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WHY DO FISH STOCKS COLLAPSE? THE EXAMPLE OF COD IN ATLANTIC CANADA

Ransom A. Myers,[1,3] Jeffrey A. Hutchings,[2] and Nicholas J. Barrowman[1]

[1]*Science Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland, Canada A1C 5X1*
[2]*Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1*

Abstract. In 1993, six Canadian populations of Atlantic cod (*Gadus morhua*) had collapsed to the point where a moratorium was declared on fishing. It has been argued that the collapses were caused by poor recruitment of cod to the fishery. Yet we are unable to detect a difference between the recruitment of year classes that should have contributed most to the spawning stock at the time of the collapse and recruitment levels in earlier years. A power analysis shows that we would have almost certainly detected an overall reduction of recruitment of 20%. There are considerable differences in the abundance trends as determined by research surveys and reconstructed from the commercial catch at age data (called ''virtual population analysis'' [VPA]) for each stock. VPA-based abundances consistently depict lower recruitment levels than do survey-based estimates in recent years. More important is the observation that from the early 1980s the VPA-based trend shows a decline where none is apparent in the survey-based trend. One explanation of these differences would be an increase in discarding of young fish as fishing mortality increased. We test the hypothesis that the mortality for young cod is unrelated to the fully recruited fishing mortality. This hypothesis is rejected; in each of the six stocks, high juvenile mortality was associated with high adult mortality. This is consistent with the discarding hypothesis. We suggest that age-specific abundance trends estimated from research surveys and VPA should be compared for all stocks where such data exist, and that high priority should be given to the measurement of discarding levels and the extent to which catch misreporting is related to changes in fishing mortality.

Key words: Atlantic cod; fishery catch surveys, accuracy of; fishing moratorium; Gadus morhua; *juvenile mortality; population collapses; power analysis; recruitment vs. fishing mortality; virtual population analysis.*

Introduction

The collapse of commercial fisheries for Atlantic cod (*Gadus morhua*) throughout eastern Canada has prompted critical evaluation of the reasons for the collapses in hopes that similar reductions in abundance can be prevented in the future. Abundance was so low for six of seven cod stocks that bans of unspecified duration were imposed on commercial exploitation in 1992 and 1993. The collapsed stocks range from southern Labrador to the continental shelf off eastern Nova Scotia (Table 1, Figs. 1 and 2). Compared to the maximum estimates for which data are available, spawner biomass at the time of the collapses had declined >75% in every stock, by >90% in three of the six stocks, and by 99% in what once was the largest cod fishery in the world, ''northern cod,'' off Labrador and northeastern Newfoundland (McGrath 1911, Thompson 1943).

The inability to control fishing mortality (the target fishing mortality was rarely obtained in any of the stocks; Fig. 2) has been identified as the primary cause for the collapse of stocks such as Labrador and northeastern Newfoundland (Hutchings and Myers 1994, Myers and Cadigan 1995*a*, *b*, Walters and Maguire 1996). However, it has been hypothesized that several years of poor recruitment, i.e., low survival from birth until age three at which individuals are vulnerable to the fishery, also played a significant role in reducing population abundance (de Young and Rose 1993, Sinclair 1994). Environmental conditions thought to effect unusually high mortality during the egg, larval, or juvenile stage(s) include low water temperatures, reduced salinity, increased seal predation, and decreased food abundance (de Young and Rose 1993, Atkinson and Bennett 1994, Mann and Drinkwater 1994).

The ''recruitment-failure'' hypothesis is that the collapse was caused by the lack of juveniles, i.e., recruits to the population. To address this, we tested whether recruitment (defined as the number of 3-yr-olds) of year classes that should have contributed to the fishery in the year the moratorium was declared was the same as recruitment levels in previous years.

There are two sources of abundance estimates from which we estimated recruitment for each of the cod stocks: research surveys and virtual population analysis (VPA). Research-survey estimates are based upon the

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[3] Address after 1 April 1997: Department of Biology, Dalhousie University, Halifax, Nova Scotia, Canada B3H 4J1.

TABLE 1. Eastern Canadian stocks of Atlantic cod, *Gadus morhua,* for which commercial fishing has been banned. Stock management units are designated by number–letter codes established by the Northwest Atlantic Fishery Organization (NAFO). The magnitude of each stock collapse is expressed as the percentage decline in spawner biomass (SB) between the maximum (SB_{max}) and that during the year in which a fishing moratorium was imposed, as estimated by virtual population analysis.

Stock	NAFO division	Year of SB_{max}	SB_{max} (Mg)	SB_{mor} (Mg)	Collapse in SB (%)†	First SB data‡	Moratorium§
Labrador and northeastern Newfoundland	2J3KL	1962	1599	22	98.9	1962	1992
Southern Grand Bank	3NO	1967	193	17	91.2	1959	1993
St. Pierre Bank	3Ps	1960	139	32	77.0	1959	1993
Northern Gulf of St. Lawrence	3Pn4RS	1984	188	10	94.7	1974	1993
Southern Gulf of St. Lawrence	4TvN	1956	429	49	88.6	1950	1993
Eastern Scotian Shelf	4VsW	1963	103	16	84.5	1958	1993

† The percentage collapse in SB is defined as $[1 - (SB_{mor}/SB_{max})] \times 100$.
‡ Earliest year for which SB data are available.
§ Year of moratorium imposition.

number and biomass of cod captured in a series of tows made by a bottom otter trawl at randomly chosen locations within each of many depth-stratified sampling strata (the maximum number of strata exists in the area determining the Labrador and northeastern Newfoundland stock where the 76 strata range in size from 376 to 7405 km^2). This survey is designed to provide unbiased estimates of the mean and variance, although the latter is often very high (e.g., standard errors of the mean ranging from 30–40% are not uncommon for Labrador and northeastern Newfoundland; however, the efficiency of the gear is less for smaller fish and the efficiency of the gear varies from year to year [Myers and Cadigan 1993, 1995*a*]).

VPA, on the other hand, relies upon commercial catch-at-age data to reconstruct past stock abundances,

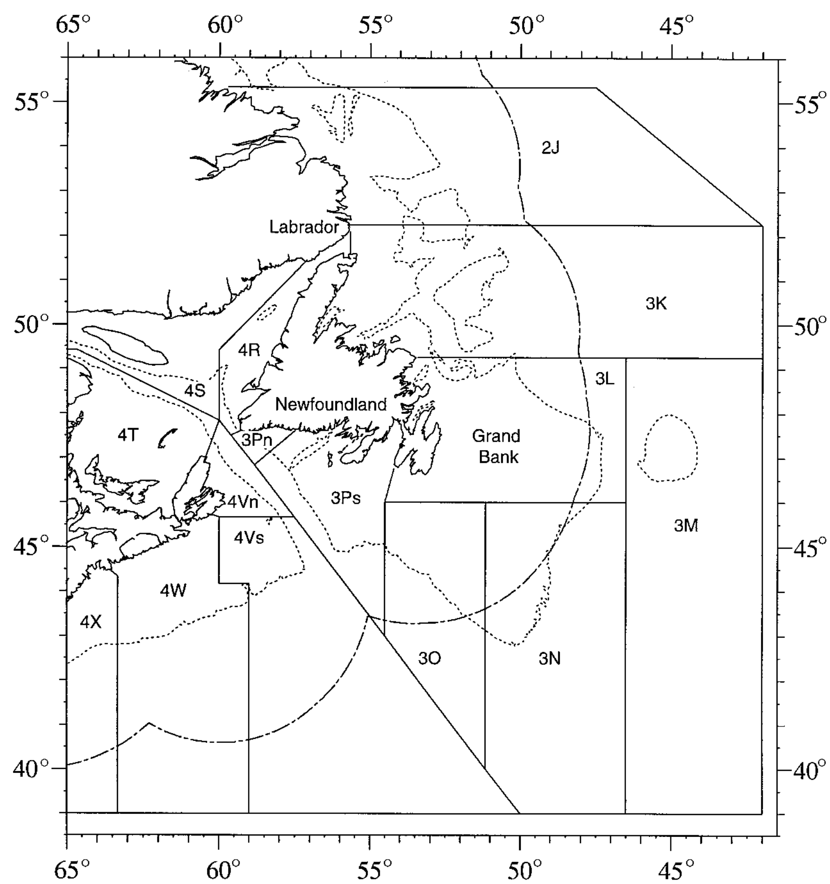

FIG. 1. Map of the Northwest Atlantic showing the cod regions used to define populations for management (Table 1), the 200 nautical mile (370.4-km) exclusive economic zone (dashed-dotted line), and 300-m isobath (dotted line).

depends upon the assumption that commercial catch-at-age is known without error, and assumes that natural mortality of cod is constant and independent of age for ages 3 and older (Hilborn and Walters 1992). VPA estimates abundance separately for each year class, or cohort, and is based on the relationship

$$N_{y,a} = e^{m}N_{y+1,a+1} + e^{m/2}C_{y,a}, \qquad (1)$$

which expresses numbers at age a in the beginning of year y, $N_{y,a}$, as a function of the numbers at age $a + 1$ in year $y + 1$, the catch, $C_{y,a}$, and the natural mortality, m. Eq. 1 makes the approximation that the catch is taken in the middle of the year and that natural mortality occurs continuously. Two sets of parameters are estimated. First, the numbers of fish alive in the last year of the analysis, $N_{Y,a}$. These estimates, and an assumption that the fishing mortality on the oldest age is equal to an average of the fishing mortalities on the younger ages, allow estimates of population numbers to be computed for every year and age for which there are catch-at-age data. Second, for each age used in the analysis, a catchability coefficient, Q_a, is estimated that allows an index of abundance, $R_{y,a}$, e.g., estimates from research surveys or catch per unit effort, to be compared to the calculated numbers-at-age. These two sets of parameters are obtained by minimizing

$$\sum_{y} \sum_{a} (\log N_{y,a} - \log(R_{y,a}Q_a))^2$$

(Myers and Cadigan 1995*a*). Once estimates of the numbers-at-age are obtained, the fishing mortality, $F_{y,a}$, is defined as the solution of

$$N_{y+1,a+1} = N_{y,a}e^{-F_{y,a}-m}.$$

The management goal for these stocks was to set quotas that reduced fishing mortality to the levels indicated on Fig. 2. These presumed sustainable levels of fishing mortality were set at the $F_{0.1}$ level which is defined as the level of fishing mortality at which the marginal increase in yield per recruit is one-tenth of its value at the origin of the curve relating yield per recruit to F (Gulland and Boerema 1973).

We compared temporal trends in recruitment as estimated from research surveys and VPA for each of the six collapsed cod stocks. In theory, the two data sources should reveal the same trends. But in the course of our analysis we found that not to be the case. One common discrepancy between the trends was a decline in recruitment as estimated by VPA concomitant with no change in recruitment as estimated from research surveys at ages 3 and below. A systematic underestimation of recruitment at age 3 by VPA would suggest that the reported catches of small fish of low market value (i.e., cod aged 3, 4, and possibly 5 yr old) are substantially lower than the actual catches. We explored this possibility by testing the hypothesis that the mortality for young cod is unrelated to the fully recruited fishing mortality. We also examined if underreporting of older, market-age fish or seal predation could also be important factors. The temporal divergence in age-specific abundance warrants examination because VPA is one of the most commonly used methods to estimate abundance in fisheries management (Hilborn and Walters 1992).

Methods and Results

Did poor recruitment effect the collapse of cod stocks?

In order to address the recruitment-failure hypothesis, we estimated recruitment at ages 1, 2, and 3 from surveys alone for the five year classes that should have contributed most of the reproductive adults to the spawner biomass in the year of the collapse (the years in which the moratoria were imposed) and compared those estimates with the mean recruitment at the same age for all previous year classes. We compiled all research trawl surveys for the region (Table 2). Specifically, if the year of the collapse is $y_{\min}$ and age at 50% maturity is A_{mat}, then we compared recruitment from year classes

$$y_{\min} - A_{\mathrm{mat}}, \cdots, y_{\min} - A_{\mathrm{mat}} - 4,$$

with all year classes before the $y_{\min} - A_{\mathrm{mat}} - 4$ year class in the survey. We used a Wilcoxon rank sum test for two-sample data (equivalent to the Mann-Whitney test; Conover 1980) to test for significant differences in recruitment. We tested this hypothesis for all research surveys in Table 2.

Recruitment, as estimated from the research surveys, of those year classes that comprised the bulk of the spawner biomass at the time of the various stock collapses differed little from long-term mean levels of recruitment (Table 3). Among the six stocks, for three the majority of the comparisons showed reduced recruitment in the mid-1980s (southern Grand Bank, northern Gulf of St. Lawrence, Eastern Scotian Shelf), two showed higher recruitment (Labrador and northeastern Newfoundland, and southern Gulf of St. Lawrence), and one was equivocal (St. Pierre Bank: fewer or more recruits according to the Canadian and French surveys, respectively).

Some of the differences in the results between different surveys may be caused by a change in survey vessel that occurred in 1983 for the spring Canadian surveys in 3L, S. Grand Bank, and St. Pierre Bank (Myers et al. 1993). The change in abundance for these three stocks is negative for 8 of the 9 comparisons, while they are positive for 8 of the 9 comparisons for the other surveys in these regions. This suggests the change in research vessel produced a negative bias in recent years caused by reduced catchability in the new vessel. Myers et al. (1993) reached a similar conclusion using alternative methods. If the alternative surveys are more reliable for these three stocks, all three appear to have increased recruitment for the cohorts that

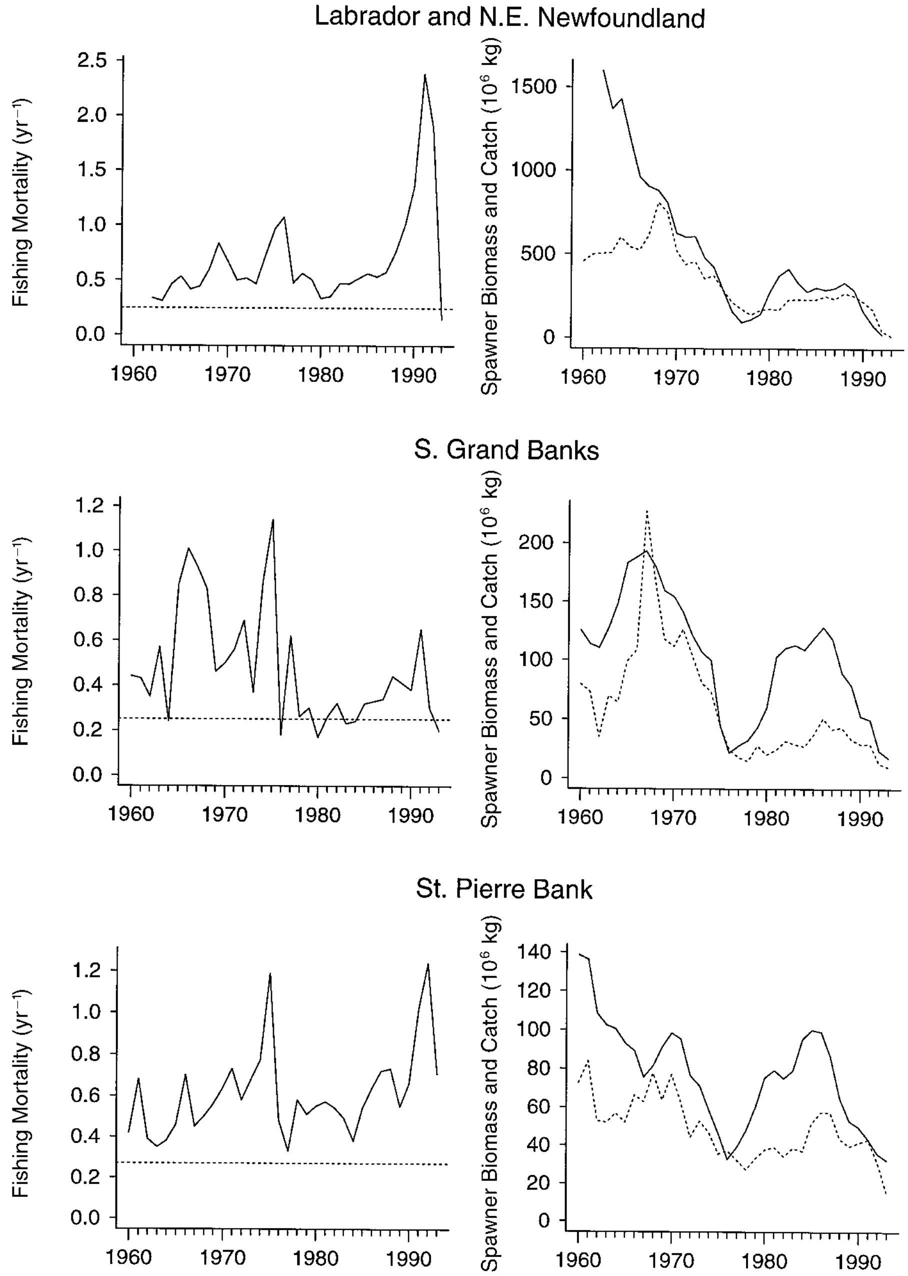

FIG. 2. Estimates of fully recruited (adult) fishing mortality (solid line) with the reference fishing mortality (dotted line), and of spawner biomass (solid line) with reported catch (dotted line) for the six stocks of Atlantic cod considered here. The fully recruited fishing mortality is the average over ages 7–9. The reference fishing mortality is the fishing mortality that represents the long-term and presumed sustainable level of fishing mortality identified by management. It is based on the $F_{0.1}$ concept as defined by Gulland and Boerema (1973) as that level of fishing mortality at which the marginal increase in yield per recruit is one-tenth of its value at the origin.

should have contributed to the collapsed stock, with the exception of the age-3 surveys in the southern Grand Bank.

In our analysis we were interested in general explanations for the collapses in the cod stocks; therefore we tested the overall significance of the hypothesis, e.g., of a positive correlation, by using Fisher's (1954) method to combine the probability levels from one-sided significance tests. Fisher's method is based upon the fact that the logarithm of the probability of a significance test is distributed as $-\frac{1}{2}\chi^2$ with df = 2, and upon additive properties of the χ^2 distribution. That is, the sum of the natural logarithm of the probability of n significance tests is distributed as $-\frac{1}{2}\chi^2_{2n}$. This allows the probabilities from one-sided significance tests to be combined, and the results tested using a χ^2 distri-

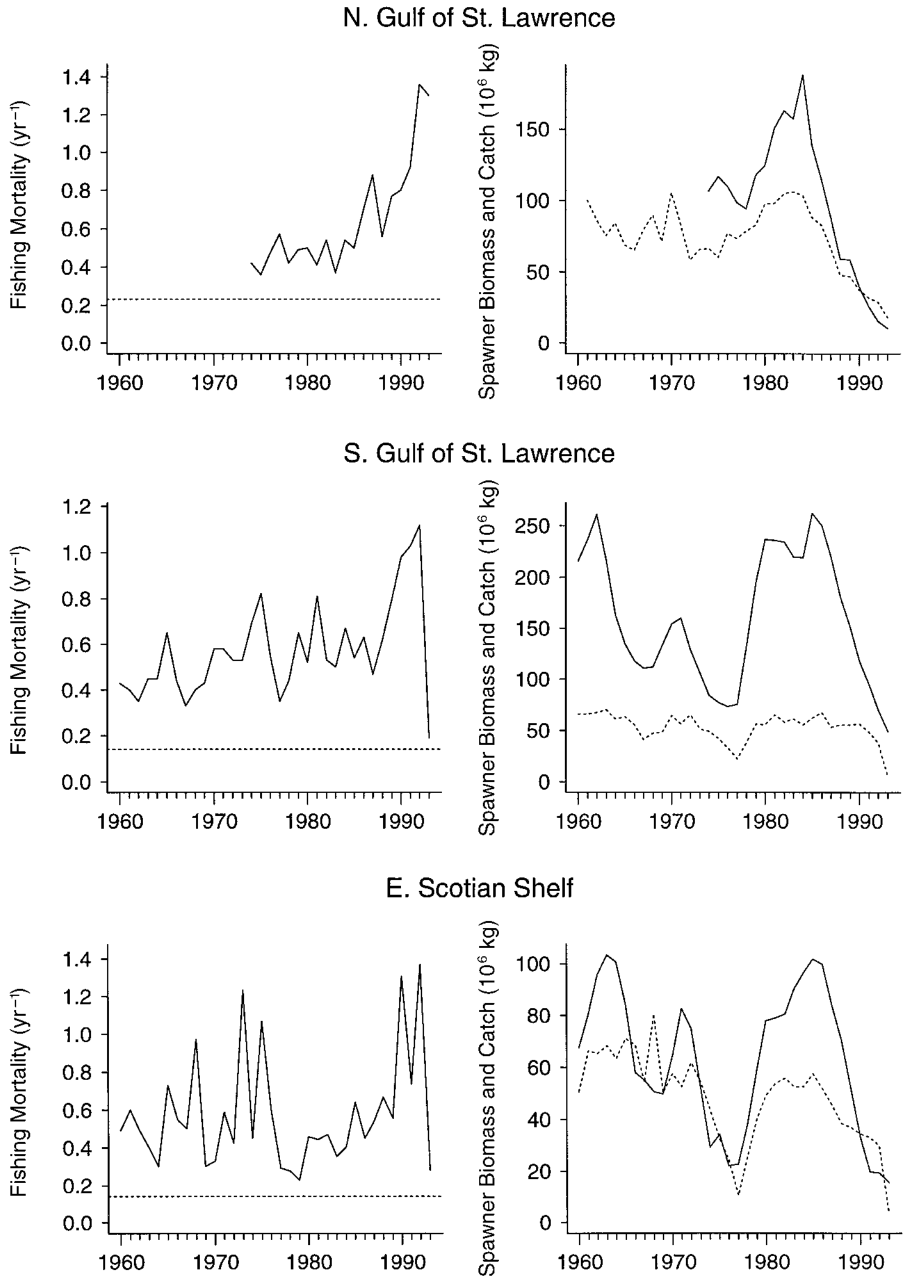

FIG. 2. Continued.

bution. When we use Fisher's method to combine significance probabilities for test statistics with discrete distributions, e.g., the Wilcoxon rank sum statistic, the discrete P values are made into continuous variates by adding to them an appropriate uniform random variable as suggested by Pearson (1950).

Statistically there was no significant difference in numbers of 3-yr-old cod between these time periods for the Labrador and northeastern Newfoundland, St. Pierre Bank, Gulf of St. Lawrence and Eastern Scotian Shelf stocks. The exception was southern Grand Bank cod for which both Canadian and Russian surveys indicated that recruitment in the mid-1980s was significantly less than the long-term mean prior to that time. If the age-3 southern Grand Bank surveys are not included in the comparison, there is no overall increase ($P = 0.15$) or decrease ($P = 0.10$) in cod recruitment for the years that should have contributed to the year of collapse using Fisher's method of combining one-sided significance tests.

We examined the power of our analysis by generating 600 pseudo-random samples with the number of observations and standard deviation of the observed research surveys for different levels of reduction in the

TABLE 2. Research surveys from the Northwest Atlantic used in the analysis. All surveys covered the entire Atlantic cod stock region except the 3L and 2J surveys. Years refer to the first and last years used in the analyses.

Stock	NAFO division	Country	Season	Years	Years missing
Labrador and northeastern Newfoundland	2J3KL	Canada	Fall	1978–1993	···
	3L	Canada	Spring	1977–1993	1983–1984
S. Grand Bank	3NO	Canada	Spring	1971–1993	1983
	3NO	Russia	Spring	1977–1993	1992
St. Pierre Bank	3Ps	Canada	Spring	1972–1994	···
	3Ps	France	Spring	1978–1992	···
N. Gulf of St. Lawrence	3Pn4RS	Canada	Winter	1978–1994	1982
S. Gulf of St. Lawrence	4TVn	Canada	Summer	1977–1993	···
Eastern Scotian Shelf	4VsW	Canada	Spring	1979–1994	1985
	4VsW	Canada	Summer	1970–1993	···

mean recruitment for the period of collapse. If the deviations in recruitment were assumed to be lognormal (Myers and Cadigan 1993) then we would have almost certainly detected an overall reduction of recruitment of 20%, and the probability is high (83%) of detecting a reduction as low as 15% (Fig. 3). Similar results were obtained if gamma variation was assumed. The power is lower if each population is considered separately; however, a large decline in recruitment, e.g., 40–50%, would have almost certainly been detected.

As an alternative to Fisher's method, we use the standard meta-analytic method to estimate the effect size, i.e., the standardized mean difference between two groups, $(\mu_1 - \mu_2)/\sigma$, where σ is the within-group standard deviation, to compare recruitment from research surveys from the two time periods described above. The mean difference in recruitment between the two periods was obtained by weighting the individual estimates by the variance (Hedges and Olkin 1985: chapter 6). The estimated effect size in this case is 0.0052, with a 95% CI of -0.254 to 0.265. That is, the effect size estimates that the true change in recruitment is overall within 25% of the observed standard deviation.

Do research survey and VPA trends in recruitment differ?

To graphically examine temporal trends in recruitment, we partitioned the variability in the log-transformed recruitment time series from VPA and research surveys into two components: low-frequency (periods >10 yr) and higher frequency (annual) variation. We estimated the low-frequency variation using a smoother known as ''Lowess'' (described by Cleveland 1979). Lowess uses robust, locally linear fits within a time window, 10 yr in our case, around each recruitment year. Recruitment estimates inside the window are weighted so that nearby points receive the most weight. The higher frequency variation was defined as the residuals from the smoothed data. This procedure was only used for graphical examination of the data; unsmoothed data were used in the statistical analyses.

Temporal divergence between the research survey and VPA abundance estimates for each stock was assessed by regressing the difference between the $\log_{10}$-transformed VPA and research survey recruitment estimates against time. Separate regressions were performed for cod aged 2 through 6 yr of age. Regression slopes significantly different from zero are indicative of divergence between the two time series. Note that these two data series are not independent for the last few years of the analysis, i.e., the numbers at age in the last year of the VPA are estimated from the research surveys. For this reason we will not include the last two years of the VPA in our analysis.

Trends in abundance as determined by VPA did not match those derived from research surveys. In recent years, the relative abundance based upon VPA is usually less than those based upon research surveys (Fig. 4). For cod aged 2 yr to 6 yr, 38 of 50 regression slopes of the difference of log survey estimates of abundance with log VPA estimates vs. time (5 ages $\times$ 10 surveys) were negative (Table 4). A negative slope indicates that VPA-based abundance estimates are declining through time at a faster rate than those based on research surveys. Of the 20 regression slopes for 2- and 3-yr-old cod, 9 of the 16 negative slopes, but none of the positive slopes, were significantly different from zero. Of the 33 regression slopes for older cod (4 to 6 yr), 10 of the 22 negative slopes and 1 of the 8 positive slopes differed significantly from zero. Where more than one research survey was available for a given stock, the signs of the regression slopes were in general agreement with one another. Again, the exception was southern Grand Bank cod (3NO). Age-specific slopes as determined from the Canadian surveys were negative, while those based upon the Russian surveys were positive (although 9 of the 10 slopes were not significantly different from zero).

We used two procedures to test the robustness of our results to potential violations of the implicit distributional assumptions underlying least-squares regression. Kendall's tau-statistic provided a nonparametric test of whether the differences are uncorrelated with time. The associated P values are very similar to those obtained from the regressions (Table 4).

If the differences between the $\log_{10}$-transformed VPA and research-survey recruitment estimates are autocorrelated then the estimates of slope will be unbiased

TABLE 3. Mean recruitment from research surveys for the year classes that should have contributed to the fishery in 1992 (collapse mean) and those before (precollapse mean), 100 times the proportional change in the two means, and the *P* value for the hypothesis that they are equal. Units of recruitment are the mean number of fish per 30-min tow of the survey trawl.

Region	Survey	Season	Age (yr)	Pre-collapse mean	Collapse mean	$100 \times \left(\frac{\Delta\ \text{Mean}}{\text{Mean}}\right)$	*P*
Labrador and northeastern Newfoundland	Canadian	Fall	1	0.11	0.42	296	0.18
			2	1.2	3.2	175	0.22
			3	5.2	5.8	11	0.79
Labrador and northeastern Newfoundland	Canadian 3L	Spring	1	0.058	0.0033	−94	0.23
			2	0.87	0.58	−32	0.75
			3	3.3	5.5	63	0.25
S. Grand Bank	Canadian	Spring	1	0.53	0.052	−90	0.20
			2	2.7	1.1	−57	0.095
			3	6.1	1.7	−72	0.014
S. Grand Bank	Russian	Spring	1	0.93	1.5	62	0.33
			2	7.8	8.9	13	0.94
			3	20	4.8	−76	0.053
St. Pierre Bank	Canadian	Spring	1	0.23	0.018	−92	0.10
			2	1.1	0.32	−71	0.075
			3	1.3	0.83	−35	0.19
St. Pierre Bank	French	Spring	1	0.96	1.8	82	0.31
			2	6.2	15	137	0.15
			3	4.8	13	173	0.030
N. Gulf of St. Lawrence	Canadian	Winter	1	0.22	0.013	−94	0.15
			2	2	1.4	−29	0.42
			3	9	5.8	−35	0.25
S. Gulf of St. Lawrence	Canadian	Summer	1	1.2	3.8	206	0.040
			2	9.9	12	23	0.29
			3	18	30	66	0.034
E. Scotian Shelf	Canadian	Spring	1	2.6	0.34	−87	0.063
			2	5.9	9.4	59	0.61
			3	12	9.5	−19	0.54
E. Scotian Shelf	Canadian	Summer	1	1.8	0.55	−69	0.19
			2	9.1	3.6	−60	0.14
			3	12	7.9	−36	0.78

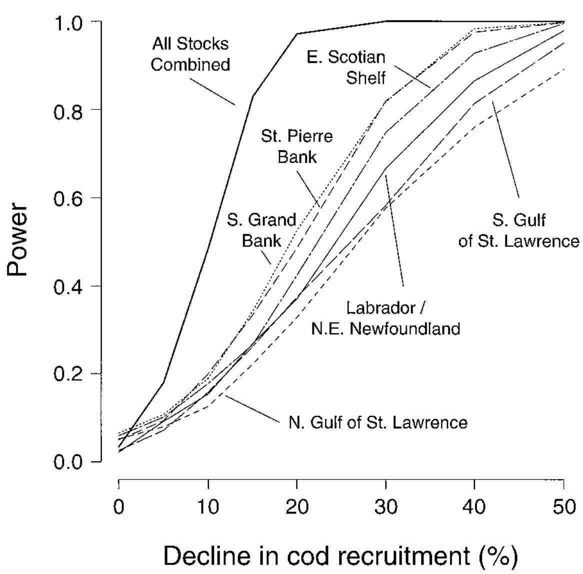

FIG. 3. Probability of detecting a decline in recruitment (i.e., power) for research trawl survey data using a Wilcoxon rank sum test with $\alpha = 0.05$. The solid curve shows the estimated power when *P* values are combined over all surveys for all six cod populations using Fisher's method. The power for detecting a decline in any one population is less than the power of detecting an overall decline in recruitment.

but the reported significance will be inflated. We used a two-step procedure to deal with this issue. First, we tested for first-order autocorrelation in the residuals from the regressions using the Durbin-Watson statistic (Judge et al. 1985). Except in the case of the Russian surveys on the southern Grand Bank, autocorrelation generally was not found to be a problem. In those cases where significant autocorrelation was detected we fitted a regression with a first-order autocorrelation term (Judge et al. 1985). The resulting *P* values for the slope are increased but do not change the overall conclusions.

Does discarding of young fish increase with fishing mortality?

As an alternative to the VPA estimates of mortality, we estimated mortality for each year and age directly from the research-survey estimates of abundance using

$$z_{y,a} = -\log\left(\frac{N_{y+1,a+1}}{N_{y,a}}\right)$$

$$\hat{z}_{y,a} = -\log\left(\frac{R_{y+1,a+1}/\tilde{Q}_{a+1}}{R_{y,a}/\tilde{Q}_a}\right)$$

$$= r_{y+1,a+1} - r_{y,a} + (\tilde{q}_{a+1} - \tilde{q}_a),$$

where we have used lower case to indicate log-trans-

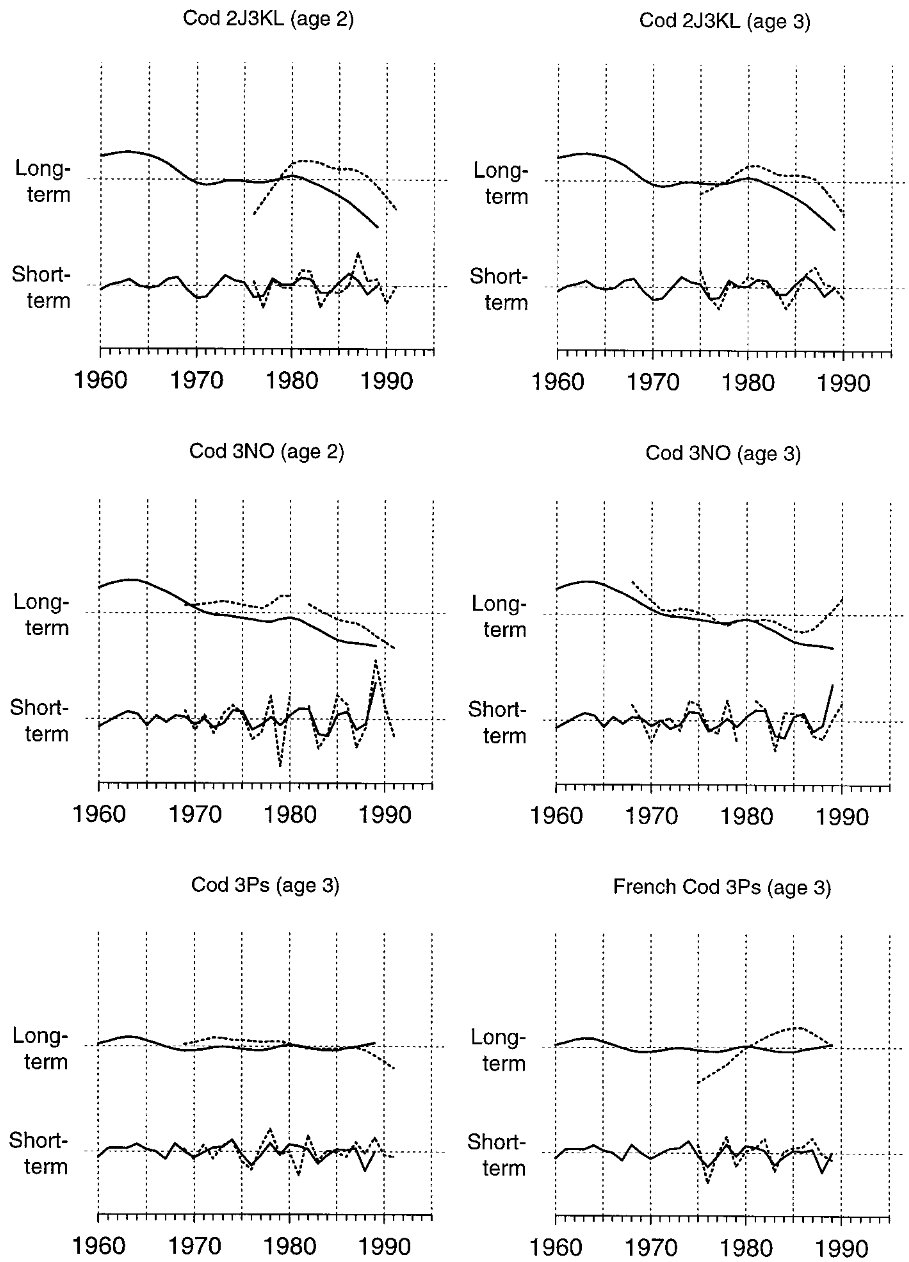

FIG. 4. The long- and short-term recruitment variability for cod at age 3 as estimated by virtual population analysis (solid line) and by research survey (dashed line). The long-term variability is estimated using the Lowess smoother with a 10-yr window; the short-term variability is represented by the residuals from the observed and the smoothed data. Estimates of numbers-at-age in a year class are $\log_{10}$-transformed with the mean removed. The mean of each series is separated by 2 units, i.e., a factor of 100, from the one below.

formed variables and parameters, the ^ symbol to indicate the parameter we estimate, and the ~ symbol to indicate a parameter we estimate from external data. The term $(\tilde{q}_{a+1} - \tilde{q}_a)$ occurs because the research surveys are not equally efficient at catching fish of all ages; this term is estimated from the VPA. It only serves to scale the graph and does not enter into our analysis.

To test the hypothesis that the discarding rate of young fish is independent of fishing mortality, we calculated the correlation coefficients between the research-survey-estimated mortality of fish younger than age 7 (the age at which cod are fully recruited to the offshore fishery, i.e., the age at which they are fully vulnerable to bottom otter trawls) and fully recruited (ages 7–9) fishing mortality as estimated by VPA. Positive associations would be consistent with the hypothesis that discarding increases with increased fish-

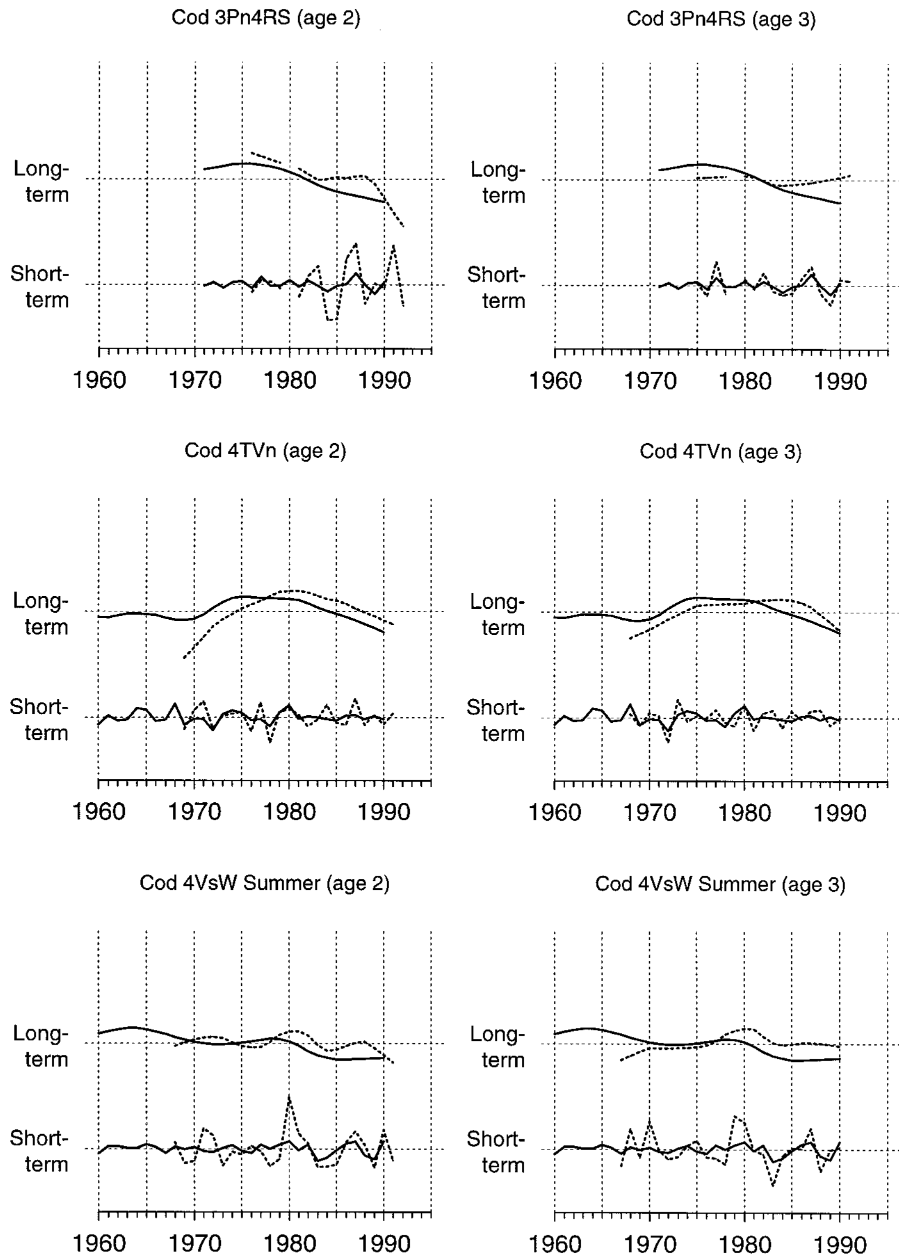

FIG. 4. Continued.

ing mortality. To test whether this increase in mortality was greater than that expected from the reported catch, we regressed the mortality estimated from the surveys at an age that discarding should be at a maximum, i.e., age 3, against the fully recruited (ages 7–9) fishing mortality as estimated by VPA, and tested whether this slope was greater than that calculated using mortality at age 3 as estimated by VPA. In the analyses we did not use VPA data after 1991, because the VPAs are unreliable in the last years of the analysis (Pope 1972).

Associations between our research-survey-based index of mortality for young cod and fully recruited fishing mortality were generally positive (Tables 5 and 6). Of the 30 correlation coefficients for ages 2, 3, and 4 (3 ages × 10 surveys), 26 were positive, significantly more than expected by chance (sign test; $P = 0.0001$). Among age-3 fish, where discarding should be at a maximum (Kulka and Stevenson 1986), 9 of the 10 correlation coefficients were positive (sign test; $P = 0.02$). We can test the overall significance of the hypothesis of a positive correlation by using Fisher's method to combine the probability levels from one-sided significance tests (Table 6). The juvenile mortality is clearly greater when adult fishing mortality is high; however, is this difference important biologically? We calculated the mean difference in juvenile mor-

TABLE 4. Slopes of age-specific regressions (for cod aged 2–6 yr) of the difference in $\log_{10}$-transformed research-survey abundance estimates and VPA estimates against time (i.e., all available years in the time series; see Fig. 1). The P value for the slope is given, along with a P value for Kendall's tau-statistic and, in cases of significant first-order autocorrelation in the residuals from the regression, the P value from a regression taking into account first-order autocorrelation.

Fish stock	Survey	Season	Age (yr)	Regression slope	P	Kendall P	P (after correction for autocorrelation)
Labrador and northeastern Newfoundland	Canadian	Fall	2	−0.25	2.8×10^{-5}	0.0005	
			3	−0.13	0.0002	0.0013	0.0025
			4	−0.056	0.081	0.15	
			5	0.029	0.3	0.7	0.27
			6	0.085	0.04	0.15	0.057
Labrador and northeastern Newfoundland	Canadian 3L	Spring	2	−0.1	0.075	0.11	
			3	−0.13	0.0024	0.019	
			4	−0.054	0.12	0.012	
			5	−0.017	0.63	0.22	
			6	0.033	0.41	0.59	0.36
S. Grand Bank	Canadian	Spring	2	−0.039	0.13	0.14	
			3	−0.0014	0.94	0.90	
			4	−0.038	0.23	0.15	
			5	−0.059	0.11	0.12	
			6	−0.1	0.0089	0.024	
S. Grand Bank	Russian	Spring	2	0.0069	0.93	0.66	0.83
			3	0.04	0.47	0.52	0.59
			4	0.022	0.71	0.93	0.97
			5	0.061	0.39	0.53	0.77
			6	0.036	0.57	0.72	0.99
St. Pierre Bank	Canadian	Spring	2	0.057	0.078	0.092	
			3	0.018	0.3	0.18	
			4	−0.017	0.47	0.32	
			5	−0.039	0.15	0.13	
			6	−0.077	0.00065	0.0017	
St. Pierre Bank	French	Spring	2	−0.21	0.013	0.014	
			3	−0.22	4.5×10^{-6}	0.00056	
			4	−0.16	0.0007	0.005	
			5	−0.084	0.053	0.09	
			6	−0.07	0.24	0.35	
N. Gulf of St. Lawrence	Canadian	Winter	2	−0.038	0.49	0.78	
			3	−0.1	8.6×10^{-5}	0.0004	
			4	−0.06	0.028	0.038	
			5	−0.043	0.2	0.5	
			6	−0.019	0.66	0.79	
S. Gulf of St. Lawrence	Canadian	Summer	2	−0.09	1.8×10^{-5}	0.0004	
			3	−0.063	0.0002	0.0004	
			4	−0.058	6.0×10^{-5}	0.0007	
			5	−0.067	1.5×10^{-5}	0.0001	0.0027
			6	−0.072	0.0007	0.0024	0.034
E. Scotian Shelf	Canadian	Spring	2	−0.051	0.54	0.46	
			3	−0.074	0.38	0.35	
			4	−0.017	0.81	0.66	
			5	0.0036	0.95	0.80	
			6	0.044	0.34	0.35	
E. Scotian Shelf	Canadian	Summer	2	−0.042	0.11	0.096	0.23
			3	−0.061	0.007	0.029	
			4	−0.084	5.7×10^{-5}	0.0004	
			5	−0.099	1.1×10^{-5}	2×10^{-5}	
			6	−0.11	1.3×10^{-5}	7.2×10^{-5}	0.0013

tality above fishing mortality of 0.5 and below, separately for each survey. The mean difference was 0.4 (1 SE = 0.12). This represents a loss of 33% of the young fish coming into the fishery when adult fishing mortality is high.

The correlation between the estimated fishing mortality on adults and the mortality on age 3 is not caused by reported catch. If it were, mortality estimated from the VPA for age 3 as a proportion of the fully recruited fishing mortality (the dotted line in Fig. 5) should increase at the same rate as the estimates from the research surveys do. However, it clearly does not; the slope of mortality estimated from the research surveys vs. the fully recruited fishing mortality from the VPA is greater than the slope of the mortality estimated at age 3 from the VPA vs. the fully recruited fishing mor-

TABLE 5. Correlation coefficients of Atlantic cod mortality by age, as determined from research surveys against virtual-population-analysis estimates of fully recruited fishing mortality. See Fig. 5 for plots of the age-3 data.

Fish stock	Survey	Season	Age (yr) 1	2	3	4	5	6	7
Labrador and northeastern Newfoundland	Canadian	Fall	0.17	0.46	0.51	−0.75	0.7	0.7	0.88
Labrador and northeastern Newfoundland	Canadian 3L	Spring	−0.44	0.023	0.22	0.2	0.62	0.67	0.75
S. Grand Bank	Canadian	Spring	−0.22	0.082	0.37	0.17	0.014	0.1	0.26
S. Grand Bank	Russian	Spring	0.24	0.34	0.21	0.073	−0.08	0.23	0.033
St. Pierre Bank	Canadian	Spring	0.10	0.038	0.087	0.073	0.13	0.14	0.24
St. Pierre Bank	French	Spring	0.37	0.27	0.80	0.54	0.45	0.41	0.55
Northern Gulf of St. Lawrence	Canadian	Winter	−0.19	−0.34	0.45	−0.02	0.067	−0.024	−0.15
Southern Gulf of St. Lawrence	Canadian	Summer	0.51	0.25	0.56	0.56	0.44	0.53	0.56
E. Scotian Shelf	Canadian	Spring	−0.56	−0.22	−0.067	0.064	0.082	0.081	0.64
E. Scotian Shelf	Canadian	Summer	−0.078	0.36	0.48	0.54	0.61	0.36	0.21

tality for 9 of the 10 comparisons. The resulting combined significance test is highly significant ($P = 1.8 \times 10^{-8}$).

It is remarkable that the increase in juvenile mortality can be detected from the research surveys, given the high estimation error apparent in Fig. 5. Note, for the two stocks where there are research-survey estimates of mortality in the early 1970s, before the extension of Canadian jurisdiction, that adult fishing mortality and discarding mortality were both high.

Is there misreporting at older ages?

The VPA should estimate mortality of older ages correctly if the catch-at-age data are correct and if the estimate of natural mortality is reasonably accurate. We examine the hypothesis that the level of underreporting of catches of juveniles increases as the fishing mortality increases in the older ages (7–9) by regressing the research-survey estimates of mortality vs. the VPA estimate of mortality, and testing if the slopes are significantly different from one. Again, we did not use data for the last 2 yr because of large statistical biases in the estimates for these years (Myers and Cadigan 1995*a*). The selectivity of the research survey sampling gear is constant at older ages, i.e., the correction of term ($\tilde{q}_{a+1} - \tilde{q}_a$) is not needed for the ages >7 yr.

The slope of the regression of mortality estimated from the surveys vs. mortality estimated from the VPA was >1 for 7 of the 10 surveys (Table 7). Two of these slopes were significantly >1 at the 0.05 level using a two-sided test. The combined significance test of the hypothesis that the slopes are >1 is marginally significant ($P = 0.041$). These results are consistent with the high VPA estimates of adult fishing mortality. In particular, the very high fishing mortalities in the late 1980s and early 1990s appear to be real, and may be underestimates because of unreported catch. Further evidence for this result is provided by an analysis of tagging data by Myers et al. (1996), which estimated higher adult fishing mortality than estimated from the VPA.

DISCUSSION

Did poor recruitment contribute to the collapse of Atlantic cod?

We could find no evidence from research surveys that poor recruitment was a contributing factor to the

TABLE 6. *P* values of the correlation coefficients of mortality by age, as determined from research surveys against virtual-population-analysis estimates of fully recruited fishing mortality. The combined *P* values are for a one-sided test of the hypothesis that the correlation is non-positive.

Fish stock	Survey	Season	Age (yr) 1	2	3	4	5	6	7
Labrador and northeastern Newfoundland	Canadian	Fall	0.61	0.098	0.061	0.0021	0.0051	0.0056	0.000027
Labrador and northeastern Newfoundland	Canadian 3L	Spring	0.46	0.94	0.49	0.54	0.032	0.017	0.0047
S. Grand Bank	Canadian	Spring	0.38	0.74	0.12	0.49	0.96	0.67	0.28
S. Grand Bank	Russian	Spring	0.44	0.23	0.47	0.81	0.79	0.94	0.91
St. Pierre Bank	Canadian	Spring	0.69	0.87	0.72	0.76	0.59	0.57	0.31
St. Pierre Bank	French	Spring	0.24	0.35	0.0006	0.046	0.11	0.14	0.42
Northern Gulf of St. Lawrence	Canadian	Winter	0.72	0.28	0.15	0.95	0.84	0.94	0.63
Southern Gulf of St. Lawrence	Canadian	Summer	0.054	0.37	0.029	0.028	0.097	0.041	0.028
E. Scotian Shelf	Canadian	Spring	0.073	0.51	0.84	0.85	0.81	0.81	0.034
E. Scotian Shelf	Canadian	Summer	0.73	0.10	0.022	0.009	0.026	0.10	0.34
Combined *P* values			0.35	0.084	0.000007	0.00009	0.00006	0.00025	0.00000007

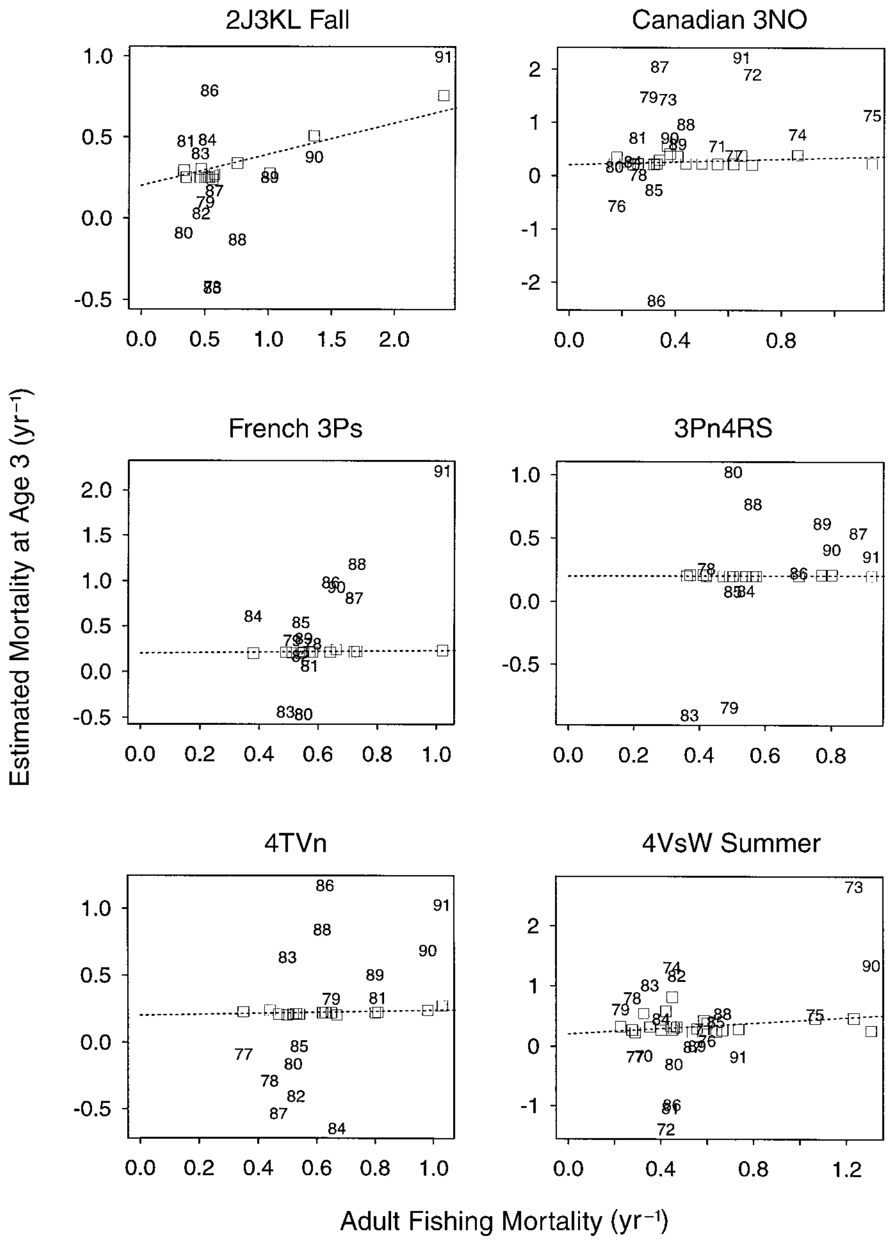

FIG. 5. Scatterplots of research survey-based estimates of mortality, identified by year class (e.g., "90" = 1990), vs. fully recruited fishing mortality estimated by virtual population analysis (VPA) for 3-yr-old cod from six eastern Canadian stocks. The dashed line is the expected mortality calculated from the reported catch-at-age data in the VPA; these data are represented by squares.

collapse of cod off eastern Canada. Recruitment from those year classes that would have comprised most of the spawners at the time of the stock collapse was not significantly different from long-term recruitment of previous year classes. Our results are consistent with those of Hutchings and Myers (1994) who concluded that overfishing alone precipitated the collapse of Labrador and northeastern Newfoundland stock off Newfoundland and Labrador. Although low recruitment levels may not have contributed to the stock collapses, the low abundance of 3-yr-old cod in the early 1990s will certainly have an inhibitory effect on the rate at which the stocks can recover. Recruitment is probably low at present largely because spawner biomass is at historical lows in all stocks (Fig. 2; Myers and Barrowman 1996). The southern Grand Bank stock for which recruitment in the mid-1980s was significantly less than previous levels was an exception to the pattern observed in other stocks. However, there is good reason to believe that this decline can be attributed to high fishing mortality on cod less than 5 yr of age. Research surveys indicate that a large proportion of the most important juvenile

TABLE 7. Slope of the regressions of mortality estimated from the research surveys vs. fishing mortality from VPA for Atlantic cod ages 7–9 yr. Also given are the standard errors and the results from the two-sided significance test that the slope does not equal 1. The combined P value is for the one-sided test of the hypothesis that the slope is ≤1.

Fish stock	Survey	Season	Regression slope	SE	P
Labrador and northeastern Newfoundland	Canadian	Fall	1.46	0.20	0.046
Labrador and northeastern Newfoundland	Canadian 3L	Spring	1.31	0.22	0.19
S. Grand Bank	Canadian	Spring	2.52	1.6	0.38
S. Grand Bank	Russian	spring	−1.57	3.7	0.51
St. Pierre Bank	Canadian	Spring	1.77	1.8	0.38
St. Pierre Bank	French	Spring	5.3	1.8	0.034
Northern Gulf of St. Lawrence	Canadian	Winter	0.16	0.48	0.37
Southern Gulf of St. Lawrence	Canadian	Summer	1.03	0.51	0.95
E. Scotian Shelf	Canadian	Spring	1.79	1.89	0.69
E. Scotian Shelf	Canadian	Summer	0.83	0.61	0.79
Combined P values			···	···	0.04

habitat on the southern Grand Bank lies outside Canada's 200-nautical-mile (370.4 km) jurisdictional limit. Although fishing in this region (known as the ''tail'' of the Grand Bank) is subject to catch quotas and mesh-size regulations established by The Northwest Atlantic Fishery Organization (NAFO), many countries routinely disregarded the quotas and mesh regulations because they were not enforced. For example, NAFO regulations stipulated a minimum mesh size of 120–130 mm. But between 1985 and 1989, as detailed by Walsh et al. (1995), fishery observers documented the use of small-mesh trawls (60 and 90 mm mesh size) in addition to the insertion of small-mesh liners into the cod-end of the trawl. European Union countries such as Spain have clearly been targeting 2- and 3-yr-old southern Grand Bank cod outside Canada's 200-mile limit since the early 1990s and, given the typically small mesh size of their trawls, perhaps as early as the mid-1980s. In 1991 almost half of the reported Spanish catch was comprised of 2-yr-olds (by number); in 1992, almost 60% was comprised of 3-yr-olds (Walsh et al. 1995). Thus, we cannot reject the hypothesis that declining recruitment of southern Grand Bank cod in the mid-1980s was a direct consequence of targeted fishing on 2- and 3-yr-old individuals.

Although we found no evidence that poor recruitment contributed to the collapse of cod in Eastern Canada, poor recruitment has certainly been a factor in slowing the recovery of these stocks. The demonstrable relationship between spawner abundance and recruitment for cod (Myers and Barrowman 1996) suggests that with spawner levels at an all-time low, recruitment will be poor. Fortunately, mortality does not generally increase at low population levels, i.e., depensation or the Allee effect, for marine populations so the populations should recover if fishing mortality is controlled (Myers et al. 1995).

Divergence in VPA and research survey abundance indices

Large discrepancies between the long-term patterns of abundance based on VPA (virtual population analysis) and research surveys are of great concern. For each of the six cod stocks considered here, VPA-based abundances consistently depict lower recruitment levels than do survey-based estimates. More important is the observation that from the early 1980s the VPA-based trend shows a decline where none is apparent in the survey-based trend. This difference appears not to be due to annual anomalies because of the generally close match between the short-term trends of the survey and VPA time series (cf. Fig. 2). An error in the estimation of natural mortality may cause trends in abundance estimated from VPA (Lapointe et al. 1989). However we have shown the differences are consistent with the hypothesis of discard mortality and unreported catches—it seems unlikely that the differences are caused by such a mis-specification of natural mortality.

The widespread use of VPA in fisheries stock assessment throughout the world makes it imperative that the reasons for the differences in long-term abundance between VPA and research-survey abundance indices be identified. We suggest that the increasing divergence between VPA and research-survey estimates of recruitment is due to increased misreporting and discarding of catches of young (i.e., 2- to 4-yr-old cod). Our observation that the mortality of 3- and 4-yr-olds increases with fishing mortality at a faster rate than predicted on the basis of VPA alone is consistent with this hypothesis. Although there is a large amount of qualitative evidence of discarding and misreporting of catches (Angel et al. 1994), there is a clear need to quantify discarding and misreporting rates and to incorporate these rates into annual stock assessments.

Did predation by seals contribute to the collapses?

It has been suggested that a major cause of the collapse of the cod stocks was seal predation (Atkinson and Bennett 1994). Harp seals (*Phoca groenlandica*) are by far the most numerous seal in the region, and there is evidence of an increase in their numbers (Stenson et al. 1993). However, cod form a small part of their diet (<4%), and nearly all of the cod in their diet is of ages <2 yr, with cod <1 yr old being the most common age (Beck et al. 1993, Lawson et al. 1995). Cod is more common in the diets of grey seals (*Halichoerus grypus*) and hooded seals (*Cystophora cristata*), which are far less common than harp seals. For both species the majority of cod consumed are <3 yr old (Mohn and Bowen 1994, Lawson et al. 1995). There is a major problem with the hypothesis that seal predation caused the collapses in that the three major seal species in the region consume cod at ages <3. Although these species may have had an impact on survival at age <3, they clearly did not cause the collapse of the cod because recruitment at age 3 was not below normal for any stock except the southern Grand Bank.

Why do fish stocks collapse?

Our results clearly indicate that mortality at age 3 is significantly correlated with the fully recruited (ages 7–9) fishing mortality. Given that the VPAs grossly underestimated the rate of increase in mortality at age 3 and that the VPAs depend upon reliable catch statistics, we conclude that high levels of discarding and catch misreporting occur and that these levels increase with declines in population abundance and the concomitant increases in fishing mortality. What are the conditions that occurred that allowed the collapse of six cod stocks in such a short time, despite attempts to regulate the fishery? We suggest that three, interrelated, common factors were responsible for the stock collapses.

Overestimation of abundance and underestimation of fishing mortality.—The target fishing mortality for these six stocks was rarely achieved (Fig. 2). One reason for this is that the fishing mortality was consistently underestimated and abundance was overestimated. The fishing mortality in the year of the assessment was typically estimated to be half of what it was estimated 5 yr later (Fig. 6). There were two reasons for this. There is a statistical bias in the estimation procedure that causes the abundance in the last years to be overestimated and fishing mortality to be underestimated (Smith and Gavaris 1993, Myers and Cadigan 1995*a*). Furthermore, there was a reliance on commercial catch-per-unit effort to estimate population numbers in the last year of the VPA; however the catch-per-unit-effort estimates of abundance were positively biased (Hutchings and Myers 1994).

The ability to catch fish efficiently at low abundance levels.—It is commonly assumed that the commercial catch-per-unit effort is proportional to the abundance, and that this provides some protection for the stock as the population declines. This assumption has been shown to be false for many stocks (Hilborn and Walters 1992) and has recently been shown to be invalid for cod along the Canadian east coast (Hutchings and Myers 1994). As the populations declined the fishing fleet was able to maintain high catches. There were two reasons for this. Firstly, the commercial catch-per-unit effort remained relatively high as the populations de-

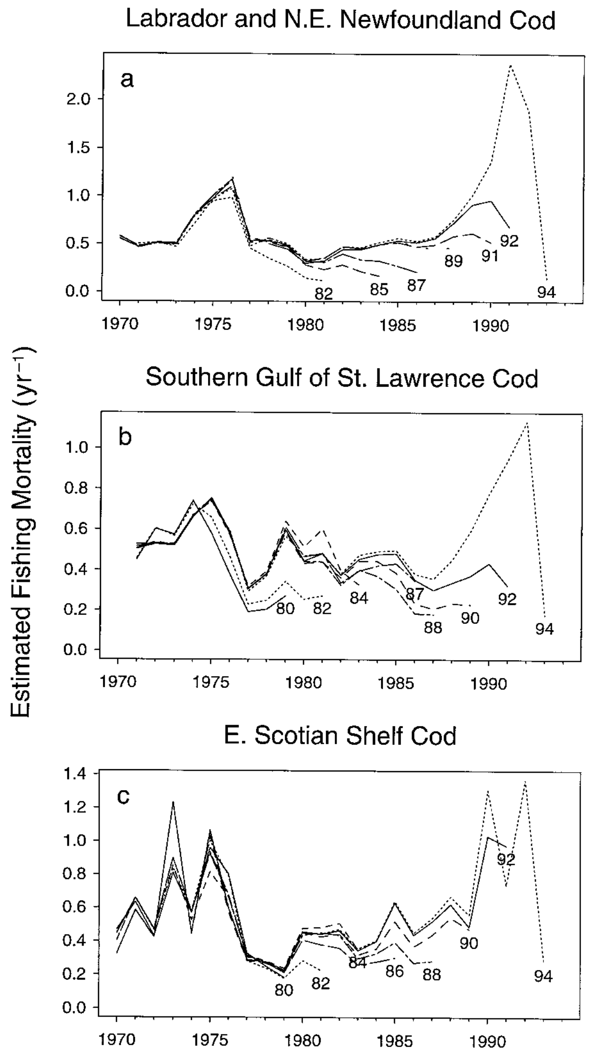

FIG. 6. Fishing mortality of cod estimated in the years 1980, 1982, . . . , 1994 for Labrador and northeastern Newfoundland, southern Gulf of St. Lawrence, and Eastern Scotian Shelf stocks. The last year of each time series represents the year in which the assessment was undertaken. Note that the fishing mortality in the most recent years in each assessment is almost always less than estimates made in later assessments. The other three stocks show similar patterns.

clined because of the ability of modern fishing vessels to find and catch fish (Hilborn and Walters 1992, Hutchings and Myers 1994, Myers and Cadigan 1995*b*). Secondly, there was an increase in effort to maintain catches as the populations declined, e.g., there was a large increase in offshore gill nets in the late 1980s on the Grand Bank after the inshore catch rates decreased (Hutchings and Myers 1994). There was a large overcapacity in the fishing fleet and strong economic incentives to maintain catch levels (Halliday et al. 1992, Schrank et al. 1992, Angel et al. 1994) that allowed the increase in fishing effort. The result is that in each of the stocks the catch remained relatively high as the abundance declined, and the fishing mortality greatly increased (Fig. 2).

Increased discarding and nonreporting of small fish as the population declined and fishing mortality increased.—The estimation of discarding and nonreported catch is inherently difficult because they are illegal activities. Nevertheless, the results of our analysis are consistent with the occurrence of such activities, in spite of the very large estimation errors in our mortality estimates. Independent confirmation of large-scale discarding of small fish has been obtained in a sociological study (Palmer and Sinclair 1996). The extent of the discarding and nonreported catches was hidden by the overestimation of abundance described above. The increase in fishing mortality was also associated with an underreporting of older, legal-sized fish; this aggravated the problem.

Another case: The collapse of herring populations

Unfortunately, the collapse of cod in Eastern Canada is not unique; the factors that led to the collapse of these stocks are commonly observed when other populations collapse. The collapse of all the major herring fisheries throughout the north Atlantic and Pacific in the 1960s and 1970s (Saville 1980) should serve to show the generality of the process. Although environmental change may have played some part in these collapses, economic factors, e.g., the demand for fish meal, were common to all. For each of these populations, the pattern of the collapse was similar to that for cod in eastern Canada. The introduction of new technology allowed younger ages to be exploited using sonar-guided purse seines (Jakobssen 1980). For example, in the British Columbia fishery, ''The fishery proceeded to remove most of the mature adults, and then large numbers of age 2 and finally age 1 fish, before depletion became evident and the fishery was stopped'' (Hourston 1980:151). Management measures were not undertaken because ''stock assessment procedures in use at the time were not sensitive enough to detect the extent of the decline in spawning'' (Hourston 1980: 151). In addition, the numbers of spawners in collapsed Atlantic and Pacific stocks were often reduced by many orders of magnitude from historical levels (Beverton 1990). Recovery for many populations is just now occurring, e.g., around Norway, or has not occurred, e.g., the Iceland spring-spawning herring.

Synthesis

The synthesis we suggest is as follows. The population abundance was overestimated and the fishing mortality was underestimated. A large overcapacity in the fishing fleet allowed the potential for very high fishing mortality. As the populations declined the fishing mortality increased, which led to higher mortality of younger fish. The decline in the populations and the high fishing mortality were not recognized because of statistical bias and over-reliance on commercial catch-per-unit-effort data that were not proportional to the true abundance. As the populations declined, fishing mortality and discarding of juveniles increased. This high discarding reduced the number of fish entering the fishery until the populations were reduced to the point of commercial extinction.

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