1887–1895.

Hilborn, R., and Walters, C.J. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.

Houghton, R.G., and Flatman, S. 1981. The exploitation pattern, density-dependent catchability, and growth of cod (*Gadus morhua*) in the west-central North Sea. J. Cons. Cons. Int. Explor. Mer, **39**: 271–287.

Hutchings, J.A. 1996. Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse. Can. J. Fish. Aquat. Sci. **53**: 943–962.

Hutchings, J.A., and Myers, R.A. 1994. What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador. Can. J. Fish. Aquat. Sci. **51**: 2126–2146.

Kulka, D.W. 1997. Discarding of cod (*Gadus morhua*) in the northern cod and northern shrimp directed trawl fisheries, 1980–94. NAFO Sci. Counc. Stud. **29**: 67–79.

Kulka, D.W., and Firth, J.R. 1987. Observer program training manual — Newfoundland region. Can. Tech. Rep. Fish. Aquat. Sci. No. 1355 (rev.).

Kulka, D.W., Wroblewski, J.S., and Narayanan, S. 1995. Recent changes in the winter distribution and movements of northern Atlantic cod (*Gadus morhua*) on the Newfoundland–Labrador shelf. ICES J. Mar. Sci. **52**: 889–902.

Kulka, D.W., Pinhorn, A.T., Halliday, R.G., Pitcher, D., and Stansbury, D. 1996. Accounting for changes in spatial distribution of groundfish when estimating abundance from commercial fishing data. Fish. Res. **28**: 321–342.

Lear, W.H., Baird, J.W., Rice, J.C., Carscadden, J.E., Lilly, G.R., and Akenhead, S.A. 1986. An examination of factors affecting the inshore cod fishery of Labrador and eastern Newfoundland. Can. Tech. Rep. Fish. Aquat. Sci. No. 1469.

MacCall, A.D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Wash.

MacLennan, D.W., and Simmonds, E.J. 1992. Fisheries acoustics. Chapman and Hall, London, U.K.

Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. Rapp. P.-v. Réun. Cons. Int. Explor. Mer, **155**: 152–163.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. No. 191.

Rose, G.A. 1993. Cod spawning on a migration highway in the north-west Atlantic. Nature (Lond.), **366**: 458–461.

Rose, G.A. 1996. Cross-shelf distributions of cod in NAFO division 2J3KL in May and June 1995: some preliminary findings of a longer term study. Can. Stock Assess. Secr. WP 96/10.

Rose, G.A., and Leggett, W.C. 1989. Predicting variability in catch-per-effort in Atlantic cod, *Gadus morhua*, trap and gillnet fisheries. J. Fish Biol. **35**(Suppl. A): 155–161.

Rose, G.A., and Leggett, W.C. 1991. Effects of biomass–range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Can. J. Fish. Aquat. Sci. **48**: 843–848.

Rose, G.A., and Porter, D.R. 1996. Target strength studies on Atlantic cod (*Gadus morhua*) in Newfoundland waters. ICES J. Mar. Sci. **53**: 259–265.

Rose, G.A., Atkinson, B., Baird, J., Bishop, C.A., and Kulka, D.W. 1994. Atlantic cod distribution changes and thermal variations in Newfoundland waters, 1980–1992. ICES Mar. Sci. Symp. **198**: 542–552.

Rose, G.A., deYoung, B., and Colbourne, E.B. 1995. Cod (*Gadus morhua*) migration speeds and transport relative to currents on the north-east Newfoundland Shelf. ICES J. Mar. Sci. **52**: 903–914.

Swain, D.P., and Wade, E.J. 1993. Density-dependent geographic distribution of Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. **50**: 725–733.

Swain, D.P., Nielsen, G.A., Sinclair, A.F., and Chouinard, G.A. 1994. Changes in catchability of Atlantic cod (*Gadus morhua*) to an otter-trawl fishery and research survey in the southern Gulf of St. Lawrence. ICES J. Mar. Sci. **51**: 493–504.

Taggart, C.T., Anderson, J., Bishop, C., Colbourne, E., Hutchings, J., Lilly, G., Morgan, J., Murphy, E., Myers, R., Rose, G., and Shelton, P. 1994. Overview of cod stocks, biology, and environment in the Northwest Atlantic region of Newfoundland, with emphasis on northern cod. ICES Mar. Sci. Symp. **198**: 140–157.

Templeman, W. 1966. Marine resources of Newfoundland. Bull. Fish. Res. Board Can. No. 154.

Walters, C., and Maguire, J.-J. 1996. Lessons for stock assessment from the northern cod collapse. Rev. Fish Biol. Fish. **6**: 125–138.

Warren, W.G. 1997. Changes in the within-survey spatio-temporal structure of the northern cod (*Gadus morhua*) population, 1985–1992. Can. J. Fish. Aquat. Sci. **54**(Suppl. 1): 139–148.

Winters, G.H., and Wheeler, J.P. 1985. Interaction between stock area, abundance, and catchability coefficient. Can. J. Fish. Aquat. Sci. **42**: 989–998.

Wroblewski, J.S., Kulka, D.W., Narayanan, S., Oake, A.M., Collier, A.G., and McGrath, B.D. 1995. Winter distribution and movements of northern Atlantic cod *(Gadus morhua*) along the Newfoundland–Labrador continental shelf edge derived from observations on commercial trawlers. Fish. Oceanogr. **4**: 128–146.