

PERSPECTIVE

What Can Be Learned from the Collapse of a Renewable Resource? Atlantic Cod, *Gadus morhua*, of Newfoundland and Labrador

Jeffrey A. Hutchings¹ and Ransom A. Myers

Department of Fisheries and Oceans, Science Branch, P.O. Box 5667, St. John's, NF A1C 5X1, Canada

Hutchings, J.A., and R.A. Myers. 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.

Temporal changes in demography, population sustainability, and harvest rates support the hypothesis that overexploitation precipitated the commercial extinction of northern cod, *Gadus morhua*, off Newfoundland and Labrador in 1992. Annual estimates of realized population growth (r) indicate that the stock was rarely sustainable at the age-specific survival and fecundity rates experienced since 1962. A twofold decline in annual survival probabilities in the 1980s was concomitant with increased inshore and offshore fishing effort, declining catch rate, and spatial shifts in gillnetting effort from areas of low (inshore) to high (offshore) catch rates. We reject hypotheses that attribute the collapse of northern cod to environmental change. Water temperature was associated neither with juvenile nor adult abundance nor with adult distribution by depth. Harvests equivalent to those of the past decade were sustainable in the nineteenth and early twentieth centuries in a considerably colder environment. An updated analysis of previous work indicates that salinity has little effect on recruitment. We conclude that the collapse of northern cod can be attributed solely to overexploitation and that population sustainability indices such as r provide a means by which the susceptibility and resilience of exploited populations can be assessed and their probability of commercial extinction reduced.

Les modifications temporelles des caractères démographiques, de la durabilité des populations et des taux de récolte soutiennent l'hypothèse selon laquelle la surexploitation a accéléré l'extinction commerciale de la morue du Nord, *Gadus morhua*, au large de Terre-Neuve et du Labrador en 1992. Les estimations annuelles de croissance réalisée des populations (r) indiquent que le stock était rarement durable aux taux de survie et de fécondité par âge qui ont existé depuis 1962. Une diminution deux fois plus importante des probabilités annuelles de survie dans les années 80 coïncidait avec une augmentation de la pêche côtière et hauturière, avec une diminution des taux de capture ainsi qu'avec les déplacements spatiaux de la pêche au filet maillant des zones à faible taux de capture (pêche côtière) vers des zones à fort taux de capture (pêche hauturière). Nous rejetons les hypothèses voulant que l'effondrement de la morue du Nord soit attribuable à des changements environnementaux. La température de l'eau n'était liée ni à l'abondance des juvéniles et des adultes ni à la distribution des adultes en fonction de la profondeur. Des récoltes équivalentes à celles des dix dernières années étaient compatibles avec la durabilité des populations au dix-neuvième siècle et au début du vingtième siècle dans un environnement considérablement plus froid. Une analyse récente des travaux antérieurs indique que la salinité n'a que peu d'effet sur le recrutement. Nous concluons que l'effondrement de la morue du Nord ne peut être attribué qu'à la surexploitation et que les indices du caractère durable des populations comme r constituent un moyen d'évaluer la sensibilité et la résilience des populations exploitées et de réduire la probabilité de leur extinction commerciale.

Received January 26, 1994

Accepted July 21, 1994
(J12254)

Reçu le 26 janvier 1994

Accepté le 21 juillet 1994

Resource management is based on the premise that the existence of harvesting regulations better ensures the long-term viability of a population under commercial exploitation than does their absence. Ideally, such regulations should depend upon sound knowledge of the harvested organism's life history (i.e., age- and size-specific schedules

of survival and fecundity), population structure (e.g., number and size of reproductively distinct populations within the geographical area of exploitation), and community ecology (i.e., the biological interactions that influence a species' abundance). In practice, the effort allocated to the collection of such biological data is limited. Instead, most management agencies concentrate on the formulation of indices of the past, present, and future states of the population (e.g., abundance, harvest-induced mortality), metrics assumed sufficient

¹Present address: Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada.

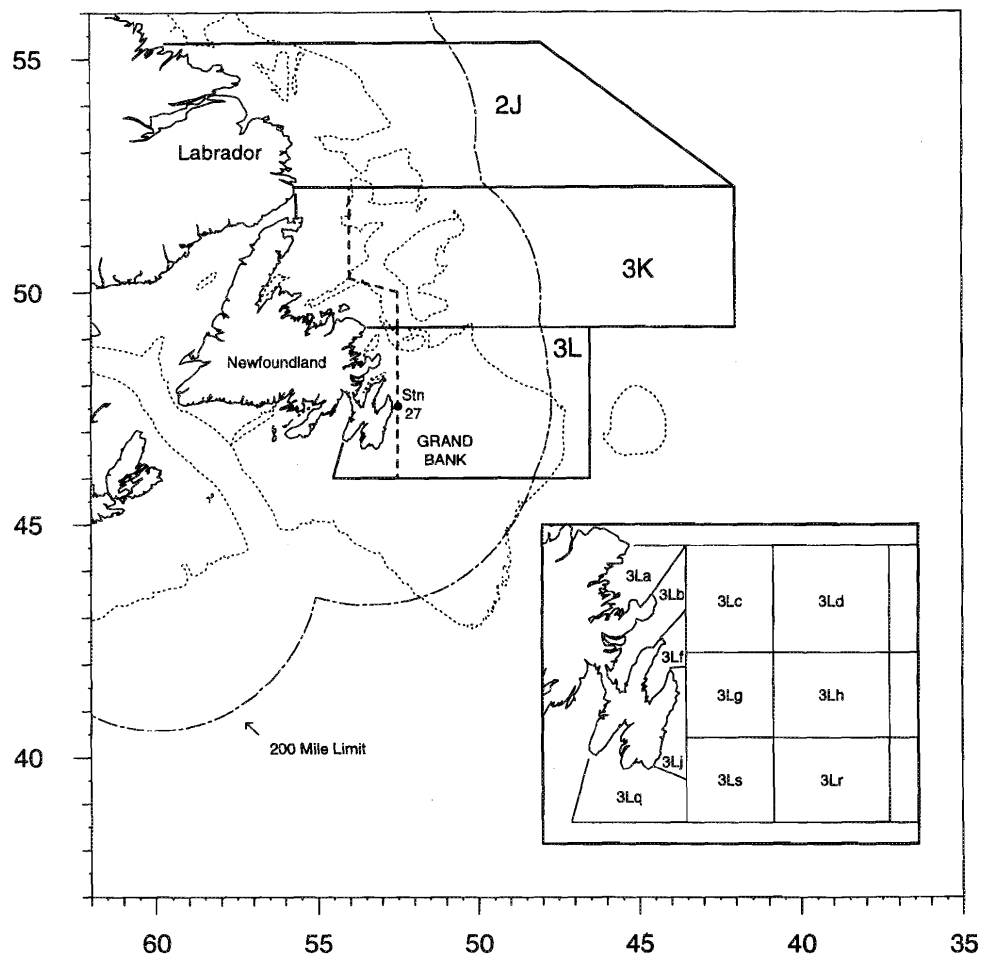


FIG. 1. Map of the study region. Cod inhabiting Northwest Atlantic Fishery Organization Divisions 2J, 3K, and 3L comprise the northern cod stock. Depth contour represents the 300-m isobath. The broken line separates the inshore and offshore jurisdictional unit areas in 3K and 3L (the latter are detailed in the inset).

to achieve long-term resource sustainability (Gulland 1983; Hilborn and Walters 1992).

The effectiveness of any management strategy can be difficult to assess. Despite the continued existence of a harvested population, it is impossible to determine whether a given management strategy is optimal because of the absence of a control (i.e., no management of a random sample of the same population) and the absence of other treatments (i.e., concurrent alternative management strategies on random replicates of the same population). It is only when a population declines in abundance to a level at which it is not economically viable for harvest (commercial extinction) and when its very existence is threatened that the reliability of a given strategy can potentially be evaluated. When a harvested population becomes commercially extinct, it is imperative that the potential causes of such biological devastation be identified and their relative contributions to the extinction evaluated (Beverton 1990; Ludwig et al. 1993; Rosenberg et al. 1993). Our objective is to determine the degree to which the commercial extinction of Atlantic cod, *Gadus morhua*, from the southern half of Labrador to northern Grand Bank of Newfoundland in 1992 was associated with temporal changes in water temperature, distribution by depth, and levels of exploitation (e.g., age-specific mortality, harvest rates, fishing effort, catch per unit effort).

Overview of the Northern Cod Fishery off Newfoundland and Labrador

Atlantic cod have been fished in Newfoundland waters since the late fifteenth century (Cell 1982). The fishery was largely a hook-and-line fishery until the development of cod traps in the 1860s and 1870s (de Loture 1949; Head 1976; Sinclair 1985). Major technological advances and increased efficiency in harvesting methods continued with the introduction of bottom trawlers in the early 1900s, particularly after the First World War (de Loture 1949), and nylon gill nets in the early 1960s (Templeman 1966). Annual landings of cod in Northwest Atlantic Fishery Organization (NAFO) Divisions 2J, 3K, and 3L (hereafter, northern cod; Fig. 1) increased from 100 000 to 150 000 t between 1805 and 1850, rose to more than 200 000 t during the latter half of the nineteenth century, and were frequently in excess of 250 000 t from 1900 to 1960 (ICNAF 1952; Harris 1990; Steele et al. 1992; Lear and Parsons 1993). With the advent of long-distance, "factory freezer", stern otter trawlers from Europe in the 1950s (Warner 1977), catches more than doubled from 360 000 t in 1959 to the historical maximum of 810 000 t in 1968. By 1977, when Canada extended its fisheries jurisdiction to 200 miles and most long-distance fishing was effectively eliminated, annual harvests had declined

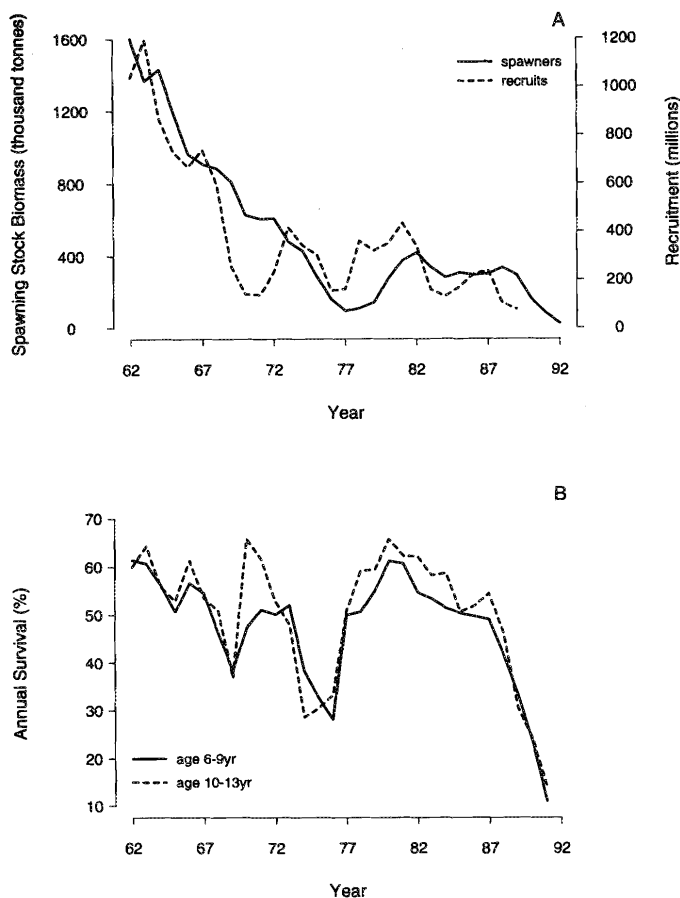


FIG. 2. (A) Variation in recruitment (numbers of 3-yr-old cod) and spawner biomass (individuals of ages 7 yr and older) of northern cod from 1962 to 1992 (data from Bishop et al. 1993b). (B) Annual survival (P) of mature northern cod aged 6–9 and 10–13 yr from 1962 to 1991. Fishing mortality (F) calculated from Baird et al. (1992) for 1962–77 and from Bishop et al. (1993b) for 1978–91; natural mortality is assumed to be constant at 18% per annum (i.e., $M = 0.2$, as defined by $P = e^{-(F+M)}$).

almost 80% from the 1968 level (Bishop et al. 1993b). During the first 11 yr of Canadian management (1978–88), commercial landings of northern cod increased from 140 000 to 270 000 t. In 1991, 1 yr before the Canadian government imposed a moratorium on commercial exploitation of northern cod, landings were 64% less than those in 1988.

The number of harvestable northern cod (i.e., aged 3 yr and older) in 1992 was approximately 3 billion fewer than the number extant in the early 1960s (Baird et al. 1991a; Bishop et al. 1993b). The enormity of this decline can also be expressed through the reduction in biomass of the spawning portion of the population (approximated in assessment documents as individuals aged 7 yr and older) and in recruitment (abundance of 3-yr-old cod). Spawner biomass declined from an estimated 1.6 million t in 1962 (the first year for which estimates are available) to 22 000 t in 1992 (Fig. 2A) (Bishop et al. 1993b). This decline was associated with large fluctuations in annual survival probability (Fig. 2B). Annual survival probabilities for reproductive individuals declined from roughly 0.6 in the early 1960s to 0.3 in the mid-1970s and increased to 0.6 again in the early 1980s before declining to 0.1–0.2 in the early 1990s. The collapse of the spawning

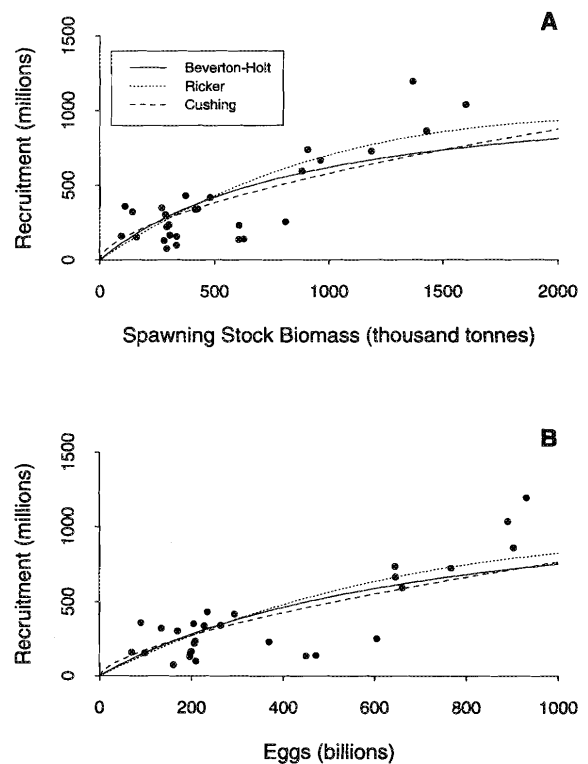


FIG. 3. (A) Three stock–recruit relationships for northern cod (Beverton–Holt, Ricker, Cushing) including recruitment year classes from 1962 to 1989. (B) Three fitted relationships (as in Fig. 3A) between recruitment and estimated number of eggs for recruitment year classes 1962–89.

stock biomass had an equally large effect on the number of juveniles recruited to the fishery (Fig. 2A); recruitment is positively associated with spawner biomass in northern cod ($r^2 = 0.73$, $p = 0.0001$, p -value corrected for autocorrelations; Fig. 3A).

Hypotheses for the Collapse of Northern Cod

When the moratorium was announced, the collapse of northern cod was considered to be sudden, drastic, and unexpected and was attributed to increased natural mortality resulting from unusual environmental conditions, primarily in the form of cold water temperatures (Lear and Parsons 1993). A second hypothesis is that colder temperatures throughout the 1980s effected a southerly shift in the distribution of spawning individuals during the 1980s that has resulted in the rearing of juveniles in suboptimal habitat (deYoung and Rose 1993). If true, we would expect a negative correlation to exist between cod abundance (adults and recruits to the fishery) and sea temperature. It has also been suggested that cod have moved to deeper water in recent years (Bishop et al. 1993b). A short-term, large-scale emigration to deeper water in the early 1990s would be evident from a temporal analysis of cod biomass in deep water relative to that in shallower water. Given that total stock failure has not been previously recorded for northern cod within the past two centuries, these hypotheses make the implicit assumption that environmental conditions experienced during the early 1990s, or the 1980s, were temporally anomalous.

These hypotheses assume either explicitly or implicitly that an environmental variable is a primary determinant of cod survival and that the dramatic reduction in annual survival probabilities throughout the 1980s and early 1990s (Fig. 2B) cannot be wholly explained by increases in fishing mortality. When the moratorium on northern cod was announced on 2 July 1992, it was noted that "the increase in fishing mortality in...recent years is inconsistent with the trends in fishing effort by Canadian fleets. The total number of hours fished by the Canadian otter trawl fleet in Div. 2J+3KL declined consistently from 63,000 [h] in 1988 to 43,000 [h] in 1991" (NAFO 1992, p. 26). This assertion was repeated in the Canadian Fisheries Resource Conservation Council's "1993 Report on the Status of Groundfish Stocks in the Northwest Atlantic" (FRCC 1993). But the implication that overfishing was not the primary contributing factor responsible for the decline of northern cod can be assessed neither in the absence of information on fishing effort *prior to 1988* (by offshore and inshore gear) nor in the absence of temporal data on population sustainability.

We wish to examine competing hypotheses for the collapse of northern cod by addressing the following questions: (1) Were water temperatures experienced by northern cod in the 1980s and early 1990s temporally anomalous? (2) Does cod mortality increase with decreasing water temperature? (3) Did cod move to deeper waters in the early 1990s? If so, can such a displacement be attributed to colder temperatures? (4) Was the temporal increase in total mortality throughout the 1980s inconsistent with observed temporal and spatial patterns in inshore and offshore fishing effort and catch rate? (5) Were observed age-specific rates of survival and fecundity sufficient to sustain the population through time?

We begin with an analysis of depth-stratified temperature data that have been collected approximately twice monthly at a single location since 1946 (Station 27, ranging in depth to 175 m, is located immediately east of St. John's; Fig. 1) as a proxy for interannual variation in water temperature throughout 2J3KL (Petrie et al. 1992). We then examine historical associations among continental shelf water temperatures (from 1910), ice clearance data (from 1803), air temperatures (from 1874), and commercial cod landings (from 1805) to provide a broad perspective of the environmental conditions in which the northern cod fishery was sustainable during the nineteenth and twentieth centuries. The relative importance of water temperature on cod population biology is assessed by statistically analyzing associations between temperature and (1) adult abundance, (2) juvenile abundance, and (3) depth distribution of cod. Research survey data are analyzed to examine temporal variation in the biomass of cod in deep water relative to that in shallow water. We analyzed NAFO fishery statistics to assess the degree to which annual increases in total mortality throughout the 1980s and early 1990s were associated (1) with yearly changes in fishing effort and catch rate by Canadian trawlers and (2) with spatial and temporal variation in the inshore and offshore gillnet fisheries. Demographic changes in northern cod are described by changes in age distribution of reproductive individuals, weight-at-age, and age-specific rates of survival and fecundity. Estimates of the latter two parameters were used to estimate r , a measure of population growth, to identify those years from 1962 to 1992 in which northern cod were able to sustain themselves, i.e., when $r \geq 0$.

Materials and Methods

Historical Temperature and Commercial Catch Data

Depth-stratified water temperature data have been recorded approximately twice monthly since 1946 at Station 27 (Fig. 1). Data are generally available at 10-m depth intervals from the surface to 50 m and at every 25 m thereafter to the bottom at 175 m. Although small-scale, short-term temperature fluctuations in 2J3KL may not be represented by these data, they do reflect large-scale variability in temperature and other environmental indices (e.g., areal ice cover, cold intermediate layer (CIL, volume of $<0^{\circ}\text{C}$ water), North Atlantic Oscillation (NOA) sea level pressure anomaly) throughout the region (Petrie et al. 1992; Colbourne et al. 1994). To remove seasonal effects on temperature, we report these data as anomalies from the long-term mean (1946–92). For analyses of adult abundance, we excluded temperatures recorded at less than 50 m, depths which demersal mature cod are unlikely to inhabit and from where abundance data are not available. Analyses involving juvenile abundance (i.e., recruitment) included temperatures recorded from 0 to 50 m (depths inhabited by larval cod; Anderson and deYoung 1993). Depth-averaged water temperature anomalies were calculated for each year using the formula

$$(1) \quad \sum_{i=1}^{N-1} ((x_i + x_{i+1})/2)(d_{i+1} - d_i)$$

where x_i represents the yearly average temperature anomalies at depth strata i, \dots, N and d_i represents the depth of stratum i . This calculation weights the mean temperature between successive strata by the difference in depth between strata. The p -values of all correlation coefficients between temperature and abundance were corrected for autocorrelation.

Long-term data on water temperatures in 3L (i.e., northern Grand Bank), dates of ice clearance, and air temperature in the region are available from 1910, 1803, and 1874, respectively. Shelf water temperatures in 3L (100 m depth) were obtained from the MEDS (Marine Environment Data Services, Ottawa, Ont., Canada) data base. Using observational data from the Labrador coast, Newell (1991, 1992, 1993) calculated an ice clearance index which reflected the day of year on which the waters off Hopedale, Labrador ($55^{\circ}05'N$), were clear of Arctic pack ice. We report these data as departures from the long-term (1800–1993) mean. The ice clearance index is correlated with depth-averaged (50–175 m) water temperature at Station 27 ($r = 0.50$, $p = 0.0004$, $n = 46$). Air temperatures have been recorded at St. John's, eastern Newfoundland (15 km from Station 27), since 1874 and are available from the Canadian Atmospheric and Environment Service. We report these data as anomalies from the long-term (1874–1992) mean. Depth-averaged water temperature at Station 27 is correlated with St. John's air temperature ($r = 0.48$, $p = 0.0006$, $n = 46$). Historical commercial catch records were derived from those estimated for northern cod by Hutchings and Myers (1995) and based upon data collated by Gosling (1910), ICNAF (1952), Harris (1990), Bishop et al. (1993b), and W.H. Lear (Department of Fisheries and Oceans, Biological Sciences Directorate, 200 Kent St., Ottawa, ON K1A 0E6, Canada, unpublished data).

Ice clearance and air temperature data were smoothed using a robust locally weighted regression, *loess*, a method recommended for scatterplot data with missing values (Cleveland 1979; Hastie and Tibshirani 1990). The value at x_k fitted by the smoothing procedure is the value of a polynomial fit to the data using weighted least squares. The weight given to (x_i, y_i) is large if x_i is close to x_k and small if it is not.

Research Survey Abundance and Biomass Data

Recent temporal changes in the abundance and biomass of adult cod were obtained from research surveys conducted in autumn by the Canadian Department of Fisheries and Oceans from 1978 to 1992 in 2J and 3K and from 1981 to 1992 in 3L. Survey estimates of abundance and biomass are based upon the actual number and biomass of cod captured in a series of tows of a bottom otter trawl within each of several depth-stratified sampling strata within each NAFO division. There are generally 5–30 sets per stratum and there are 24, 23, and 29 strata within Divisions 2J, 3K, and 3L, respectively. The number (or biomass) of cod in division i is simply the sum of the numbers of cod estimated for all strata j in that division:

$$(2) \quad N_i = \sum_{j=1}^s N_j.$$

The number of cod in stratum j , N_j , is estimated as the mean number of cod captured per tow in stratum j (summed over tows $t = 1 \dots x$) increased by a proportion equal to the area of stratum j , A_j , divided by the total area sampled by the tows, i.e.,

$$(3) \quad N_j = \bar{N}_j \left(A_j / \sum_{t=1}^x A_t \right).$$

Abundance data were also obtained from depth-stratified random research surveys conducted by German vessels from 1972 to 1983 in 2J (Messtorff 1984). Their survey designs are comparable with the later Canadian surveys. German researchers also employed 30-min tows of otter trawls and conducted their surveys during late autumn in the same strata sampled by the Canadian vessels from 1978 to 1992.

VPA Estimates of Abundance and Biomass

Unless identified as being based solely upon research vessel survey data, indices of cod abundance and biomass were those determined from a virtual population analysis (VPA) conducted using a process called ADAPT (described by Mohn and Cook 1993). For northern cod, this procedure combines age-specific indices of population size from both commercial and research vessels, or more recently from research vessels only, to estimate historical stock sizes from 1962 to the present (Gavaris 1988; Conser 1993). The age-specific groups of cod referred to in the text for which abundance or biomass was estimated from the VPA are *recruits* or *recruitment* to the fishery (abundance of cod of age 3 yr), *spawner* or *spawning stock biomass* (cod of age 7 yr and older), and *harvestable biomass* or *abundance* (cod of age 3 yr and older).

Distribution by Depth of Cod Biomass

Cod biomass was estimated from the autumn research surveys conducted in 2J3KL (data in Bishop et al. 1993b).

Temporal changes in biomass were documented for the four main depth classes in each region in which surveys were conducted. These depth classes ranged from 100 to 500 m, in increments of 100 m in 2J and 3K, and 57–92, 93–183, 184–275, and 276–366 m in 3L. Associations between water temperature and cod biomass in deep water relative to that in shallow water were determined by calculating correlation coefficients between depth-averaged Station 27 temperature anomalies and two indices of deepwater cod biomass. The latter were biomass between 300 and 500 m relative to that between 100 and 300 m in 2J and 3K and biomass between 184 and 366 m relative to that between 57 and 184 m in 3L.

Catch and Effort Data

Commercial catch and effort data on Canadian offshore trawlers were obtained from fishery statistics compiled by NAFO from 1979 to 1991 (1979–90 data are from NAFO (1984–94); 1991 data are available from NAFO although they have not yet been published). These statistical summaries report the catch of all species caught in each NAFO division. Catches are further subdivided by country of origin, by gear type, by vessel tonnage, and by the target species being fished. We restricted our analyses to vessels for which cod constituted the largest biomass of species caught. From 1978 to 1991, nominal effort data were available for 87–100% of the annual cod biomass caught by otter trawls in 2J, 82–100% in 3K, and 91–100% in 3L. Most of the harvested cod was caught by vessels fishing primarily for cod (as percentages of the annual harvested cod biomass: 85–100% in 2J, 86–94% in 3K, and 64–88% in 3L). From 1981 to 1991, Canadian trawlers accounted for an average 52% of the Canadian catch and 44% of the total catch of northern cod (calculated from Bishop et al. 1993b).

Catch and effort data were also analyzed for cod captured by traps and gill nets. The data were compiled by STACAC (Statistical Co-ordinating Committee for the Atlantic Coast, Department of Fisheries and Oceans, Ottawa, Ont., Canada) and are available from 1985 to 1992. These data report catches on a considerably smaller spatial scale than those in the aforementioned NAFO records; data are summarized for 14 unit areas in 2J, 11 in 3K, and 14 in 3L. Effort is reported as number of trap days and number of clearances per 100-m gill net.

Population Sustainability

The instantaneous rate of change of the northern cod stock was estimated as r and given by the discrete-time version of the Euler-Lotka equation

$$(4) \quad 1 = \sum l_x m_x e^{-rx},$$

where l_x represents survival from the zygote to the beginning of the breeding season at age x and m_x is the number of female zygotes produced by a female breeding at age x (Cole 1954; Schaffer 1974). r is frequently used as a measure of fitness in evolutionary ecology (Charlesworth 1980; Stearns 1992; Hutchings 1993). As a measure of the rate of change in population abundance, population size at time $t + 1$ can be estimated from population size at time t from the equation $N_{t+1} = N_t e^r$ (Caughley 1977; Roff 1992). Thus, $r = 0$ for a population that is neither increasing nor decreasing, i.e., sustainable through time.

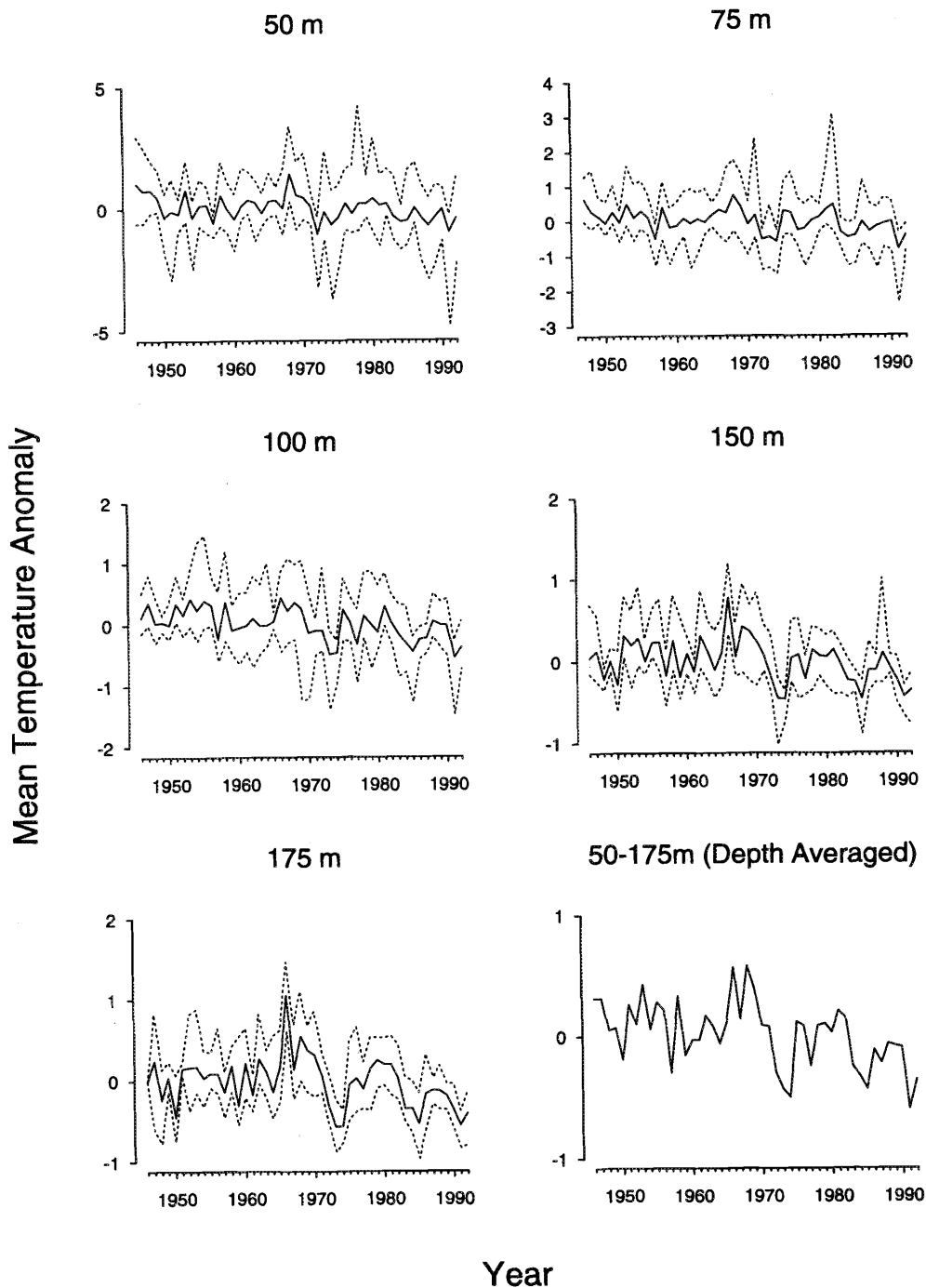


FIG. 4. Water temperature anomalies from the long-term mean (1946–92) at Station 27, immediately east of St. John's, Newfoundland, at depths of 50, 75, 100, 150, and 175 m and averaged across depths between 50 and 175 m. Solid lines represent annual temperature anomalies; broken lines indicate the maximum and minimum monthly temperature anomalies for each year.

We included age-specific rates of survival, l_x , and fecundity, m_x , for northern cod from 1962 to 1992. Fishing mortality estimates for ages 3–13 yr are available in Baird et al. (1991a) for the 1962–77 period and from Bishop et al. (1993b) for the 1978–92 period. Natural mortality per annum for all ages was assumed to be 18% (Baird et al. 1992; Bishop et al. 1993b). To allow for estimation errors in fishing mortality, F , we calculated r at F -values 30% greater and less than those provided in the assessment documents

(Baird et al. 1991a; Bishop et al. 1993b). For comparison, an independent review of the northern cod stock suggested an error rate of $\pm 22\%$ for the overall fishing mortality rate estimated for 1988 (Harris 1990).

Age-specific fecundities were estimated from the fecundity versus weight regressions calculated by May (1967). Weight-at-age data from the commercial fishery are available from 1972 to 1992 (Bishop et al. 1993b). Data from 1962 to 1971 were approximated by the average weight-at-age from 1972

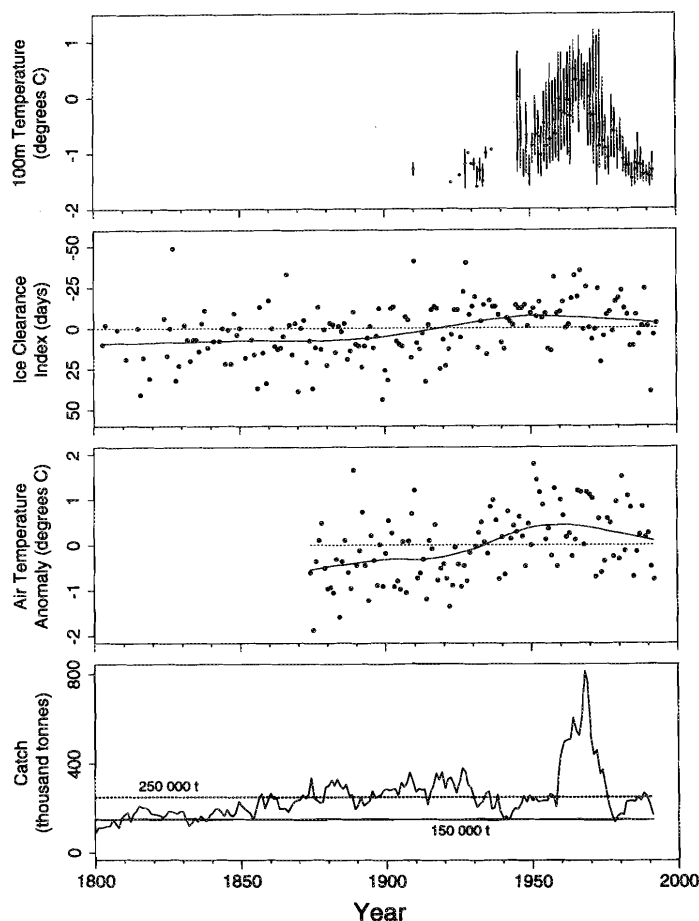


FIG. 5. Temporal variation in water temperatures on the continental shelf in 3L, date of ice clearance, air temperature, and commercial catch of Atlantic cod in NAFO Divisions 2J3KL. Shelf temperatures in 3L at 100 m (1910–92; MEDS data base) are represented by the median with the upper and lower quartiles represented by the lines above and below each median, respectively. Ice clearance index (1800–1993) represents the departure in days from the 1964–84 median clearing date at Hopedale, Labrador (data from Newell 1991). Air temperature anomalies from the long-term mean (1874–1992) recorded by Canadian Atmospheric and Environment Service at St. John's, Newfoundland. Estimated commercial catch of Atlantic cod from the region corresponding to 2J3KL from 1800 to 1992 (data from Hutchings and Myers 1995).

to 1992. The similarity between the 1972–92 averaged weights-at-age and those estimated from autumn sampling by Canadian research vessels in 2J and 3K in the early 1950s and early 1960s suggests that such an approximation is a reasonable one (unpublished data). Based upon empirical data available from 1973 to 1992 (Shelton and Morgan 1993), we assumed that 0% of females reproduce prior to age 5 yr, 10% at age 5, 50% at age 6, and 100% at age 7 and at all subsequent ages until death following reproduction at age 15 (fish older than 15 yr constituted a median 1% of the total harvested biomass from 1962 to 1991; Bishop et al. 1993b).

To estimate survival from birth to age 3 yr (ages for which we do not have data), we plotted recruitment (number of 3-yr-old cod) against the expected fecundity contribution of the reproductive portion of the population (i.e., the summed product of age-specific fecundities and age-specific

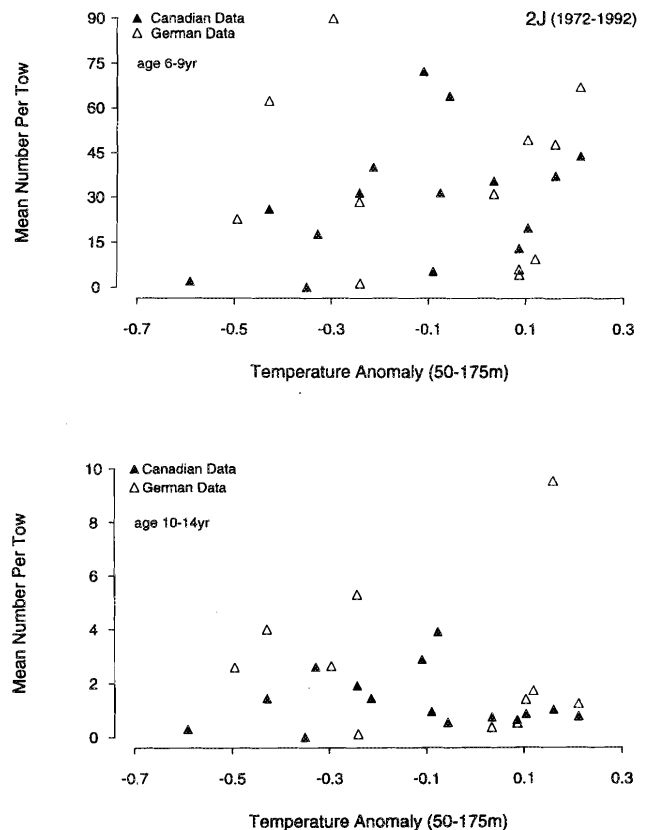


FIG. 6. Scatterplots of mature cod abundance against Station 27 water temperature anomaly in NAFO Division 2J. Data are from autumn research surveys conducted by German and Canadian vessels from 1972 to 1992.

abundances). Three stock–recruit relationships were applied to the data (Fig. 3B): the Ricker, Beverton–Holt, and Cushing models (described by Cushing (1971) and Hilborn and Walters (1992)). Survival from birth to age 3 was estimated from the Ricker and Cushing models which generally encompassed the stock and recruit values predicted by the Beverton–Holt model. By using these models, the influence of density on juvenile survival (Myers and Cadigan 1993) is explicitly included in our estimates of sustainability.

Results

Interannual Variation in Water Temperature

Significant interannual variation exists among the 47 consecutive years of water temperature data at Station 27 in 3L ($F_{[46,463]} = 12.17, p = 0.0001$; Fig. 4). The time series of depth-averaged data indicates that temperatures were below the long-term mean in the early 1970s, the mid-1980s, and the early 1990s (lower right panel in Fig. 4). These relatively cold years (1972–74, 1984–85, and 1991–92) are evident within each depth interval and did not differ in temperature ($F_{[6,73]} = 1.94, p = 0.09$; depth-averaged temperatures from 20 to 175 m did not differ among these years either ($F_{[6,73]} = 1.91, p = 0.09$)). Thus, as measured by annual, depth-averaged temperature anomalies, the environmental conditions of 1991 and 1992 were also experienced from 1972 to 1974 and during 1984 and 1985. Minimum monthly anomalies at 50 and 75 m were lowest in 1991. However, those at 100, 150, and 175 m in 1991 were similar to or

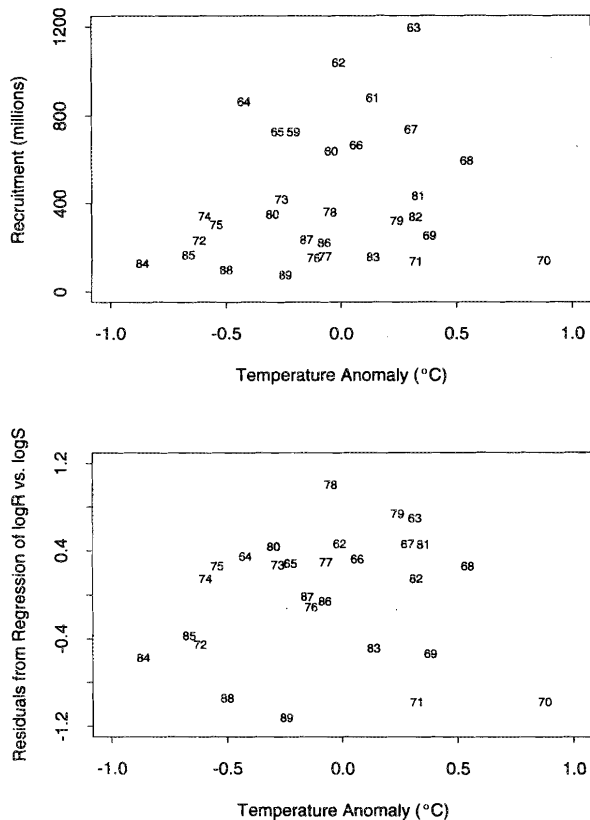


FIG. 7. Scatterplots of two indices of recruitment to the northern cod fishery against Station 27 water temperature anomaly (depth-averaged from 0 to 50 m). Upper panel: dependent variable represents millions of cod aged 3 yrs. Lower panel: dependent variable represents residuals from the linear regression of $\log_{10}(\text{recruitment})$ versus $\log_{10}(\text{spawning stock biomass})$. Data are indicated by year class.

less than those experienced in the early 1970s, the mid-1980s, and, for the 175 m depth, the late 1940s.

There was no indication that cod landings throughout the nineteenth century were deleteriously affected on the scale of the major fishery collapse experienced in 1991 despite environmental conditions colder than those of recent years (Fig. 5). Shelf water temperatures in 3L similar to or less than those of the early 1990s were experienced in the 1920s, 1930s, and late 1940s when commercial landings averaged roughly 250 000 t. Dates of ice clearance from the Labrador coast and air temperature at St. John's have been considerably earlier and warmer, respectively, in the past several decades than they were throughout the nineteenth and early twentieth centuries when northern cod landings ranged from 100 000 to 300 000 t. Thus, landings that were not sustainable in the 1980s were sustainable in colder environments during the nineteenth and early twentieth centuries.

Water Temperature and Cod Abundance

The German and Canadian surveys conducted over 21 yr (1972–92) in 2J constitute the longest continuous time series of research abundance estimates available for northern cod. Scatterplots of abundance (combined data sets) versus temperature anomaly indicate that abundance of mature cod during this period was not associated with water temperature (Fig. 6; cod aged 6–9 yr: $r = 0.08$, $p = 0.72$; cod aged 10–14 yr: $r = -0.03$, $p = 0.89$). The absence of significant

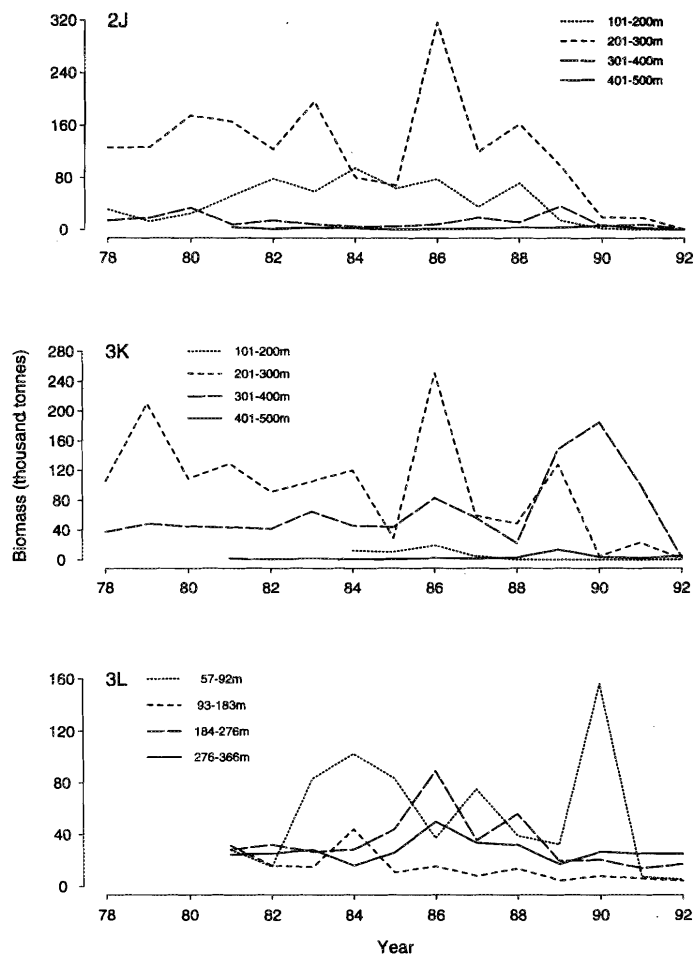


FIG. 8. Temporal changes in cod biomass at four depth intervals for which extensive sampling was conducted during autumn research surveys in NAFO Divisions 2J, 3K, and 3L. Standard errors of the annual total biomass estimates (all depths included) averaged $\pm 37\%$ in 2J, $\pm 41\%$ in 3K, and $\pm 16\%$ in 3L (data from Bishop et al. 1993b).

associations persists if the German and Canadian data are examined separately (cod aged 6–9 yr: $r_{\text{CAN}} = 0.39$ ($p = 0.15$), $r_{\text{GER}} = -0.13$ ($p = 0.68$); cod aged 10–14 yr: $r_{\text{CAN}} = -0.04$ ($p = 0.89$), $r_{\text{GER}} = -0.08$ ($p = 0.80$)).

The association between water temperature and juvenile cod abundance was examined by plotting numbers of recruits to the fishery (i.e., cod aged 3 yr) against the depth-averaged temperature anomalies recorded at Station 27 for the upper 50 m of the water column (depths at which cod eggs and larvae are found on the Newfoundland Shelf; Anderson and deYoung 1993) (Fig. 7, upper panel). The correlation coefficient between temperature and recruitment is not significant ($r = 0.19$, $p = 0.54$). When the effect of spawning stock size on recruitment is removed from the analysis, there is still no evidence that recruitment is associated with any range of water temperature during the first year of life ($r = 0.08$, $p = 0.78$; Fig. 7, lower panel). Nor are there significant associations between recruitment (effects of spawner stock removed) and depth-averaged temperature anomalies in the upper 10 m ($r = -0.14$, $p = 0.58$), upper 20 m ($r = -0.09$, $p = 0.74$), or the entire water column from 0 to 175 m ($r = 0.18$, $p = 0.47$). Similar nonsignificant associations exist between recruitment and temperature experienced during

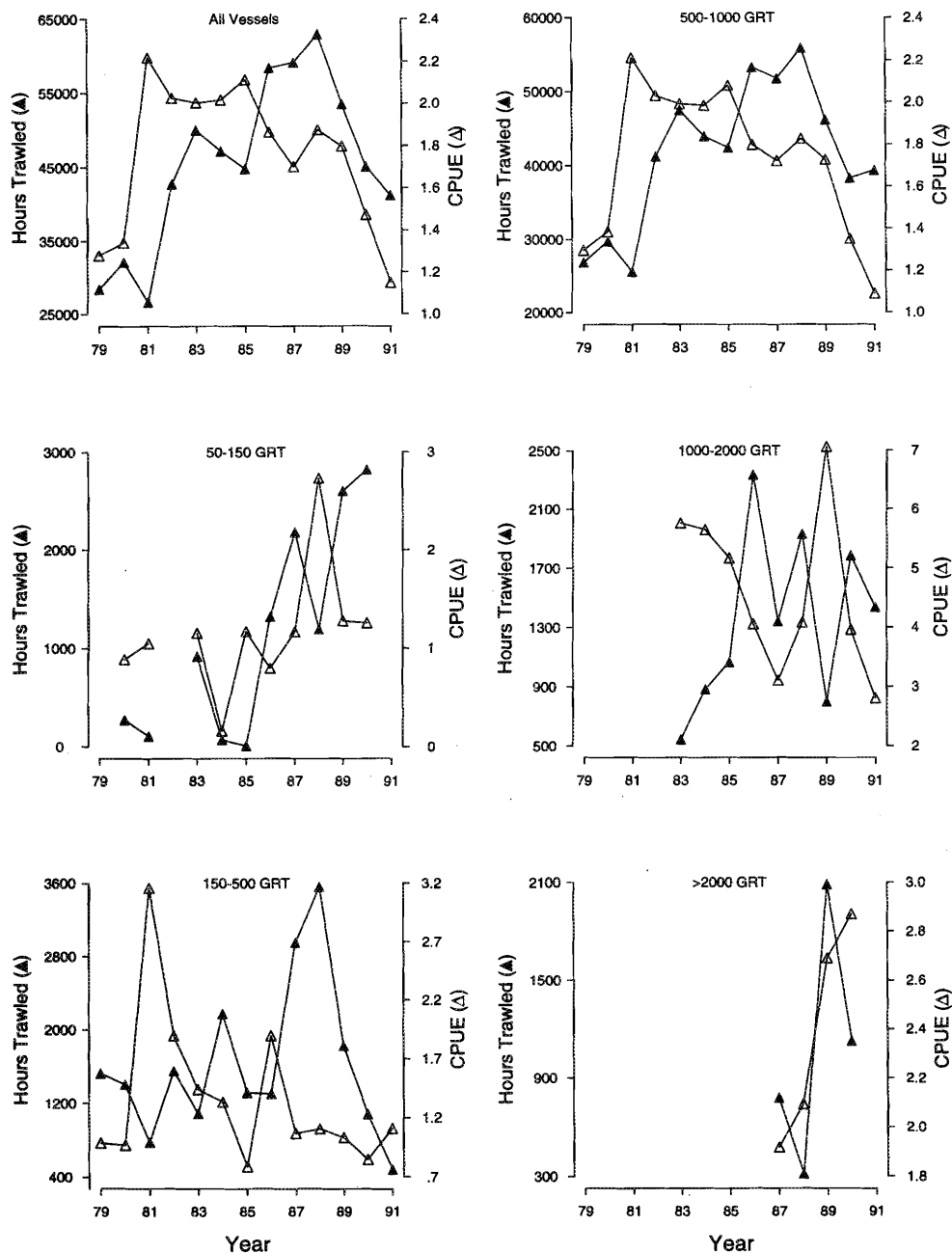


FIG. 9. Temporal variation in nominal commercial fishing effort (hours trawled; solid triangles) and catch per unit effort (CPUE, metric tonnes of cod per trawling hour; open triangles) for Canadian otter trawlers fishing for Atlantic cod in NAFO Divisions 2J3KL from 1979 to 1991 (GRT = gross registered tonnage).

the second and third years of life (upper 50 m of water, $r = 0.23$, $p = 0.40$ and $r = 0.46$, $p = 0.08$, respectively).

Interannual Variation in Depth Distribution of Cod

The biomass of northern cod in deep water, relative to that in shallow water, has not been significantly greater in the 1990s than in previous years and there is no evidence that the depth distribution of cod is related to water temperature. Any apparent proportional increase in cod biomass in deep water is due to the near absence of fish in shallow water (Fig. 8). In 2J, cod biomass from 100 to 300 m has declined by at least two orders of magnitude since 1978 whereas biomass between 300 and 500 m has changed little through

time. Biomass at depths 300–400 m in 3K increased between 1989 and 1991 whereas that between 400 and 500 m was consistently low. Shallow water (100–300 m) biomass in 3K declined almost 100-fold over the 15-yr period. In 3L, cod biomass in deep water (184–366 m) in the early 1990s was lower than or similar to estimates from 1981 to 1989. As with the other two regions, biomass in shallow water (57–183 m) in 3L declined by almost two orders of magnitude through the 1980s and early 1990s. Water temperature was not significantly associated with deepwater cod biomass (>300 m in 2J and 3K, >184 m in 3L), relative to biomass in shallower water, in any of the regions (2J: $r = -0.35$, $p = 0.27$; 3K: $r = -0.28$, $p = -0.47$; 3L: $r = -0.08$, $p = 0.80$).

Temporal Trends in Fishing Effort and Nominal Catch per Unit Effort of Canadian Trawlers

The harvesting pressure imposed by offshore trawlers on northern cod was assessed by examining temporal changes in fishing effort (number of trawling hours by Canadian vessels) and catch per unit effort (CPUE, expressed as tonnes of cod captured per hour trawling) (Fig. 9). Catch and effort data are presented for all vessels and for five of the six tonnage classes of Canadian stern trawlers separately (the smallest tonnage class, not shown here, caught less than 1% of the annual trawler harvest from 1979 to 1991). Annually, more than 90% of the cod biomass caught by Canadian trawlers was harvested by vessels between 500 and 1000 gross registered tonnage (GRT, upper right panel of Fig. 9). From 1981 to 1988, fishing effort for these vessels more than doubled from 25 544 to 55 923 trawling hours whereas CPUE declined 23% over the same time period. Hours trawled and CPUE were negatively correlated for the 500–1000 GRT vessels ($r = -0.90$, $p = 0.01$, p -value corrected for autocorrelation) and for all vessels combined ($r = -0.89$, $p = 0.02$). The 54% increase in trawling hours between 1981 and 1991 for 500–1000 GRT vessels was associated with a halving of CPUE. Negative associations between effort and CPUE are also evident for 150–500 GRT vessels and among most years for 1000–2000 GRT vessels. It is noteworthy that during the first 4 yr of operation of the latter vessels, whose harvesting efficiency was generally more than double that of other vessels, a 30% decline in CPUE was associated with an almost fivefold increase in effort.

Temporal Trends in Gillnet Catches and Nominal CPUE

Gillnet landings of cod throughout 2J3KL increased from 11 435 to 47 000 t between 1974 and 1982, declined rapidly between 1982 and 1985 to 20 500 t, and increased again to almost 47 000 t in 1989 before decreasing to 17 300 t in 1991 (Fig. 10A). Temporal variation in gillnet catches in 2J3KL is reflected largely by catches in 3L. Inshore landings in 3L increased from 19 500 to 31 000 t in 1987 and remained at that level for two more years before declining by 50% in each of 1990 and 1991 (Fig. 10B). Offshore gillnet catches increased dramatically from 8 t in 1985 to 19 448 t in 1990, comprising 45 and 71% of the total gillnet catch in 2J3KL in 1990 and 1991, respectively. The dramatic spatial changes that occurred during the late 1980s in the fixed-gear fishery are well illustrated by the observation that between 1985 and 1990, offshore gillnet catches of northern cod increased from less than 1 to 18% of the total fixed-gear landings of northern cod.

Inshore trap and gillnet catches were associated with declining catch rates throughout the latter half of the 1980s (Fig. 11). Catch rates in the 3K and 3L trap fisheries decreased from 1986 to 1991 with the decline clearly evident by 1989. Notably, a tripling of trap catches in 3L between 1987 and 1990 was associated with a 70% reduction in catch rate. Significant reductions in gillnet catch rate were evident in Trinity Bay by 1988, Bonavista and Conception bays by 1989, and between St. Mary's Bay and the Southern Shore by 1990. Stable or declining gillnet catches were associated with declines in catch rate of 80, 60, and 76% in Bonavista (1986–89), Conception (1987–89), and Trinity (1985–89) bays, respectively. Between 1986 and 1990, catches from

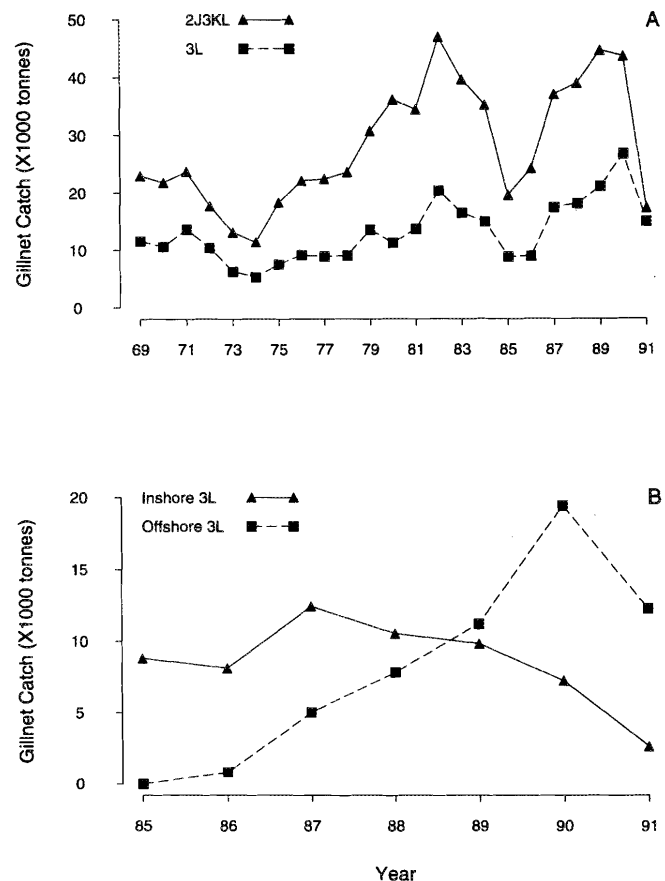


FIG. 10. Temporal variation in gillnet catches of northern cod in (A) 2J3KL and 3L and (B) inshore and offshore unit areas (defined in text) in 3L.

St. Mary's Bay and along the Southern Shore declined 21% whereas catch rate declined 30%.

Offshore harvest of cod by gill nets began after the sharp decline in inshore gillnet landings in 2J3KL between 1982 and 1985 (Fig. 10B). The majority of offshore cod captured by gill net were harvested in the Virgin Rocks area in central Grand Bank (unit area 3Lr) (Fig. 1 and 12). The increase in catch from Virgin Rocks from nil in 1985 to 17 257 t in 1990 was associated with a 53% reduction in catch rate. This pattern of rapid decline from initially high catch rates that exceeded those experienced inshore to relatively low rates was evident throughout the Northeast Newfoundland Shelf (unit areas 3Kbcefg) and throughout north and central Grand Bank (Fig. 12).

Temporal Changes in Age-Specific Weight and Abundance

Temporal changes in age-specific body weight are evident for northern cod of reproductive age from 1972 to 1992 with variability generally increasing with age (Fig. 13). In general, weight-at-age increased from the early 1970s to the late 1970s before declining thereafter. The lowest weights-at-age occurred between 1972 and 1975 for all age classes except the 10- and 11-yr-olds whose lowest weights-at-age were experienced in 1992. Although these commercial data represent the longest continuous time series of weight-at-age data for northern cod, it should be noted that the representation of cod from each division differs somewhat annually.

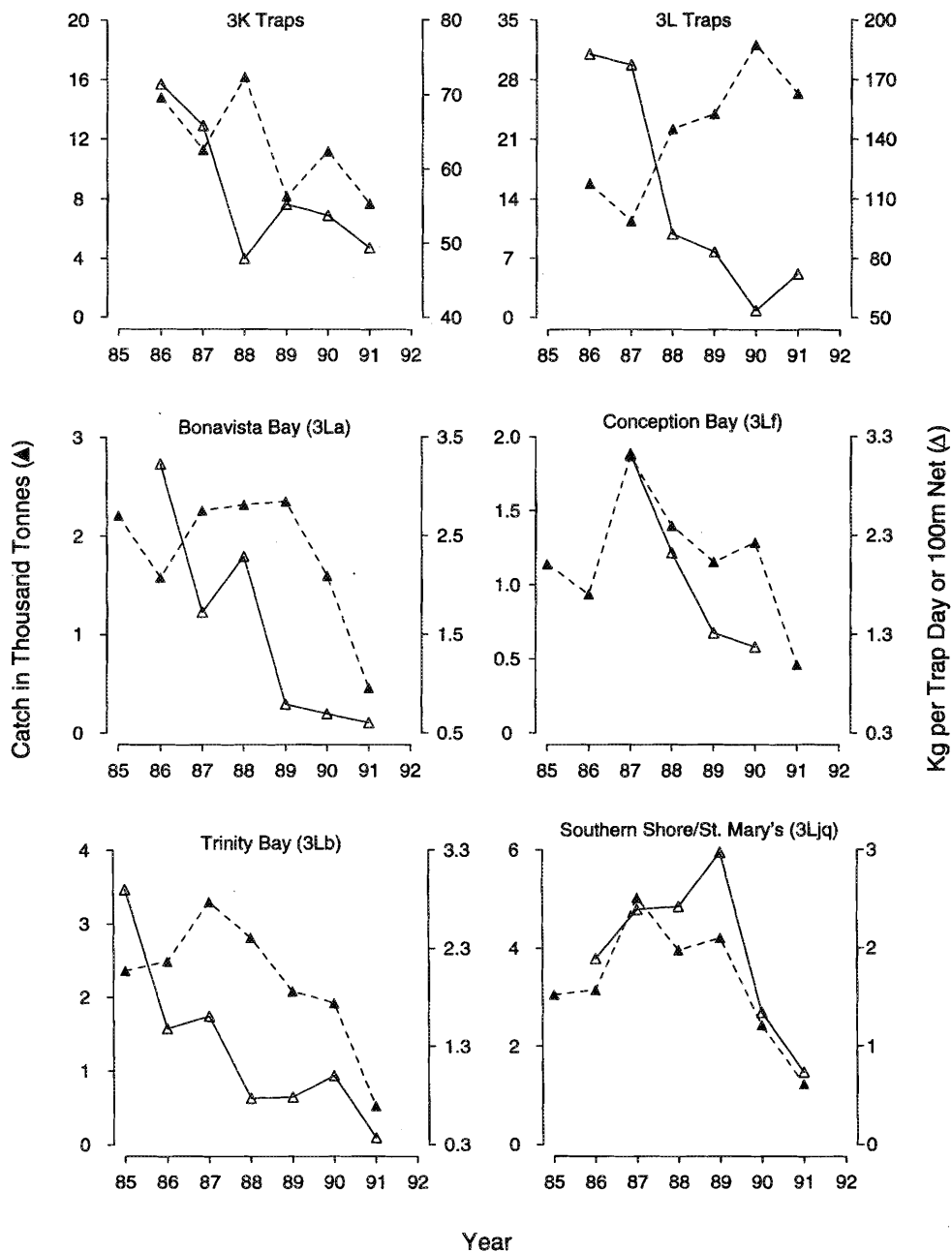


FIG. 11. Inshore catches (solid triangles) and catch rate (open triangles) for the trap (3K and 3L) and gillnet (3L unit areas) fisheries for northern cod.

Temporal changes in age structure are evident from age-specific variation in fecundity contribution to the northern cod stock (i.e., age-specific abundance multiplied by age-specific fecundity; Fig. 14). Independent of time, most eggs are produced by 6-, 7-, and 8-yr-old females. The fecundity contribution of older individuals has declined dramatically since the 1960s (1962–69) when an annual average 30% of all eggs (46% in 1962) were produced by 10- to 14-yr-old cod. This percentage dropped by almost one half to 17% in the 1970s before declining further to 12% in the 1980s and 11% in the last 2 yr of the fishery (1990 and 1991). Changes in age structure during the last 5 yr of the fishery (1987–91) were very similar to those of the 5 yr leading up to the extension of Canada's jurisdiction to 200 miles (1973–77; Fig. 14, lower two panels). In addition

to similar collapses in age structure, total estimated fecundity declined 23% during both 5-yr periods.

Annual Variation in the Realized Rate of Natural Increase

Age-specific survival probabilities imposed on northern cod since 1962, and corresponding age-specific fecundities, have rarely been sufficiently high to allow northern cod to sustain themselves (Fig. 15). Independent of the survival estimate to age 3 (Fig. 15A and 15B), the annual rate of change in cod abundance declined steadily from 1962 to 1976, increased to 1980 following Canada's jurisdictional extension to 200 miles, and then declined again from 1981 to 1991. The two periods in which r rose dramatically, i.e., 1976–80 and 1991–92, were associated with significant reductions in fishing pressure by non-Canadian and Canadian vessels, respectively.

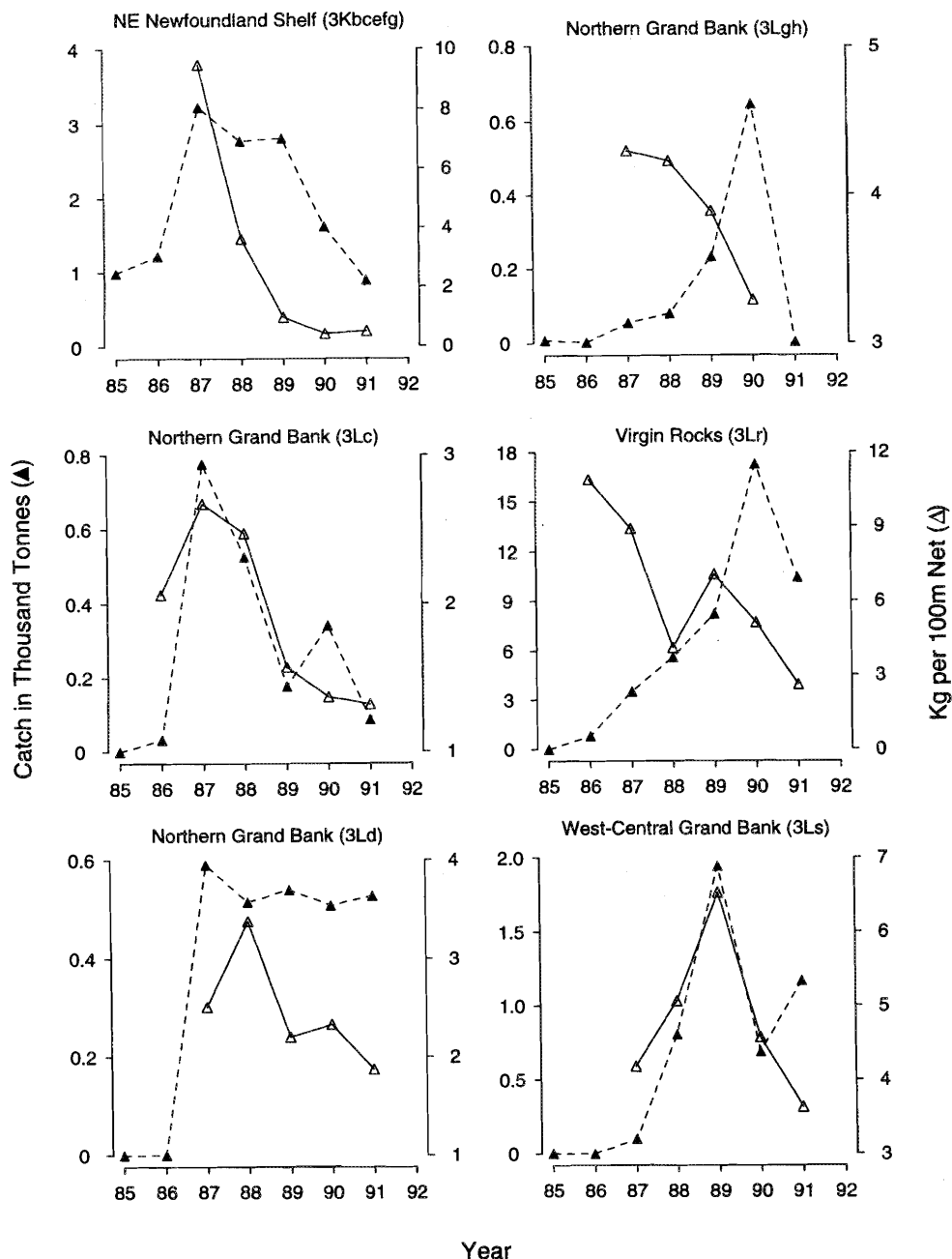


FIG. 12. Offshore gillnet catches (solid triangles) and catch rate (open triangles) in 3K (all offshore unit areas combined) and in six unit areas throughout 3L. See Fig. 1 for location of unit areas.

Harvestable abundance (cod aged 3 yr and older) from 1962 to 1992 estimated from yearly estimates of r , independent of survival to age 3 yr, is highly correlated with estimates based upon the VPA (Fig. 15C; 1962–77 data from Baird et al. 1991a; 1978–92 data from Bishop et al. 1993b). Although the VPA- and r -based estimates of abundance are not independent (both use the same survival data), their concordance suggests that predicted changes in population sustainability reflect temporal changes in cod abundance.

Discussion

Collapse of the Northern Cod Stock

The demographic changes that northern cod have incurred since 1962 have rarely allowed the stock to sustain itself over

the past three decades. This lack of sustainability coupled with historically high commercial catches and technological expertise, an age structure that has collapsed with respect to number of reproductive age classes and numbers of individuals per age class, declining inshore and offshore catch rates during the past decade, and a lack of evidence for environmentally related influences on cod survival lend overwhelming support to the hypothesis that human overexploitation precipitated the commercial extinction of northern cod.

Unsustainable Harvesting of Northern Cod

The inability of northern cod to achieve sustainability is not surprising given the harvest rates (i.e., commercial catch/harvestable biomass) imposed on the stock since 1962

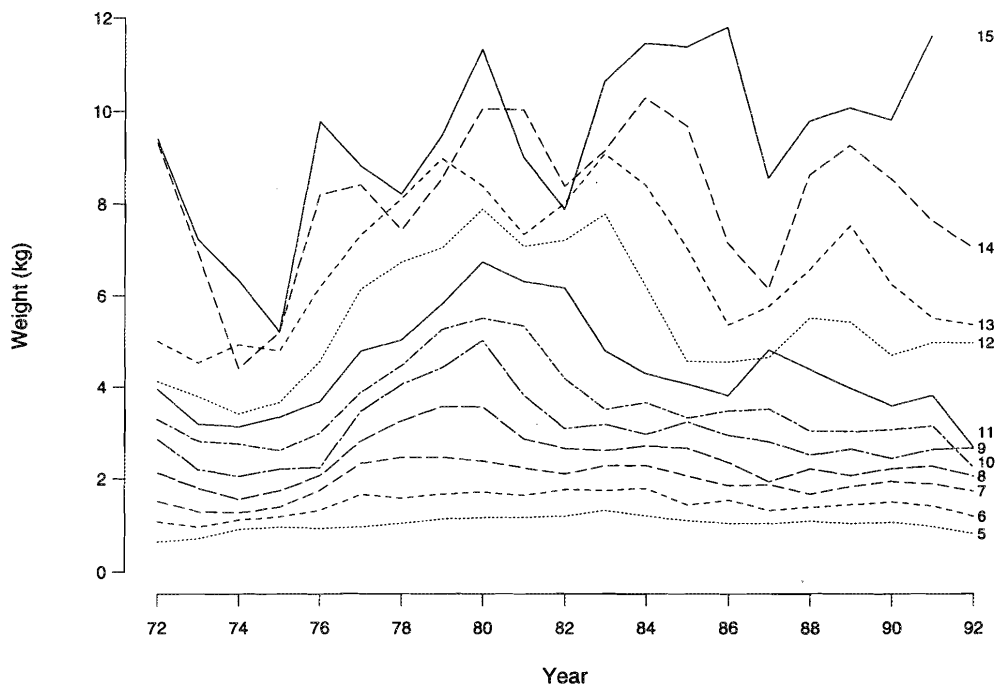


FIG. 13. Weight-at-age data for northern cod of ages 5–15 yr as determined from commercial catches from 1972 to 1992.

(Fig. 16A). A comparison of Fig. 15A, 15B, and 16A indicates that harvest rates less than 17% (the 1962 estimate) will permit the stock to sustain itself. The approximate linearity of the stock–recruit relationship for northern cod (Fig. 3A) suggests that the sustainable harvest rate will be relatively constant with changes in stock size. The data suggest that the stock was sustainable at harvest rates between 19 and 25% from 1978 to 1984. However, this interpretation should be treated with caution, as this period coincided with the largest age-specific weights, and hence the largest age-specific fecundities (and thus increased r), since 1972. These large weights-at-age may be attributable to the high growth rates associated with low density for northern cod (Millar and Myers 1990) and may not be representative of the average age-specific weights (or fecundities) experienced by the stock. It is also noteworthy that age-specific weights in the late 1980s and early 1990s are similar to or greater than those recorded between 1947 and 1950 (Fleming 1952). It should be noted that our estimates of harvest rate are probably underestimates because they do not include age-specific vulnerabilities to the fishery (younger fish tend to be less vulnerable to the fishery than older fish).

A total allowable catch (TAC) was first established for northern cod by the International Commission for the Northwest Atlantic Fisheries (ICNAF) in 1973 (temporal changes in management criteria for northern cod are detailed by Steele et al. (1992) and by Lear and Parsons (1993)). The TAC was based upon the management strategy of fishing at the maximum sustainable yield, i.e., at $F_{\max} = 0.35$. Increased concern about the conservation of the resource led to the establishment of $F_{0.1}$ (described by Gulland and Boerema 1973) as the target fishing mortality rate in 1977. The $F_{0.1}$ for northern cod was set at 0.2 which corresponded to a harvest rate of 18%. TACs were set at the $F_{0.1}$ level in 1977 and 1978, at 80% $F_{0.1}$ from 1979 to 1983, and again at 100% $F_{0.1}$ from 1984 to 1986. Following 2 yr during which

TACs were once again based upon fishing mortality less than $F_{0.1}$, it was realized that fishing mortalities throughout the 1980s had consistently exceeded $F_{0.1}$ because of overestimation of stock size (Baird et al. 1991b). Concomitant with these excessive fishing mortalities were the high proportions of the commercial catches composed of largely prereproductive individuals, i.e., less than 7 yr of age. These percentages increased from 55% in each of 1980, 1981, and 1982 to a mean of $66 \pm 4(\text{SE})\%$ from 1983 to 1992 (range 46–84%) (data from annual stock assessment documents for the 2J3KL stock). The extent to which TACs since 1977 have exceeded the sustainable harvest rate of 17% suggested here is illustrated in Fig. 16B.

Perhaps the most direct question related to the relative importance of overfishing to the recent collapse of northern cod is: How much of the variation in abundance in the past decade can be explained solely on the basis of changes in harvest rate? Although a temporal analysis of changes in fishing mortality in the 1980s indicates that harvest rates were exceedingly high, these harvest rate data are based upon estimates of age-specific abundance derived from VPA in which natural mortality is assumed to be constant.

One means of assessing the validity of the harvest rates estimated for the 1980s is to calculate changes in the abundance of northern cod based upon changes in harvest rate and then compare these with independent estimates of abundance such as those derived from the autumn research surveys. Annual changes in abundance N from year t to year $t + 1$ as a consequence of changes in harvest rate in year t , H_t , can be estimated as

$$(5) \quad N_{t+1} = N_t e^{r_t^*} (1 - H_t).$$

Thus, abundance is predicted to increase between years t and $t + 1$ by the expected rate of population increase *in the absence of fishing* in year t , $e^{r_t^*}$, and to decline by an amount proportional to the harvest rate experienced in that

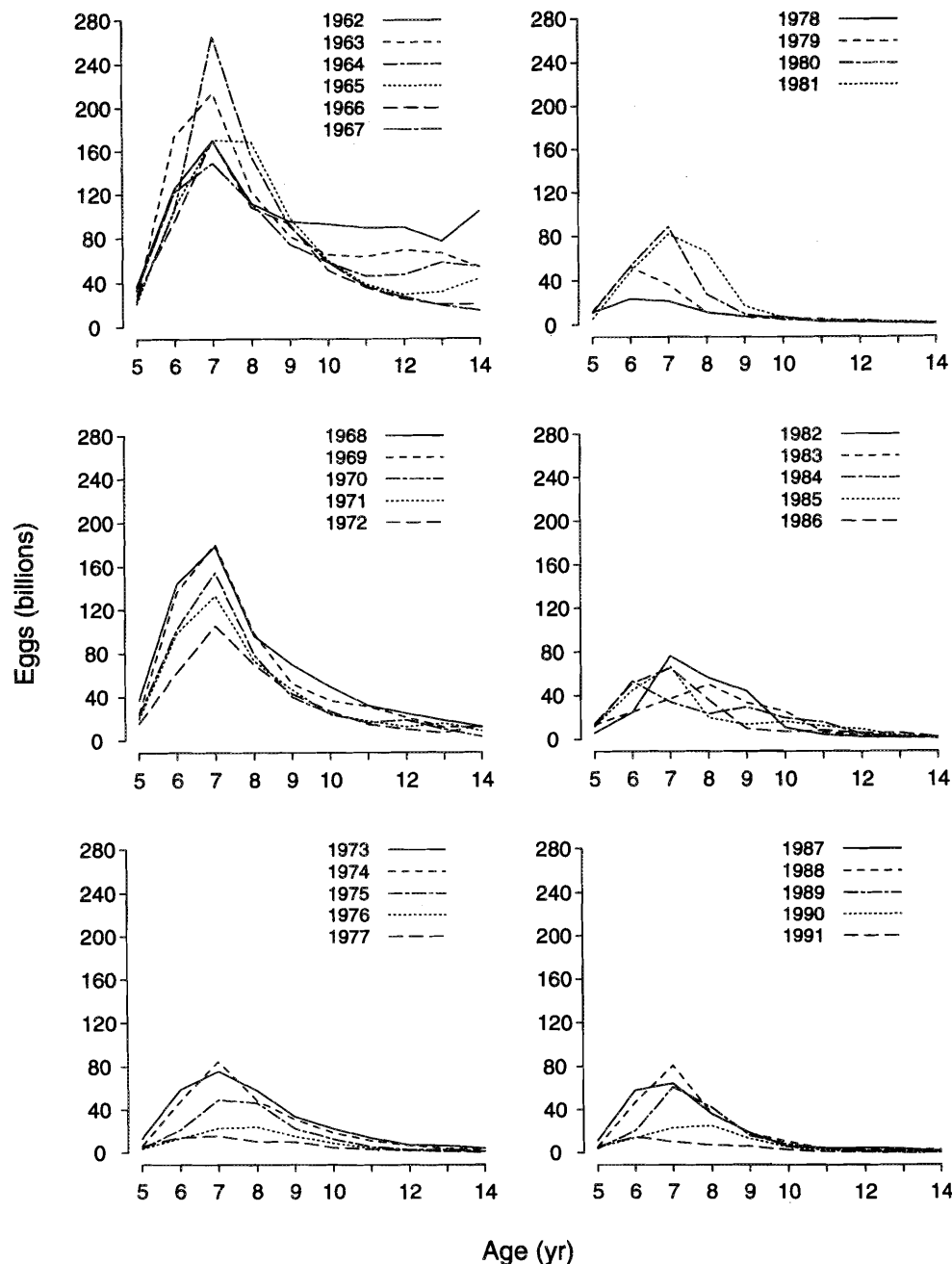


FIG. 14. Estimated age-specific fecundity contributions for northern cod from 1962 to 1991.

year (cf. Lockwood 1987). e_t^* is estimated by assuming constant natural mortality of 18% (i.e., $M = 0.2$) and no fishing mortality (i.e., $F = 0$).

The longest continual decline in abundance of exploited northern cod in the 1980s occurred from 1985 to 1992 (Fig. 15C). Predicted changes in abundance during this period, as estimated from Equation (5), can be compared with those derived from the autumn research surveys (for which annual changes in abundance are a consequence of both natural and fishing mortality). To account for sampling error, observed mean number of harvestable cod per tow in year t was approximated by the mean number per tow in years $t - 1$, t , and $t + 1$, i.e., as a 3-yr running mean (data from Bishop et al. 1993b). The predicted numbers of cod per tow are highly correlated with those observed during the research surveys ($r = 0.78$, $p = 0.02$, p -value corrected

for autocorrelation; Fig. 17). This concordance suggests that 61% of the variation in abundance from 1985 to 1991 can be accounted by harvest rate and lends strong support to the hypothesis that the decline of northern cod in the 1980s can be attributed primarily to overexploitation. This conclusion is supported by an independent analysis which indicates that the natural mortality of northern cod did not increase prior to the imposition of the moratorium in 1992 (Myers and Cadigan 1995).

Long-term Demographic Collapse of Northern Cod

By any demographic measure, the viability of northern cod has been seriously threatened since the introduction of European-based offshore trawlers in the late 1950s and early 1960s. By 1977, when compared with 1962 estimates, (1) harvestable biomass had declined 82% (2 961 000 versus

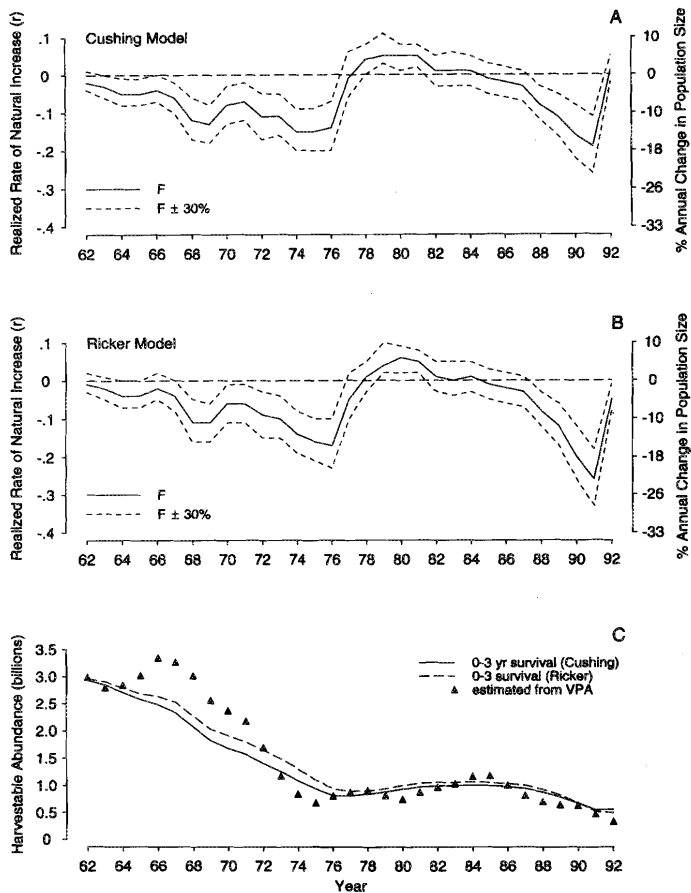


FIG. 15. Temporal variation in r , the realized rate of natural increase (left ordinate), from 1962 to 1992 and its relationship to harvestable abundance (cod aged 3 yr and older) from 1978 to 1992. At $r = 0$, the population replaces itself through time. When r is greater or less than 0, the population increases or decreases, respectively, at the annual rates of change indicated on the right ordinate (note that the right ordinates are not linearly scaled). (A) Survival from birth to age 3 yr estimated from the Cushing spawner–recruit relationship. (B) Survival from birth to age 3 yr estimated from the Ricker spawner–recruit relationship. (C) Temporal change in harvestable abundance as estimated by VPA (Bishop et al. 1993b) and as calculated assuming annual rates of change in population size corresponding to the annual estimates of r with survival from birth to age 3 yr estimated from the Ricker and Cushing stock–recruit relationships.

526 000 t), (2) spawner biomass had declined 94% (1.6 million versus 93 000 t), (3) recruitment had declined 84% (1 billion versus 168 million), (4) fecundity contribution of 10- to 14-yr-old fish had declined from 46 to 18%, and (5) harvest rates had yet to attain levels at which the stock was sustainable. For most populations, the 82% reduction in harvestable northern cod biomass experienced between 1962 and 1977 would have been considered a collapse! If not for the large reduction in harvest rate by 1978 (less than half the 1975 rate of 51%) concomitant with the establishment of the 200-mile limit and the fortuitously high recruitment (relative to spawner abundance) provided by the 1978–81 year classes (cf. Fig. 7), northern cod would probably have collapsed by 1980. The remarkably similar patterns of decline in r (Fig. 15), in age-specific fecundity contributions, and in total fecundity between the 1973–77 and 1987–91 time

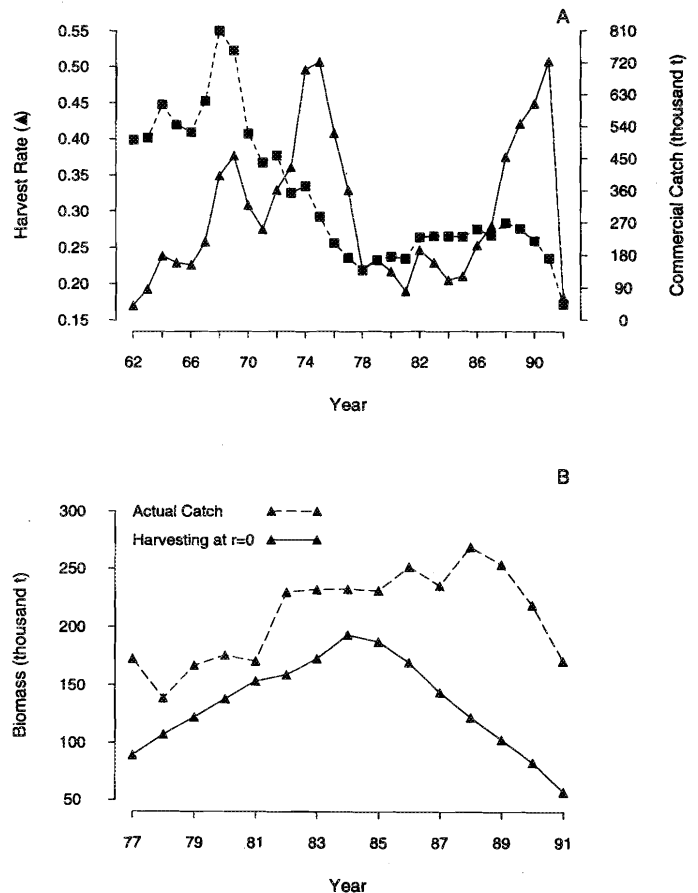


FIG. 16. (A) Temporal variation in harvest rate (commercial catch/harvestable biomass) of commercial vessels (triangles) and in reported commercial catches (squares) from 1962 to 1992. (B) Changes in actual and estimated sustainable catches (harvest rate = 17%, see text) for northern cod from 1977 to 1991.

periods (cf. Fig. 14, lowest two panels) are consistent with this hypothesis. Given the near collapse of the stock in 1977, it is not surprising that there was little margin for error in establishing sustainable harvest rates in the early 1980s. However, harvest rates in the 1980s greatly exceeded the targeted $F_{0.1}$ level, largely because of overestimation of stock size (described by Baird et al. (1991b) and by Hilborn and Walters (1992, p. 533–535) and discussed further below) coupled with great uncertainty in abundance estimates derived from the research surveys (standard errors of 30–40% of the mean are not uncommon; data in Bishop et al. 1993b).

Changes in Catch Rate and Spatial Allocation of Effort as Metrics of Stock Health

The decline in northern cod abundance in the 1980s was reflected by changes in fishing effort and catch rate. During the decade preceding the northern cod moratorium, a twofold decline in annual survival probability (cf. Fig. 2) was associated with increased inshore and offshore fishing effort, a spatial change in allocation of gillnet effort, and dramatic declines in catch rate of inshore and offshore fishing gear. The observed doubling of hours trawled and the halving of trawler catch rate may be conservative estimates of the temporal increase in fishing effort and decline in harvesting efficiency (cf. Rothschild 1977). One hour of trawling in

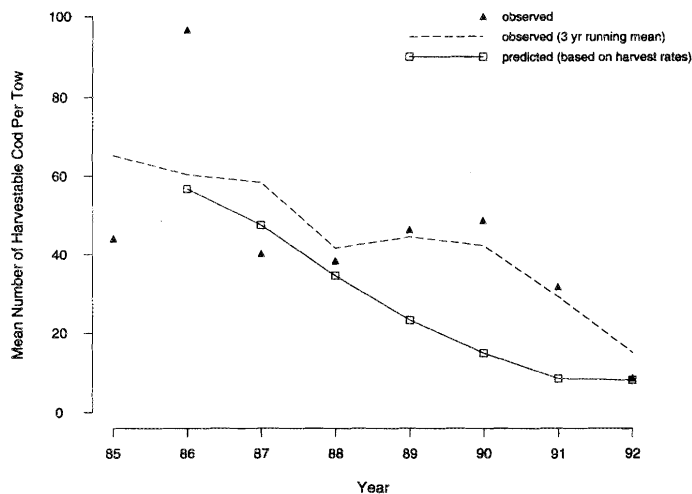


FIG. 17. Mean number of harvestable cod (cod aged 3 yr and older) per tow in 2J3KL from 1985 to 1991 as observed from autumn research surveys and as predicted from annual estimates of harvest rate.

1991 may have exerted considerably more mortality on the stock than one trawling hour in 1981 because of increased ability to locate and harvest cod through advances in technology and learning by those exploiting the resource. Temporal changes may also, however, have been affected by changes in trawling practices and gear operation which can combine to decrease trawling effort (e.g., the employment of windows on trawls to allow for increased escapement of fish).

Increasing inshore catches combined with declining catch rates were indicative of dramatic increases in effort in the mid- to late 1980s (and possibly as early as the 1960s; cf. Templeman 1966). Initiation of the use of gill nets offshore in 1987, where catch rates declined at even faster rates than they did inshore, would appear to have been a direct consequence of declining catch rates inshore. Thus, despite increases in both gillnet and trap catches of northern cod from the mid-1980s (Fig. 10; Bishop et al. 1993b), these patterns did not reflect the health of the stock because they obscured the underlying dynamics of spatial and temporal changes in the allocation of effort.

The influence of changes in gear technology on catch rates of northern cod, and on management's perception of stock health, has not received the attention it warrants. It is clear that the ability of inshore fishers to catch fish has increased dramatically with time, particularly during the 1980s, and any interpretation of temporal changes in landings should reflect these changes in effort. For example, echo sounders can permit the employment of greater number of cod traps per fisher because of the avoidance of hauling empty traps. Sounders also reduce the time handline fishers spend on locating cod. Throughout the 1980s, there was increased use of "Japanese" cod traps whose design allows for reduced escapement of fish and permits their placement in areas unsuitable for regular cod traps (Neis 1992). Advanced navigation equipment such as Loran C enables fishers to record electronically the location of large fish assemblages, sites of previously large catches, and the precise orientation of gillnet sets. The necessity of having to increase effort significantly throughout the 1970s and 1980s in order to maintain catches is amply reflected in interviews with inshore cod fishers (e.g., Neis 1992; Davis et al. 1994).

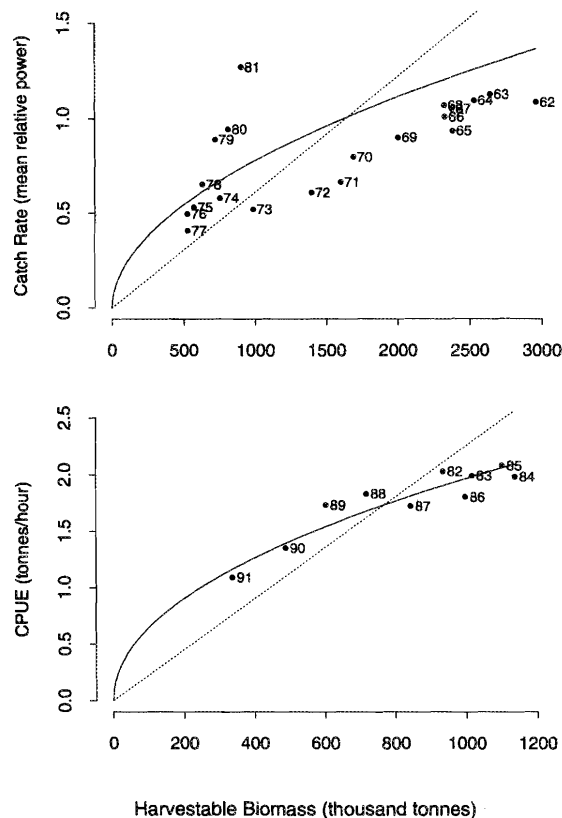


FIG. 18. Relationship between catch rate (estimated from a multiplicative model by Bishop and Gavaris 1982) and harvestable biomass of northern cod (biomass of cod aged 3 yr and older) from 1962 to 1981 (upper panel) and between nominal catch per unit effort (CPUE) of Canadian stern otter trawlers and harvestable biomass from 1982 to 1991 (lower panel).

High trawler catch rates can be maintained despite declining stock size for the simple reason that fishers do not exploit fish in a random manner. Increased ability to locate large assemblages of fish coupled with an apparent increase in the concentration of northern cod in the 1980s (Bishop et al. 1993b) can also lead to nonlinear relationships between catch rate and stock abundance, thus violating one of the implicit assumptions of most analyses of commercial catch data (Hilborn and Walters 1992). Such nonlinearity is evident in plots of catch rate against harvestable biomass of northern cod during the 10 yr immediately preceding the moratorium (1982–91) and during the previous 20 yr (1962–81). (Fig. 18). Catch rates from 1982 to 1991 represent the nominal CPUE estimated from 500–1000 GRT Canadian trawlers; catch rates from 1962 to 1981 were those estimated by Bishop and Gavaris (1982). For both time periods, a curvilinear relationship between CPUE and harvestable biomass (HB) ($CPUE = \alpha HB^\beta$) provided a significantly better fit to the data than did the model with β constrained to be 1 (1962–81 data: $CPUE = 0.001HB^{0.52}$, $F_{[2,17]} = 64.6$, $p < 0.00001$; 1982–91 data: $CPUE = 0.070HB^{0.48}$, $F_{[1,8]} = 69.3$, $p = 0.00003$) such that the probability of overestimating abundance increases as CPUE declines (note the similarity in the slopes, β , of the two models). The first-order autocorrelation coefficient was significant ($p = 0.0006$) in the 1962–81 data but not for the 1982–91 data. Thus, the parameters for the model describing the 1962–81 data were estimated under the assumption that the error term is an autoregressive process.

We also assumed that all estimation errors were in CPUE (following Richards and Schnute 1986). If estimation errors are assumed to be in HB, similar and highly significant regressions are obtained. The pattern of nonlinearity illustrated in Fig. 18 is expected in fisheries (such as the offshore trawler fishery for northern cod) where search is highly efficient, effort is concentrated in areas in which fish are most abundant, and fish remain concentrated as abundance declines (Hilborn and Walters 1992). There is a growing literature which indicates that β is less than 1 for many gadoid stocks with the result that fishing mortalities can remain high despite declines in stock size (e.g., Cooke and Beddington 1985; Crecco and Overholtz 1990; Rose and Leggett 1991).

Increased search and harvesting efficiency of Canadian trawlers contributed to the serious overestimates of northern cod abundance in the 1980s. This is well illustrated from 1977 to 1981 (Fig. 18, upper panel) in which a more than threefold increase in catch rate was associated with a relatively small increase in stock abundance. The potential for overestimation of stock size is clear given that technological advances had increased catch rates from 1979 to 1981 to levels previously realized in the 1960s when abundance was considerably higher. From 1978 to 1986, the abundance of northern cod was usually approximated by the midpoint of the VPA estimates derived from both commercial CPUE data and data from research vessel surveys (Baird et al. 1991b). However, abundance estimates based upon the commercial data indicated that the stock had increased threefold from 1978 to 1988 whereas those based upon the research surveys suggested that the stock had changed little in size (Baird et al. 1991b; Hilborn and Walters 1992, p. 533–535). The main consequence of this overestimation of stock size was that actual fishing mortality rates exceeded the targeted $F_{0.1}$ level of $F = 0.2$ more than twofold from 1978 to 1983 (average of $F = 0.41 \pm 0.03$ (SE) for cod aged 7–9 yr) and more than threefold from 1984 to 1989 (average of $F = 0.65 \pm 0.08$) (data in Bishop et al. 1993b).

Relative Importance of Environmental Change to the Collapse of Northern Cod

Water temperature and sustainable harvests

How much of the variation in northern cod abundance in the decade preceding the moratorium can be attributed to variability in the environment? More specifically, to what extent did “ecological factors” in 1991 (Lear and Parsons 1993) or cold temperatures throughout the 1980s (deYoung and Rose 1993) predicate the collapse in cod abundance? Long-term data for a variety of environmental indices including the NOA index (data on sea level air pressure) (Drinkwater 1994), areal extent of the CIL on the Northeast Newfoundland Shelf (Drinkwater 1994), Station 27 water temperatures (Fig. 4), 100 m depth water temperatures throughout 3L, pack ice persistence off Labrador, and air temperature in St. John’s (Fig. 5) indicate that while it was relatively cold and ice cover relatively extensive in 1991, similar conditions had been experienced during the previous two decades and considerably colder conditions had prevailed throughout the nineteenth and early twentieth centuries. Evidence of a colder environment in the 1800s is also supported by ground borehole data from Newfoundland (Beltrami and Mareschal 1992) and by long-term (1550–1978) tree-ring data from northern Canada and Alaska (which indicate that most of the nineteenth century

was characterized by slower than average growth whereas better than average growth has occurred since 1925; Jacoby and Cook 1983).

Despite the colder environment from 1800 to the 1920s, it was possible to sustain a fishery of the size that was not sustainable in the 1980s. There is no evidence of extraordinarily high natural mortalities leading to a major stock collapse in the past two centuries of the kind experienced in the early 1990s. Extant historical records of mass cod mortalities (Templeman 1965) were reported during years (1876, 1934, 1960) in which catches were relatively high (~160 000, ~260 000, and 459 000 t, respectively). If the reduction in cod abundance in the 1980s and early 1990s was due to increased natural mortality resulting from cold temperature, then similar population declines should have been evident during years with similarly cold temperatures (e.g., 1972–74, 1984–85, 1991–92). Despite encompassing all three cold periods, the longest continuous research time series (in region 2J) did not yield a significant correlation between water temperature and cod abundance. It is also worth noting that the large 1.7°C decline in water temperature on St. Pierre Bank (NAFO division 3Ps) off the south coast of Newfoundland from the 1981–84 average of 1.4°C to the 1985–91 average of -0.7°C (mean temperature at 50 m between January and June; data in Hutchings and Myers 1994) was not associated with a precipitous decline in cod biomass (Bishop et al. 1993a).

Water temperature and depth distribution of cod

Data from the autumn research surveys are not consistent with a directed movement of large numbers of cod to deeper water (Fig. 8). Any apparent increase in the proportion of cod biomass in deep water in the late 1980s and early 1990s can be attributed to the near absence of cod in shallow water. In addition, the distribution of cod with depth appears to be unrelated to water temperature. Although the water temperature data in our analysis were those from Station 27, and as such do not extend to some of the deeper depths at which fish were caught in the research surveys, our results agree with those of Lilly (1994) who examined the relationship between bottom temperatures recorded at the time of the research surveys and the abundance of cod in the shallowest strata in division 2J. He concluded that there was no support for the postulate that the reduced abundance of cod in the north and west sections of 2J and 3K was the result of avoidance of cold water. Hutchings and Myers (1994) could also find no association between late and winter/spring temperatures and cod biomass on the shelf relative to that on the slope in 3L (the latter being a metric of the spring migration from the slope to shelf).

Water temperature and recruitment

We are unable to document any association between water temperature and recruitment of cod to the fishery (Fig. 7). Of the five cold years for which data are available (1972–74, 1984, 1985), two year classes were greater than average whereas three were less than average (Fig. 7, lower panel). Myers et al. (1992) were also unable to find any consistent relationship between Station 27 water temperature or the extent of the CIL with either VPA or research survey estimates of recruitment. In contrast, deYoung and Rose (1993) reported a positive correlation between northern cod recruitment and temperature between 1972 and 1988. Their exclusion of data from 1962 to 1971 notwithstanding, deYoung and Rose (1993)

removed the effects of spawner abundance on recruitment by dividing the number of 3-yr-olds by the *number* of cod aged 6 yr and older. This means of accounting for changes in the fecundity of a stock can be justified only if the age and size distributions of reproductive individuals remain constant with time, i.e., if fecundity is a function of the numbers of individuals and neither their age nor size. It is clear, however, that both mean age and body size have declined over the past two and three decades (cf. Fig. 14). Decreasing age and body size will have the effect of continually underestimating recruitment with ever-increasing bias when number of recruits is divided by number of spawners. If the effect of spawner biomass (a more reliable metric of fecundity than abundance) on recruitment is removed from the analysis, there is no significant association between recruitment and water temperature (depth-averaged over 0–50 m) for the 1972–89 year classes of northern cod ($r = 0.31$, $p = 0.210$). Again, if water temperature in the upper 50 m (the usual location of cod larvae; Anderson and deYoung 1993) has a significantly detrimental effect on larval survival, a significant decline in recruitment in 3Ps should have been observed following the 1.4°C decline in temperature (greater than *any* annual decline recorded at Station 27) at 50 m between 1984 and 1985. However, there is no significant association between water temperature (January through June at 50 m; data in Hutchings and Myers 1994) and the residuals from the regression of $\log_{10}(\text{recruitment})$ against $\log_{10}(\text{spawner biomass})$ (data in Bishop et al. 1993a) for cod in 3Ps from 1972 to 1989 ($r = 0.11$, $p = 0.662$).

It has been argued that cold temperatures effect southerly shifts in the location of spawning cod and lead to recruitment failures (deYoung and Rose 1993). Empirical support for the argument is primarily of three kinds. The first was an apparent association between water temperature and recruitment which, as outlined above, is problematic in its interpretation. Second, cod larvae in 2J3KL were purported to be more southerly distributed in a cold year (1935) than in a warm year (1934). However, this observation must be tempered by the observation that there was no difference in water temperatures on the Northeast Newfoundland Shelf in 1934 and 1935 (MEDS data base; $t_{1761} = 0.95$, $p = 0.35$). Third, deYoung and Rose (1993) also argued, citing data on spring distributions of cod on the Northeast Newfoundland Shelf, that cod were more southerly distributed in two cold years (1984 and 1985) than in two warm years (1986 and 1987). However, given that the hydroacoustic samples upon which these data are based were not conducted north of 51°30'N in 1984 and 1985 because of ice conditions, the finding of cod north of this latitude in 1986 and 1987 does not constitute evidence that cod are more northerly distributed in warm years (a caveat noted also by deYoung and Rose 1993). The claim that cod are more widely dispersed in warm years cannot be assessed in the absence of data on actual locations and sampling effort of the ship(s) involved.

Salinity and recruitment

Even if there is an effect of water temperature on recruitment, although not detectable with data presently available, it will likely be small relative to that of the size of the spawning stock. This can be illustrated by an analysis of the effects of salinity on northern cod recruitment. Based upon a model proposed by Sutcliffe et al. (1983), Myers et al. (1993) found that salinity experienced during the second year of life was significantly related to recruitment

from 1976 to 1987 when spawning stock biomass was included in the analysis. We repeated their multiple regression analysis because the most recent VPA estimates of recruitment and spawner biomass (Bishop et al. 1993b) indicated that recruitment from the 1984 to 1988 year classes was substantially less than had been estimated in 1992 (Baird et al. 1992). The percentage reductions in the 1993 recruitment estimates relative to those from 1992 were 16% (1984 year class), 23% (1985), 42% (1986), 55% (1987), and 43% (1988).

Our reanalysis indicates that salinity has little effect on recruitment relative to that of spawner biomass. Comparing one-variable models, the r^2 of the regression of log-transformed spawner biomass against log-transformed recruitment ($r^2 = 0.39$, $p = 0.0004$; untransformed recruitment and spawner biomass data: $r^2 = 0.73$, $p < 0.0001$) is highly significant whereas that of the regression of salinity against log-transformed recruitment is not ($r^2 = 0.11$, $p = 0.08$; untransformed recruitment data: $r^2 = 0.15$, $p = 0.04$). The marginal significance of salinity suggested by the regression of salinity against the untransformed recruitment data is not evident in the multiple regression model (i.e., recruitment = $\alpha(\text{spawner biomass}) + \beta(\text{salinity}) + \epsilon$). Following the stepwise addition of spawner biomass, inclusion of salinity does not significantly improve the r^2 of the multiple regression for either the transformed ($p = 0.10$) or untransformed data ($p = 0.07$).

Resistance and resilience to environmental variation

We conclude that, relative to the effect of spawner biomass, neither temperature nor salinity had a significant influence on recruitment of northern cod prior to the moratorium in 1992. However, one consequence of the dramatic reductions in abundance experienced by northern cod over the past three decades may have been increased susceptibility to environmentally induced stochasticity in age-specific survival rates (Harrison 1979; Lande 1988). Populations with low r can have reduced ability to return to their equilibrium density following a disturbance from equilibrium, i.e., they have low resilience (Holling 1973; May et al. 1974; Harrison 1979; Pimm 1991). Low resilience of northern cod is implied by their low intrinsic rates of increase during the 1970s and mid- to late 1980s (Harwood 1978; Harrison 1979). Thus, the negative association between resilience and harvesting mortality (Beddington 1978; Harwood 1978) may have increased the susceptibility of cod in recent years to changes in water temperature to which larger, more resilient populations would not have been affected. Thus, the extremely low abundance of northern cod in the 1990s raises justified concern that increased vulnerability to both fishing (within and without the 200-mile limit) and naturally occurring environmental variation may significantly increase the probability of extinction of this stock.

Population resilience would also be expected to decline with increased variability in juvenile survival. Based upon their finding that age is positively correlated with spawning duration in cod, Hutchings and Myers (1993) identified a mechanism by which the size-selective mortality against larger, older individuals characteristic of most fisheries can increase variability in recruitment. Selective mortality against larger individuals is reflected by the observation that relative to the early 1960s, the expected fecundity contribution of older cod (15–20 yr) in the late 1980s had declined by two orders of magnitude relative to that of younger (7–9 yr)

individuals, i.e., for every 100 eggs produced by younger cod, older cod produced 40 eggs in the early 1960s but only 4 eggs in the late 1980s (Fig. 1B in Hutchings and Myers 1993). Given that younger cod spawn for a shorter period than older cod (Hutchings and Myers 1993), this bias towards younger ages coupled with a decline in the number of age classes during spawning would be expected to shorten the effective spawning season, reducing the likelihood that larvae could initiate feeding during the period of peak zooplankton abundance and thereby increasing variation in juvenile survival.

Conclusions

Our analyses of realized population growth (r) indicate that northern cod have rarely been fished at sustainable levels since at least 1962. Overfishing by long-distance trawlers in the 1960s and 1970s had reduced the stock to near commercial extinction in 1977. Since Canada's extension of fisheries jurisdiction to 200 miles, two factors were of prime importance in contributing to the overexploitation of the stock from 1977 to 1991. First, management estimated that recruitment from 1977 would equal the average maintained from 1962 to 1972 (see Steele et al. (1992) and Lear and Parsons (1993) for more details). Given that the stock (i.e., harvestable abundance) was three to four times larger in the 1960s than in 1977, and that recruitment was *not* corrected for changes in spawner biomass, the predicted rate of growth of the stock was greatly overestimated (see harvest predictions in Kirby 1982). Nonetheless, the predicted growth of the stock led to markedly increased industrial and government investment which fuelled a socioeconomic and political optimism in the fishery whose momentum could not easily be abated. The second factor was the overestimation of stock size (described earlier) and the concomitant excess of actual fishing mortality over targeted rates. As noted by Finlayson (1994), reliance upon commercial data, whose catch rates indicated that the stock was increasing in size, to "fine-tune" the VPAs (at least until 1986) was probably a reflection of management's prediction of rapid growth of the stock in the late 1970s.

The temporal changes in demography, population sustainability, harvest rates, and inshore/offshore catch rates documented here provide strong evidence that overexploitation was the primary cause of the collapse of northern cod in the early 1990s. The inability to identify unambiguous and significant associations between water temperature and both spatial and depth-related indices of juvenile and adult cod abundance (Myers et al. 1992; deYoung and Rose 1993; Lilly 1994; present paper), the collapse in population structure defined primarily by fewer reproductive age classes and fewer individuals per age class (Fig. 14), the observation that cod did not have anomalously low age-specific weights in the early 1990s (Fig. 13; Fleming 1952), the observation that the population decline can be predicted solely from harvest rates and cannot be attributed to increased natural mortality (Fig. 17; Myers and Cadigan 1995), the low amount of recruitment variability that can be attributed to water temperature and salinity, and the fact that large harvests were sustainable during a colder environment in the nineteenth and early twentieth centuries underscore our postulate that the environment contributed relatively little to the collapse of northern cod relative to that imposed by the fishery.

The cod collapse and previous commercial extinctions in

the history of fisheries management (e.g., California sardine (Radovitch 1981); Peruvian anchovy (Hilborn and Walters 1992); African/Namibian pilchard (Cram 1981)) should provide ample justification for politicians, policy-makers, industry, and management to limit the urge to attribute resource collapses to vaguely understood or even imagined environmental causes. The ecological and socioeconomic consequences of so responding to repeated failure are too great.

Acknowledgements

We very much appreciate the assistance of those presently involved in the assessment of northern cod, notably Claude Bishop, Eugene Murphy, and Don Stansbury. Nick Barrowman and Noel Cadigan provided invaluable statistical and computing assistance; David Arenillas assisted us in digitizing some of the data. We thank John Newell for permission to use the ice clearance data presented in Fig. 5 and Darryl Janes for compiling and updating these data. Ken Drinkwater provided the air temperature data in Fig. 5. Financial support for this work was provided by the Northern Cod Science Programme and a NSERC Visiting Fellowship to J.A.H. Carl Walters provided extremely useful comments and criticism on an earlier version of the manuscript. Bruce Atkinson, Ray Beverton, Claude Bishop, Michael Fogarty, Richard Haedrich, George Lilly, Gordon Mertz, Bill Montevecchi, Doug Morris, Barbara Neis, Andy Rosenberg, Nancy Shackell, Chris Taggart, and George Winters also provided very helpful comments and discussion.

References

- ANDERSON, J.T., AND B. DEYOUNG. 1993. Application of a 1-dimensional model to vertical distributions of cod eggs and larvae on the north-east Newfoundland shelf. ICES Symp. Cod and Climate Change, Poster 11. 14 p.
- BAIRD, J.W., C.A. BISHOP, W.B. BRODIE, AND E.F. MURPHY. 1992. An assessment of the cod stock in NAFO divisions 2J3KL. NAFO Sci. Council. Res. Doc. 92/18, Ser. No. N2063.
- BAIRD, J.W., C.A. BISHOP, AND E.F. MURPHY. 1991a. An assessment of the cod stock in NAFO Divisions 2J3KL. CAFSAC Res. Doc. 91/53: 84 p.
- BAIRD, J.W., C.A. BISHOP, AND E.F. MURPHY. 1991b. Sudden changes in the perception of stock size and reference catch levels for cod in north-eastern Newfoundland shelves. NAFO Sci. Council. Stud. 16: 111-119.
- BEDDINGTON, J.R. 1978. On the risks associated with different harvesting strategies. Rep. Int. Whaling Comm. 28: 165-167.
- BELTRAMI, H., AND J.-C. MARESCHAL. 1992. Ground temperature changes in eastern Canada: borehole temperature evidence compared with proxy data. Terra Nova 5: 21-28.
- BEVERTON, R.J.H. 1990. Small marine pelagic fish and the threat of fishing; are they endangered? J. Fish Biol. 37: 5-16.
- BISHOP, C.A., AND S. GAVARIS. 1982. Assessment of the cod stock in NAFO Divisions 2J3KL. NAFO Sci. Council. Res. Doc. 82/VI/68, Ser. No. N561: 12 p.
- BISHOP, C.A., E.F. MURPHY, AND M.B. DAVIS. 1993a. An assessment of the cod stock in NAFO Subdivision 3Ps. DFO Atl. Fish. Res. Doc. 93/70: 39 p.
- BISHOP, C.A., E.F. MURPHY, M.B. DAVIS, J.W. BAIRD, AND G.A. ROSE. 1993b. An assessment of the cod stock in NAFO Divisions 2J+3KL. NAFO Sci. Council. Res. Doc. 93/86, Ser. No. N2271: 51 p.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. Wiley & Sons, New York, N.Y. 234 p.
- CELL, G.T. [ED.] 1982. Newfoundland discovered: English attempts at colonisation, 1610-1630. The Hakluyt Society, London. 310 p.
- CHARLESWORTH, B. 1980. Evolution in age-structured populations. Cambridge University Press, Cambridge. 300 p.
- CLEVELAND, W.S. 1979. Robust locally weighted regression and smoothing scatterplots. J. Am. Stat. Assoc. 74: 829-836.
- COLBOURNE, E., S. NARAYANAN, AND S. PRINSENBURG. 1994. Climatic change and environmental conditions in the Northwest Atlantic during the period 1970-1993. ICES Mar. Sci. Symp. (In press)
- COLE, L.C. 1954. The population consequences of life history phenomena. Q. Rev. Biol. 29: 103-137.

- CONSER, R. 1993. A brief history of ADAPT, p. 83–87. In R.K. Mohn and R. Cook [ed.] Introduction to sequential population analysis. NAFO Sci. Coun. Stud. No. 17, Dartmouth, N.S.
- COOKE, J.G., AND J.R. BEDDINGTON. 1985. The relationship between catch rates and abundance in fishes. IMA J. Math. Appl. Med. Biol. 2: 1–15.
- CRAM, D. 1981. Hidden elements in the development and implementation of marine resource conservation policy: the case of the southwest Africa/Namibian fisheries, p. 137–156. In M.R. Glantz and J.D. Thompson [ed.] Resource management and environmental uncertainty. Wiley & Sons, New York, N.Y.
- CRECCO, V., AND W.J. OVERHOLTZ. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Can. J. Fish. Aquat. Sci. 47: 385–394.
- CUSHING, D.H. 1971. The dependence of recruitment on parent stock in different groups of fishes. J. Cons. Int. Explor. Mer 33: 340–362.
- DAVIS, M.B., P. LUNDRIGAN, AND P. RIPLEY. 1994. A description of the cod stock structure in Placentia Bay, NAFO Subdivision 3Ps. DFO Atl. Fish. Res. Doc. 94/32: 16 p.
- DE LOTURE, R. 1949. History of the great fishery of Newfoundland. Gallimard, France. (Transl. from French by C.C. Taylor. U.S. Fish Wildl. Serv. Spec. Sci. Rep. (Fish.) No. 213, 1957).
- DE YOUNG, B., AND G.A. ROSE. 1993. On recruitment and distribution of Atlantic cod (*Gadus morhua*) off Newfoundland. Can. J. Fish. Aquat. Sci. 50: 2729–2741.
- DRINKWATER, K.F. 1994. Overview of environmental conditions in the Northwest Atlantic in 1993. DFO Atl. Fish. Res. Doc. 94/11.
- FINLAYSON, A.C. 1994. Fishing for truth: a sociological analysis of northern cod assessments from 1977–1990. Inst. Soc. Econ. Res., Memorial University of Newfoundland, St. John's, Nfld. 176 p.
- FLEMING, A.M. 1952. A study of the age and growth of the cod (*Gadus callarias* L.) in the Newfoundland area. M.A. thesis, University of Toronto, Toronto, Ont. 119 p.
- FRCC. 1993. Report on the status of groundfish stocks in the Canadian Northwest Atlantic. Fisheries Resource Conservation Council. Department of Fisheries and Oceans, Ottawa, Ont.
- GAVARIS, S. 1988. An adaptive framework for the estimation of population size. CAFSAC Res. Doc. 88/29: 12 p.
- GOSLING, W.G. 1910. Labrador: its discovery, exploration, and development. Rivers, London. 574 p.
- GULLAND, J.A. 1983. Fish stock assessment: a manual of basic methods. Wiley & Sons, New York, N.Y. 223 p.
- GULLAND, J.A., AND L.K. BOEREMA. 1973. Scientific advice on catch levels. Fish. Bull. 71: 325–335.
- HARRIS, L. 1990. Independent review of the state of the northern cod stock. Communications Directorate, Department of Fisheries and Oceans, Ottawa, Ont. 154 p.
- HARRISON, G.W. 1979. Stability under environmental stress: resistance, resilience, persistence, and variability. Am. Nat. 113: 659–669.
- HARWOOD, J. 1978. The effect of management policies on the stability and resilience of British grey seal populations. J. Appl. Ecol. 15: 413–421.
- HASTIE, T.J., AND R.J. TIBSHIRANI. 1990. Generalized additive models. Chapman & Hall, New York, N.Y. 335 p.
- HEAD, C.G. 1976. Eighteenth century Newfoundland. Macmillan & Stewart, Toronto, Ont.
- HILBORN, R., AND C.J. WALTERS. 1992. Quantitative fisheries stock assessment. Chapman & Hall, New York, N.Y. 570 p.
- HOLLING, C.S. 1973. Resilience and stability of ecological systems. Ann. Rev. Ecol. Syst. 4: 1–24.
- HUTCHINGS, J.A. 1993. Adaptive life histories effected by age-specific survival and growth rate. Ecology 74: 673–684.
- HUTCHINGS, J.A., AND R.A. MYERS. 1993. The effect of age on the seasonality of maturation and spawning of Atlantic cod, *Gadus morhua*, in the Northwest Atlantic. Can. J. Fish. Aquat. Sci. 50: 2468–2474.
- HUTCHINGS, J.A., AND R.A. MYERS. 1994. The timing of cod reproduction: interannual variability and the influence of temperature. Mar. Ecol. Prog. Ser. 108: 21–31.
- HUTCHINGS, J.A., AND R.A. MYERS. 1995. The biological collapse of Atlantic cod off Newfoundland and Labrador: an exploration of historical changes in exploitation, harvesting technology, and management. In R. Arnason and L. Felt [ed.] Island fisheries of the North Atlantic. University of Malta Press, Malta. (In press)
- ICNAF. 1952. Statistics of landings of groundfish from the convention area. Second annual report for the year 1951–52. ICNAF, St. Andrews, N.B.
- JACOBY, G.C., AND E.R. COOK. 1983. Past temperature variations inferred from a 400-year tree-ring chronology from Yukon Territory, Canada. Arct. Alp. Res. 13: 409–418.
- KIRBY, M.J.L. 1982. Navigating troubled waters. A new policy for the Atlantic fisheries. Supply and Services Canada, Ottawa, Ont.
- LANDE, R. 1988. Genetics and demography in biological conservation. Science (Wash., D.C.) 241: 1455–1459.
- LEAR, W.H., AND L.S. PARSONS. 1993. History and management of the fishery for northern cod in NAFO Divisions 2J, 3K and 3L, p. 55–89. In L.S. Parsons and W.H. Lear [ed.] Perspectives on Canadian marine fisheries management. Can. Bull. Fish. Aquat. Sci. 226.
- LILLY, G.R. 1994. Predation by Atlantic cod on capelin on the southern Labrador and northeast Newfoundland shelves during a period of changing spatial distributions. ICES Mar. Sci. Symp. (In press)
- LOCKWOOD, S.J. 1987. A simple method for analysing trends in recruitment. J. Cons. Int. Explor. Mer 43: 279–284.
- LUDWIG, D., R. HILBORN, AND C. WALTERS. 1993. Uncertainty, resource exploitation, and conservation: lessons from history. Science (Wash., D.C.) 260: 17, 36.
- MAY, A.W. 1967. Fecundity of Atlantic cod. J. Fish. Res. Board Can. 24: 1531–1551.
- MAY, R.M., G.R. CONWAY, M.P. HASSELL, AND T.R.E. SOUTHWOOD. 1974. Time delays, density dependence, and single species oscillations. J. Anim. Ecol. 43: 747–770.
- MESSTORFF, J. 1984. Research vessel survey results for cod in division 2J as obtained by RV *Anton Dohrn* and RV *Walther Herwig* in autumn 1972–83. NAFO Sci. Coun. Res. Doc. 84/VI/91, Ser. No. N882: 7 p.
- MILLAR, R.B., AND R.A. MYERS. 1990. Modelling environmentally induced change in growth for Atlantic Canada cod stocks. Int. Coun. Explor. Sea C.M. 1990/G:24: 13 p.
- MOHN, R.K., AND R. COOK. 1993. Introduction to sequential population analysis. NAFO Sci. Coun. Stud. No. 17, Dartmouth, N.S. 110 p.
- MYERS, R.A., K. DRINKWATER, AND N. BARROWMAN. 1992. Cold water and recruitment in 2J3KL cod. CAFSAC Res. Doc. 92/97: 13 p.
- MYERS, R.A., AND N.G. CADIGAN. 1993. Density-dependent juvenile mortality in marine demersal fish. Can. J. Fish. Aquat. Sci. 50: 1576–1590.
- MYERS, R.A., AND N.G. CADIGAN. 1995. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. 52. (In press)
- MYERS, R.A., K.F. DRINKWATER, N.J. BARROWMAN, AND J.W. BAIRD. 1993. Salinity and recruitment of Atlantic cod (*Gadus morhua*) in the Newfoundland region. Can. J. Fish. Aquat. Sci. 50: 1599–1609.
- NAFO. 1984–94. Fishery statistics for 1979–1990. Statistical Bulletins 29–40, Dartmouth, N.S.
- NAFO. 1992. Report of the special meeting scientific council, 1–4 June 1992. NAFO Sci. Coun. Stud. Doc. 92/20, Ser. No. N2112: 39 p.
- NEIS, B. 1992. Fishers' ecological knowledge and stock assessment in Newfoundland. Nfld. Stud. 8: 155–178.
- NEWELL, J.P. 1991. Spring and summer ice and climate conditions in the Labrador Sea, 1800-present. Ph.D. thesis, University of Colorado, Boulder, Colo. Univ. Microfilm Inc., Ann Arbor, Mich., Order No. 9122631.
- NEWELL, J.P. 1992. Climate change in northeast Canada and the northwest Atlantic: new insights from a long term sea ice data set, p. 87–90. In Proc. 5th Int. Meet. Statistical Climatology, Toronto Environment Canada, Atmospheric Environment Service, Toronto, Ont.
- NEWELL, J.P. 1993. Exceptionally large icebergs and ice islands in eastern Canadian waters: a review of sightings from 1900 to present. Arctic 46: 205–211.
- PETRIE, B., J.W. LODER, J. LAZIER, AND S.A. AKENHEAD. 1992. Temperature and salinity variability on the eastern Newfoundland shelf: the residual field. Atmos. Ocean 30: 120–139.
- PIMM, S.L. 1991. The balance of nature?: ecological issues in the conservation of species and communities. University of Chicago Press, Chicago, Ill. 434 p.
- RADOVITCH, J. 1981. Lessons from coastal upwelling fisheries, p. 107–136. In M.R. Glantz and J.D. Thompson [ed.] Resource management and environmental uncertainty. Wiley & Sons, New York, N.Y.
- RICHARDS, L.J., AND J.T. SCHNUTE. 1986. An experimental and statistical approach to the question: is CPUE an index of abundance? Can. J. Fish. Aquat. Sci. 43: 1214–1227.
- ROFF, D.A. 1992. The evolution of life histories: theory and analysis. Chapman & Hall, New York, N.Y. 535 p.
- ROSE, G.A., AND W.C. LEGGETT. 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.
- ROSENBERG, A.A., M.J. FOGARTY, M.P. SISSEWINE, J.R., BEDDINGTON, AND J.G. SHEPHERD. 1993. Achieving sustainable use of renewable resources. Science (Wash., D.C.) 262: 828–829.
- ROTHSCHILD, B.J. 1977. Fishing effort, p. 97–115. In J.A. Gulland [ed.]

- Fish population dynamics. Wiley & Sons, New York, N.Y.
- SCHAFFER, W.M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55: 291-303.
- SHELTON, P.A., AND M.J. MORGAN. 1993. An analysis of NAFO Division 2J3KL cod spawner biomass and recruitment. NAFO Sci. Council. Res/Doc. 93/37, Ser. No. N2217: 14 p.
- SINCLAIR, P.R. 1985. From traps to dragnets: domestic commodity production in northwest Newfoundland, 1850-1982. *Inst. Soc. Econ. Res., Memorial University of Newfoundland, St. John's, Nfld.* 171 p.
- STEARNS, S.C. 1992. *The evolution of life histories.* Oxford University Press, Oxford. 249 p.
- STEELE, D.H., R. ANDERSEN, AND J.M. GREEN. 1992. The managed commercial annihilation of northern cod. *Nfld. Stud.* 8: 34-68.
- SUTCLIFFE, W.H., R.H. LOUCKS, K.F. DRINKWATER, AND A.R. COOTE. 1983. Nutrient flux onto the Labrador Shelf from Hudson Strait and its biological consequences. *Can. J. Fish. Aquat. Sci.* 40: 1692-1701.
- TEMPLEMAN, W. 1965. Mass mortalities of marine fishes in the Newfoundland area presumably due to low temperature. *ICNAF Spec. Publ. No. 6:* 137-147.
- TEMPLEMAN, W. 1966. Marine resources of Newfoundland. *Bull. Fish. Res. Board Can.* 154: 170 p.
- WARNER, W.W. 1977. *Distant water: the fate of North Atlantic fishermen.* Little, Brown & Co., Boston, Mass. 338 p.