ICES J. mar. Sci., 51: 493–504. 1994

Changes in catchability of Atlantic cod (*Gadus morhua*) to an otter-trawl fishery and research survey in the southern Gulf of St Lawrence

D. P. Swain, G. A. Nielsen, A. F. Sinclair, and
G. A. Chouinard

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

For each year from 1971 to 1991 and each age from 3 to 8+, we estimated catchability of Atlantic cod (*Gadus morhua*) to an otter-trawl fishery (q) and a research survey (k) using SPA-based abundance estimates (N) and catch rates to the fishery (U) or survey (R). q tended to be highest early in the time series for young cod (ages 3 and 4), late in the time series for old cod (ages 7 and 8+), and at the two extremes of the time series for cod of intermediate ages (5 and 6). k tended to be higher later in the time series for all ages of cod. We tested for density dependence of q and k by comparing lnU or lnR to lnN. The slope of the regression of lnU versus lnN was significantly less than 1.0 for ages 3 to 5 and greater than 1.0 for age 8+, indicating an inverse relationship between q and N for the younger ages and a positive relationship for the older age. The slope of the regression of lnR on lnN was significantly greater than 1.0 for ages 5 to 7, indicating a positive relationship between k and N for these ages of cod. An SPA calibration model assuming a non-linear relationship between catch rate and abundance led to the same conclusions about the density dependence of q and k. We discuss possible causes of these apparent changes in q and k, and relate the density-dependent changes in k to previous reports of density-dependent changes in spatial distribution for this population.

Key words: catchability, Atlantic cod, bottom trawl, density-dependent.

Received 31 May 1993; accepted 14 April 1994.

D. P. Swain, G. A. Nielsen, A. F. Sinclair, and G. A. Chouinard: Department of Fisheries and Oceans, Gulf Fisheries Centre, PO Box 5030, Moncton, New Brunswick E1C 9B6, Canada.

Introduction

Catch rates (catch per unit effort) in commercial fisheries and research surveys are used to provide information on the abundance of commercially exploited fish species. For example, these catch rates are often used as indices of relative abundance to calibrate or constrain virtual population analyses (e.g. Gulland, 1983; Gavaris, 1988). However, this use of catch rates requires that catchability, the proportion of the population captured by a unit of effort, is constant or its variation known.

A growing number of studies have demonstrated variation in catchability to commercial fisheries (e.g. Pope and Garrod, 1975; MacCall, 1976; Ulltang, 1980; Winters and Wheeler, 1985; Crecco and Overholtz, 1990; Gordoa and Hightower, 1991). Factors that may contribute to variation in catchability include changes in fishing power and diurnal, seasonal, and geographic variation in fish distribution (Garrod, 1964; Gulland, 1964, 1983). These factors can often be measured and accounted for in standardized catch rates (e.g. Gavaris, 1980). Another source of variation in catchability is the relationship between abundance and geographic range of fish populations. Paloheimo and Dickie (1964) noted that catchability is inversely proportional to the area occupied by a stock. A positive correlation between abundance and geographic range has been demonstrated for both pelagic (reviewed by Winters and Wheeler, 1985; MacCall, 1990) and demersal fishes (Crecco and Overholtz, 1990; Rose and Leggett, 1991; Swain and Wade, 1993; Swain and Sinclair, 1994). Thus, catchability is predicted to increase as population size decreases. This prediction has been confirmed by a number of empirical studies (e.g. Pope and Garrod, 1975; MacCall, 1976; Houghton and Flatman, 1980; Ulltang, 1980; Cook and Armstrong, 1985; Winters and Wheeler, 1985; Crecco and Overholtz, 1990; Rose and Leggett, 1991).

1054–3139/94/040493+12 $08.00/0

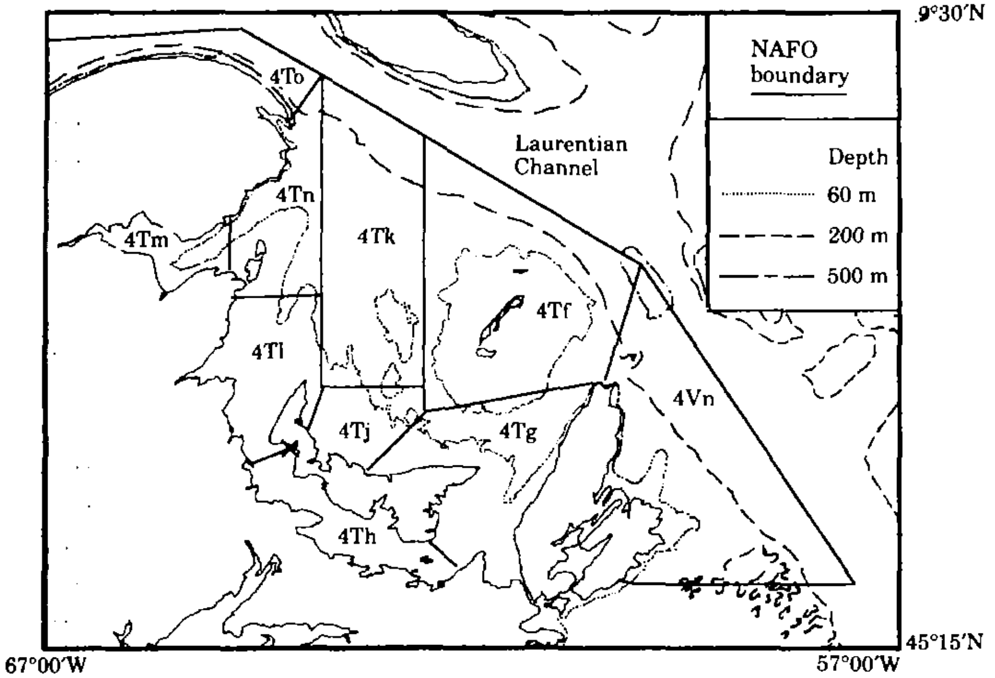

Figure 1. Map of the southern Gulf of St Lawrence and Sidney Bight, showing bathymetry and North Atlantic Fisheries Organization division 4T and subdivision 4Vn.

Abundance indices provided by research surveys are expected to be free of many of the difficulties caused by changes in catchability to commercial fisheries (e.g. Gulland, 1983). These surveys typically use the same standard methods and gear each year, so catchability in surveys should not vary due to changes in fishing power or efficiency. However, catchability in surveys may vary due to variation in fish availability. This may occur because of annual variation in the vertical distribution of fish, or in the proportion of the population that occurs outside of the survey area.

Where possible, Atlantic Canadian groundfish stock assessments have estimated fish stock size using sequential population analysis (SPA) calibrated using catch-rate indices (e.g. Sinclair, 1993). SPA consists of adding up the catches of cohorts of fish while adjusting for natural mortality (Pope, 1972). Estimates of the survivors (or fishing mortalities) in the last year of the time series are needed to begin SPA. Calibration consists of finding the survivor estimates that produce the best match between the SPA estimates of population size and the catch-rate indices. The SPA model and calibration framework most commonly used assumes that: (1) there is no error in the catch-at-age data; (2) natural mortality is constant (usually $M=0.2$); (3) fishing mortality (F) of the oldest age group in a particular year is equal to the average of the values for fully recruited ages in that year; and (4) catchability is constant. For several stocks, estimates of recent population sizes calculated in this way tend to decrease as additional years of data are included in the analysis (e.g. Sinclair, 1993). This "retrospective" pattern suggests an error in the SPA or calibration assumptions.

In this paper we compare estimates of abundance from SPA to catch rates in a commercial fishery and research survey for Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence. This stock has shown a strong retrospective pattern in recent assessments (e.g. Hanson *et al.*, 1992). We present evidence of apparent changes in catchability to both the commercial fishery and research survey.

Material and methods

Study population

The southern Gulf of St Lawrence (North Atlantic Fisheries Organization Division 4T) comprises a shallow shelf (mostly less than 75 m in depth) bordered on the north by the Laurentian Channel (Fig. 1). In summer, three distinct water layers are present: a warm surface layer, a cold (−0.5–1°C) intermediate layer, and a warm (4–6°C) deep layer (Strain, 1988). In winter, two layers are present: a surface mixed layer (50–100 m thick) with temperatures near the freezing point (−1.5°C) and the warm deep layer along the edge of the Laurentian Channel. Juvenile cod are protected by anti-freeze proteins (Kao and Fletcher, 1988) and most are thought to remain in the Gulf throughout the year (Jean, 1964; Paloheimo and Kohler, 1968). Adult cod migrate between summer spawning and feeding grounds in the southern Gulf and overwintering grounds in the deeper, warmer water of the Sydney Bight–Laurentian Channel area of NAFO subdivision 4Vn (Martin and Jean, 1964; Jean, 1964). Because of this annual migration, the southern Gulf cod population is referred to as the 4T–4Vn (Jan–Apr) stock (abbreviated here to 4TVn).

The estimated abundance of 4TVn cod aged 3 and older has varied four-fold during the period 1971–1991 (Chouinard *et al.*, 1992). Abundance was lowest in the mid-1970s and highest in the mid-1980s. Growth rate has also varied widely over this period, declining from the 1970s to the 1980s (Hanson and Chouinard, 1992). The spatial distribution of this stock is density-dependent. September geographic range expands from the western region of the southern Gulf at low population sizes to include central and north-eastern regions of the southern Gulf at high population sizes (Swain and Wade, 1993). Peak cod densities in September shift from shallow water when abundance is low to intermediate depths when abundance is high (Swain, 1993).

Commercial fishery

A description of the fishery on 4TVn cod is given by Hanson *et al.* (1992). The fishery has focused on the interception of cod in areas 4Tf and 4Tg (Fig. 1) during their annual migration into the Gulf in spring and out of the Gulf in autumn, on winter concentrations in the Sidney Bight area (NAFO 4Vn), and on early summer concentrations off the Gaspé Peninsula (4Tn). Monthly catches are usually highest during either the spring migration in May or the autumn migration in November. About 60% of the annual catch of 4TVn cod is landed by otter trawls. Catch rates by this gear are generally highest in the winter fishery in 4Vn and lowest during the August–October period when cod are believed to be most widely dispersed throughout the southern Gulf (Clay, 1991). Minimum mesh-size regulations for otter trawls have varied over the 1971–1991 period. Before June 1977, the minimum size was 105 mm diamond mesh for cotton, hemp, polyamide, and polyester nets and 114 mm for nets of other materials; between June 1977 and July 1981, minimum sizes were 120 and 130 mm, respectively; since July 1981, the minimum size has been 130 mm for all materials.

Research survey

A bottom-trawl survey of the southern Gulf has been conducted each September since 1971. Surveys used a stratified random design (Fig. 2), with stratification based on depth and geographic region. Station allocation has been roughly proportional to stratum area. Sample size has ranged from 61 to 186 trawl tows per survey. Surveys were conducted by the stern trawler "E. E. Prince" using a Yankee 36 trawl during the period 1971–1985, and by the stern trawler "Lady Hammond" using a Western IIA trawl during the period 1986–1991. Both trawls were equipped with a small-mesh cod-end liner. See Carrothers (1988) for detailed trawl specifications. A comparative fishing experiment in 1985 failed to reveal a significant difference in the average catch rate for cod between the two vessels and gears (Nielsen, 1994). The target fishing procedure was a 30-min tow at 3.5 knots in all years. All catches were adjusted to a standard tow of 3.24 km. Further details of survey procedures are given by Hurlbut and Clay (1990).

Catch rates

Two catch rate time series are available for the 4TVn cod stock: U, the standardized catch per unit effort (number of fish per h) in the otter-trawl fishery, and R, the stratified mean catch per tow in the research survey. U is calculated using effort standardized on tonnage class of vessel, month, and area of capture (4T or 4Vn) following Gavaris (1980).

Abundance and catchability

In most recent assessments of the 4TVn cod stock, abundance has been estimated using SPA and a calibration framework known as ADAPT (Gavaris, 1988). In this framework, catch rates from a research survey and/or commercial fishery are taken as observed values and SPA is used to produce predicted values, e.g.:

$$\hat{u}_{ij} = q_j N_{ij}, \tag{1}$$

where û is predicted catch rate, N is abundance estimated by SPA, q is catchability, i indexes year, and j indexes age. Calibration consists of finding the set of input parameters for SPA (i.e. the survivors in the last year of analysis) and the q_j that minimize an objective function tabulating the discrepancy between observed and predicted values, typically:

$$\sum_i \sum_j (\ln U_{ij} - \ln \hat{u}_{ij})^2,$$

where U_{ij} is the observed catch rate in year i for age j.

If q_j is not constant, a different approach to calibration needs to be taken. One possibility is the catch curve approach on which the estimates of Chouinard *et al.* (1992) were based. This approach is based on a multiplicative analysis of the catch rate indices (Sinclair, 1992). The survey and fishery catch rate indices were each analysed using a model with age (A) and year-class (Y) terms, e.g.:

$$\ln U_{ik} = A_i + Y_k + \varepsilon. \tag{2}$$

For calibration purposes, the model was restricted to the 1986–1991 period. Model fit was good according to r^2

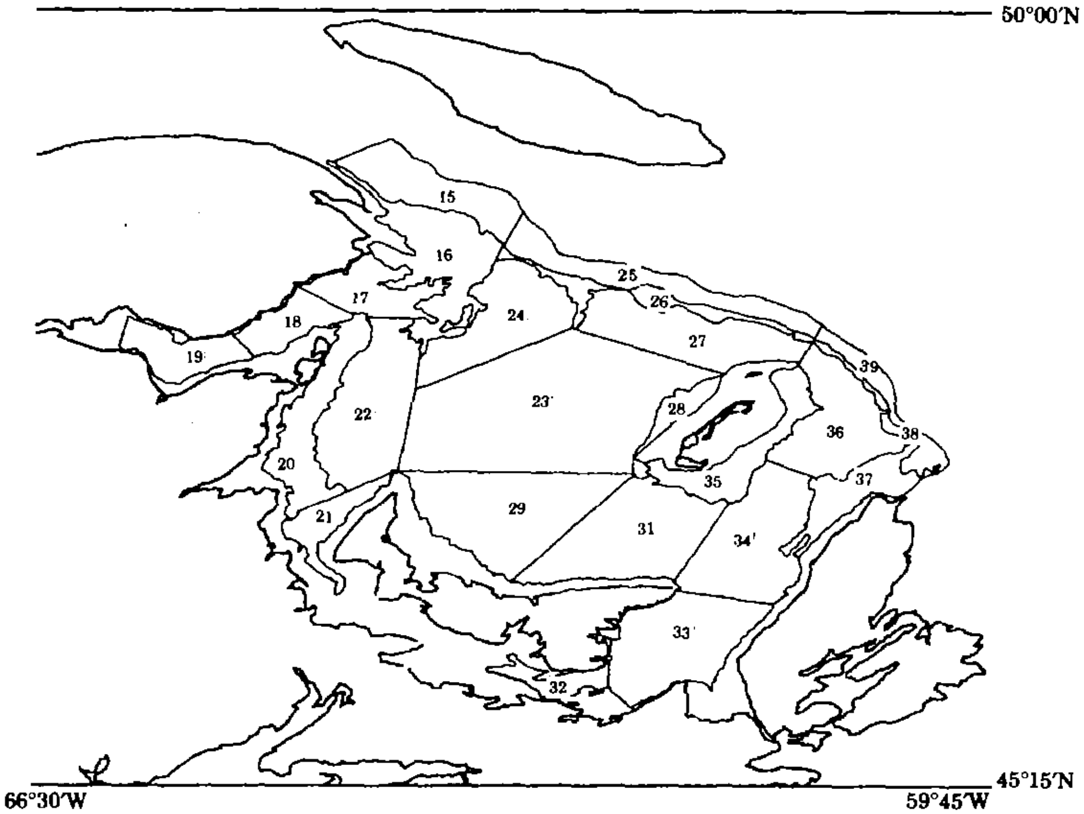

Figure 2. Strata used in groundfish abundance surveys of the southern Gulf of St Lawrence, 1971–1991.

values (0.93 for the survey and 0.97 for the fishery index) and normal probability plots of the residuals (Sinclair, 1992). The estimated age effects A_i were used for catch curves normalized for variation in year-class strength (Shepherd and Nicholson, 1991). For each index, Sinclair (1992) calculated the regression of A_i versus i for fully recruited ages (i=5–10 for the survey and 7–12 for the fishery index). The slopes of these lines indicated a total instantaneous mortality rate (Z) near 0.7 in recent years (Z=0.73 for the survey and 0.71 for the fishery index). Assuming an instantaneous natural mortality rate (M) of 0.2, Chouinard *et al.* (1992) concluded that fishing mortality was approximately 0.5 in recent years. Using this estimate and a partial recruitment vector derived from an analysis of fishing mortality for the years 1987–1990, they assigned age-specific fishing mortalities for 1991 to begin the SPA. In this SPA, they assumed an M of 0.2 for all ages (3–14+) and years and that the instantaneous fishing mortality rate (F) of the oldest ages (13 and 14+) was equal to the average F of ages 7 to 12.

Using the abundance estimates calculated by Chouinard *et al.* (1992), we estimated catchability to the otter-trawl fishery and research survey for each age class from 3 to 8+ in each year from 1971 to 1991 as follows:

$$q_{ij}=\frac{U_{ij}}{N_{ij}} \tag{3}$$

$$k_{ij}=\frac{R_{ij}}{N_{ij}}, \tag{4}$$

where q is catchability to the otter-trawl fishery, k is catchability to the research survey, N is population size, U is the fishery catch rate, R is the survey catch rate, j indexes age (3 to 8+), and i indexes year (1971 to 1991). The N_{ij} were adjusted to values for the end of September to coincide with the timing of the research survey and approximate midpoint of the fishery.

The values used for F in the last year of analysis have a large effect on SPA estimates of abundance for later years in the time series, but not for earlier years provided that fishing mortality is high enough (Pope, 1972). That is, SPA abundance estimates "converge" to values that are insensitive to the input values. A cumulative F of 2.0 or more is often used as a criterion of convergence. Based on this criterion, all the N_{ij} estimated by Chouinard *et al.* (1992) were converged for the 1971–1986 period except for the 1983 year class (age 3 in 1986, cumulative F=1.6). To test the sensitivity of our results to the input values used for the SPA, we performed all analyses described below using both the converged portion of the series (1971–1986) and the full 1971–1991 time series. Analyses using the converged portion of the time series led to the same conclusions as those using the entire time series, and only the latter analyses are reported here.

We tested for temporal trends in q and k using regression analyses with year as the independent variable. A quadratic year term was included in the model when the type I sum of squares for this term indicated a significant ($p<0.05$) improvement over models with a linear term only. q and k were log transformed for these analyses.

We wanted to test whether catchability depended on population size. Comparisons between catchability and population size are of the form y/x versus x [recall Equations (3) and (4)]. To avoid the statistical difficulties associated with comparisons of this form (e.g. Atchley *et al.*, 1976), we tested this question by examining the relationship between catch rate and abundance. Previous workers have assumed a non-linear relationship between catchability and abundance (e.g. Winters and Wheeler, 1985; Crecco and Overholtz, 1990):

$$q=\alpha N^{\beta}. \tag{5}$$

This gives the following relationship between catch rate and abundance:

$$U=\alpha N^{\beta+1}. \tag{6}$$

We tested for a relationship between q and N by linear regression analysis of the logarithmic transformation of Equation (6). A slope ($\beta+1$) significantly ($p<0.05$) different from 1.0 was taken as evidence of a relationship between q and N; values significantly less than 1.0 indicated an inverse relationship, those significantly greater than 1.0 a positive relationship. Analyses used the REG procedure of SAS (SAS, 1990). We used the same approach to test for a relationship between k and N. An assumption of this analysis is that the relationship between U or R and N has an intercept of zero (when $\beta+1>0$). Plots of U or R versus N suggested that this assumption was reasonable. Correlations between q or k and N, which do not depend on this assumption, led to the same conclusions regarding the density dependence of q and k, as did this analysis of catch rates and abundance. We do not report the correlation analysis here due to the previously noted statistical problems.

A second approach is to try to estimate N and the patterns in catchability simultaneously using the SPA and its calibration model. We used this approach as a second test for density dependence of catchability. We performed SPA, calibrating with either the fishery or survey catch rate index. Following from Equation (6), we calibrated with the fishery index by selecting the parameter estimates that minimized:

$$\sum_{i=71}^{91}\sum_{j=5}^{12}(\ln U_{ij} - \ln(Q_{1j}N_{ij}^{Q_{2j}+1}))^2, \tag{7}$$

where the parameters to be estimated were Q_{1j}, Q_{2j}, and N_{91j}. A value for Q_{2j} significantly different from zero was taken as evidence of density-dependent catchability for age j. We used the same approach to test for the density dependence of catchability to the survey, except that calibration with the survey index used ages 3 to 10.

Results

Population size

The SPA from Chouinard *et al.* (1992) indicated a period of low abundance in the 1970s and a period of high abundance in the 1980s (Fig. 3). For age 3, abundance was lowest in the early 1970s and highest in the late 1970s and early 1980s. For age 8+, abundance was low throughout the 1970s and high for most of the 1980s.

Catch rates in both the commercial fishery and research survey suggest the same trends in abundance as the SPA for older ages but not for younger ages (Fig. 4). For ages 6 to 8+, both catch rate indices indicate a period of low abundance in the 1970s, a period of high abundance in the 1980s, and a recent decline in abundance. For age 5, the survey index and SPA (Fig. 3) indicate similar patterns in relative abundance. On the other hand, commercial catch rates of age 5 cod suggest no strong trend in abundance. For ages 3 and 4, the survey catch rates suggest a period of low abundance in the early 1970s and a period of relatively high abundance since then. In contrast, commercial catch rates of age 3 and 4 cod were relatively high in the early 1970s and low in the 1980s.

Catchability

Annual trends in q were strongly age-dependent (Fig. 5). For ages 3 and 4, q tended to be relatively high in the early to mid 1970s and low thereafter. For ages 5 and 6, q tended to be relatively high in the early to mid 1970s and relatively low in the early to mid 1980s, increasing to intermediate or high values in recent years. For ages 7 and 8+, q tended to increase from 1971 to 1991. These relationships between q and year were statistically significant for ages 4, 5, 7, and 8+ (Table 1). A linear model adequately described annual trends in q for ages 7 and 8+, while a quadratic term significantly improved models for ages 4 and 5.

Annual trends in k were similar for all six age groups (Fig. 5). k tended to be higher in the 1980s than in the 1970s. Relationships between k and year were highly significant for all age groups (Table 1). A linear model adequately described annual trends in k for ages 3 to 7,

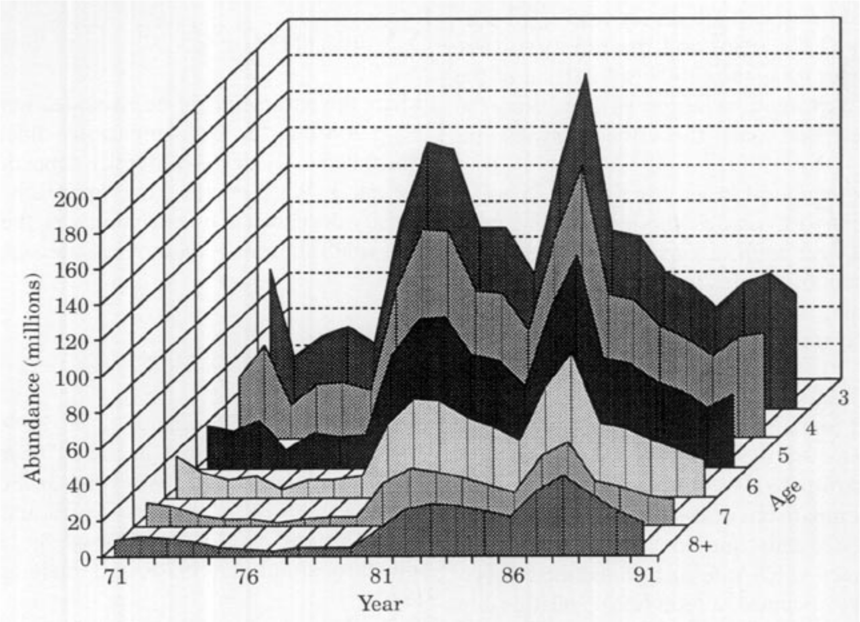

Figure 3. Abundance estimates of the southern Gulf of St Lawrence [4TVn (Jan–Apr)] cod stock for ages 3 to 8+ (from Chouinard *et al.*, 1992).

while a quadratic term significantly improved the model for age 8+.

Catchability and abundance

Estimates of the slope of the relationship between lnU and lnN were significantly less than 1.0 for ages 3 to 5, and significantly greater than 1.0 for age 8+ (Table 2). This indicates an inverse relationship between q and N for ages 3 to 5 and a positive relationship for age 8+.

Estimates of the slope of the relationship between lnR and lnN did not differ significantly from 1.0 for ages 3, 4, and 8+, but were significantly greater than 1.0 for ages 5 to 7 (Table 2). These results indicate a positive relationship between k and N for ages 5 to 7.

Calibration using the objective function given by expression 7 led to the same conclusions about the density dependence of catchability (Table 3). Catchability to the fishery was inversely related to abundance for age 5 and positively related to abundance for ages 9–11. The positive relationship between abundance and catchability to the survey was significant for ages 5 and 6 and nearly so for age 7.

Discussion

Catchability to the fishery tended to be highest early in the time series for young cod (ages 3 and 4) and late in the time series for old cod (ages 7 and 8+). q showed an intermediate pattern, with highest values early and late in the time series, for cod of intermediate ages (5 and 6). This pattern of variation may be explained by the opposing effects of known changes in mesh size and size-at-age on the one hand and of possible changes in vessel fishing power on the other hand. Mesh size has increased and size-at-age decreased during the 1971–1991 time series (see Material and methods). These changes are expected to result in a decrease in q during the time series, particularly for the younger, partially recruited ages. Effort standardization on vessel tonnage corrected for one source of variation in fishing power in our analysis, but other potential sources of variation (e.g. fish targetting capabilities) were not measured or corrected for. Increases in fishing power during the 1971–1991 time series due to these other sources of variation are likely and may explain the temporal trend toward increasing q apparent for older cod.

A negative relationship between abundance and catchability to commercial fisheries has been predicted on theoretical grounds (Paloheimo and Dickie, 1964) and widely observed in empirical studies (e.g. Winters and Wheeler, 1985; Crecco and Overholtz, 1990; Rose and Leggett, 1991; and references therein). We observed the predicted negative relationship for younger cod (ages 3 to 5) but not for older cod. For the oldest age group, we observed the opposite effect, a positive relationship between q and abundance. We believe that the relationships between q and N reported here may be spurious, resulting from confounding between abundance and temporal changes in mesh size, size-at-age, and fishing power. Perhaps confounding with these other factors

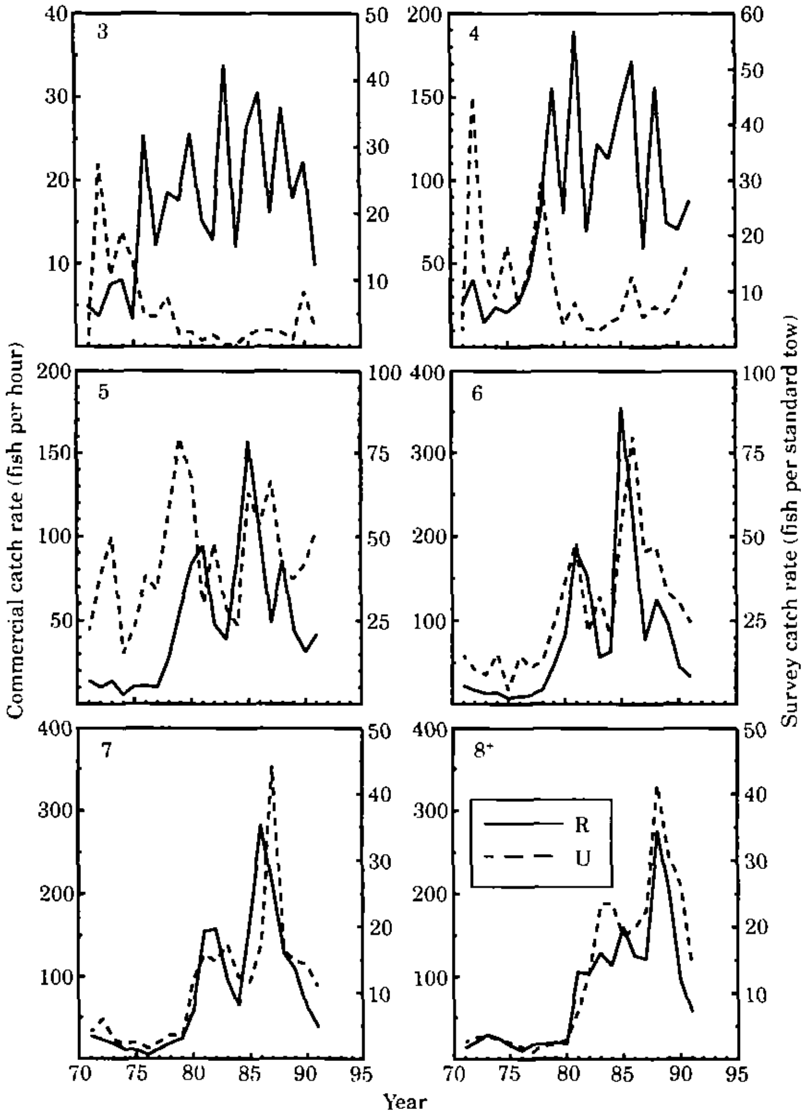

Figure 4. Catch rates of 4TVn (Jan–Apr) cod to the otter-trawl fishery (U) and research survey (R) for ages 3 to 8+.

has obscured the expected negative relationship between q and abundance for older cod. Alternatively, a functional relationship between q and N may not occur for 4TVn cod because of the nature of the otter-trawl fishery for this stock. Effort in this fishery is concentrated in periods of highest cod aggregation: the migration into the Gulf in spring and out of the Gulf in autumn, spring spawning aggregations in the Gulf, and overwintering concentrations in the Sidney Bight area. The prediction that q and abundance should be inversely related is based on the prediction that geographic range or stock area should be density-dependent, expanding as abundance increases (e.g. Paloheimo and Dickie, 1964; Winters and Wheeler, 1985). Expansion of stock area as abundance increases is expected because of competition for density-dependent resources like food (MacCall, 1990). The main feeding period for 4TVn cod is the summer and early autumn (K. Schwalme and G. Chouinard, unpublished data), and stock area during this season does expand as abundance increases (Swain and Wade, 1993; Swain and Sinclair, 1994). However, little fishing by the otter-trawl fleet occurs during this feeding period, and stock area during periods of greater fishing activity is not well known for 4TVn cod. Because competition for density-dependent resources is not expected to be strong during migration, spawning, and overwintering (when 4TVn cod appear to feed little), the prediction for stock area (and thus q) to be density-dependent may not apply during these periods of greatest fishing activity.

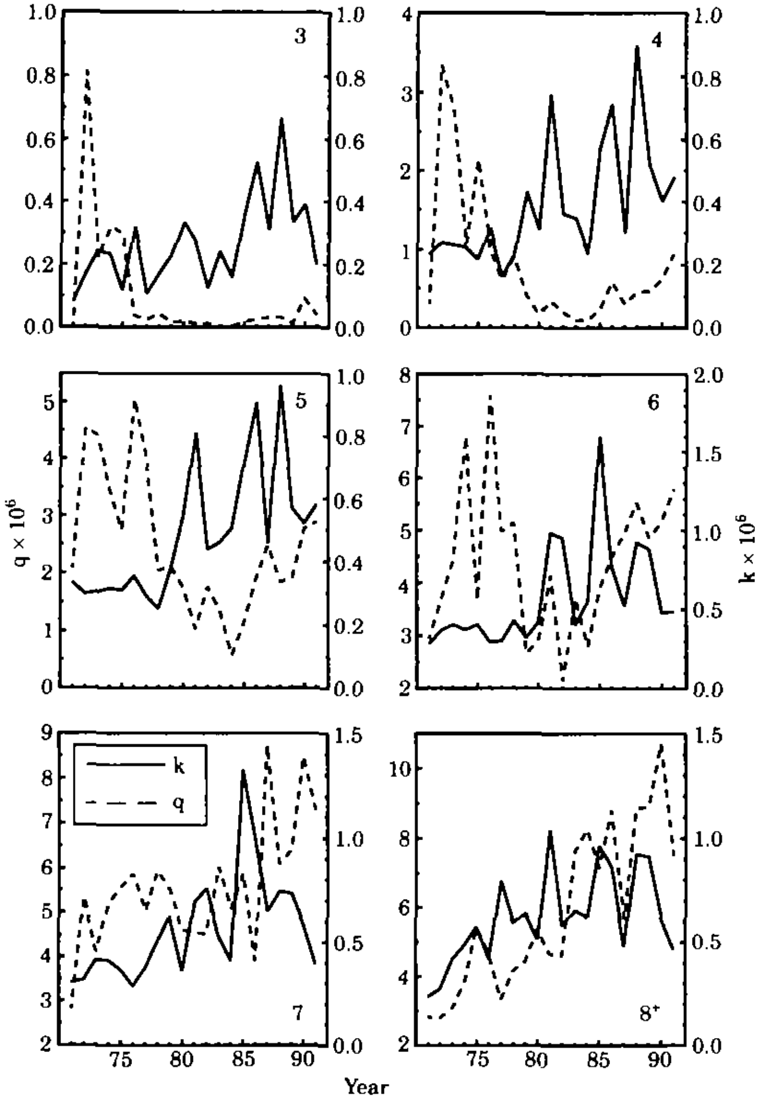

Figure 5. Catchability of 4TVn (Jan–Apr) cod to the otter-trawl fishery (q) and research survey (k) for ages 3 to 8+.

Catchability of cod to the research survey in the southern Gulf increased from the 1970s to the 1980s. This indicates a change in availability of cod to the survey. Changes in availability to the survey may be related to changes in the proportion of the population occurring: (*1*) outside of the survey area; (*2*) on "untrawlable" bottom; or (3) high in the water column.

Chouinard and Sinclair (1987) also suspected a change in the catchability of cod to the southern Gulf research survey between the 1970s and the 1980s. They suggested that the relationship between SPA and survey estimates of abundance may be non-linear and recommended research to identify possible mechanisms for such a relationship. We found that k was significantly density-dependent for ages 5 to 7, increasing as abundance increased. The spatial distribution of cod in the southern Gulf is also density-dependent (Swain, 1993; Swain and Wade, 1993). The observed changes in distribution are consistent with the observed changes in k. Peak cod densities occur in shallow water when abundance is low and at intermediate depths when abundance is high (Swain, 1993). The survey area does not include shallow inshore areas. Thus, a higher proportion of the population is predicted to occur in shallow water outside of the survey area when abundance is low, resulting in reduced availability and catchability to the survey at low abundance. Age-dependent variation in bathymetric pattern may also explain why density-dependent changes in k were most significant for ages 5 to 7. When abundance is high, peak densities occur at

Table 1. Annual trends in q and k during the period 1971–1991. r^2_{adj} is adjusted for the number of parameters included in the model. Parameter estimates are shown only for the significant ($p<0.05$) models.

		Sequential probabilities		Model					
Series	Age	Year	$Year^2$|Year	Predictors	r^2_{adj}	P	β_0	β_1	β_2
q	3	0.58	0.50	Year		0.57			
	4	0.027	0.011	Year, $Year^2$	0.37	0.0059	101.31783	− 2.46408	0.014793
	5	0.037	0.019	Year, $Year^2$	0.33	0.011	52.64518	− 1.251797	0.007507
	6	0.52	0.17	Year		0.53			
	7	0.0041	0.73	Year	0.34	0.0032	− 0.34492	0.025082	
	8^+	0.0001	0.56	Year	0.79	0.0001	− 3.13855	0.059553	
k	3	0.0065	0.71	Year	0.31	0.0053	− 5.49475	0.049846	
	4	0.0026	0.87	Year	0.37	0.0020	− 4.80201	0.046461	
	5	0.0002	0.49	Year	0.52	0.0001	− 4.60533	0.047099	
	6	0.0037	0.23	Year	0.33	0.0039	− 4.41677	0.046297	
	7	0.0019	0.081	Year	0.35	0.0029	− 3.95658	0.040661	
	8^+	0.0006	0.0015	Year, $Year^2$	0.59	0.0001	− 16.71994	0.336393	− 0.001745

Table 2. Estimates of slope ($\beta+1$) from the linear regression between ln(catch rate) and ln(N). SE=standard error of the slope. F is the F-statistic testing for a slope of 1. p is the probability that slope equals 1.

Catch rate	Age	Estimate	SE	F	p
U	3	− 1.457	0.708	12.05	0.0026
	4	− 0.177	0.304	15.02	0.0010
	5	0.389	0.115	28.37	0.0001
	6	0.837	0.086	3.57	0.074
	7	1.014	0.067	0.05	0.83
	8^+	1.313	0.085	13.48	0.0016
R	3	0.903	0.249	0.15	0.70
	4	1.132	0.185	0.51	0.49
	5	1.337	0.109	9.50	0.0061
	6	1.387	0.108	12.85	0.0020
	7	1.275	0.088	9.84	0.0054
	8^+	1.150	0.099	2.28	0.15

progressively greater depths for older cod (Swain, 1993). Thus, changes in k may be relatively small for younger cod (i.e. ages 3 and 4) because density-dependent shifts in spatial distribution are relatively small for these ages. Older cod, particularly age 8+, tended to be relatively widely distributed with respect to depth at low abundance. This may explain why changes in k were less strong for age 8+ than for ages 5 to 7.

Other explanations for changes in availability to the survey can also be suggested. For example, if cod prefer "untrawlable" bottom (e.g. rocky, irregular bottom) and this bottom type is limiting, then availability of cod should increase with abundance. Alternatively, the observed relationship between k and abundance may be coincidental, and the changes in availability to the survey may be related to density-independent factors such as environmental conditions. The 4TVn cod stock

Table 3. Estimates of the exponent parameter in the calibration model given by Equation (7) in the text. Q_2 and K_2 are the parameter estimates from calibrations with the fishery and survey catch rate indices, respectively. Asterisks indicate estimates more than two standard errors (SE) from zero.

Age	Q_2	SE	K_2	SE
3			− 0.0168	0.2144
4			0.1304	0.1842
5	− 0.5944*	0.1627	0.3185*	0.1512
6	− 0.1391	0.1385	0.3516*	0.1304
7	0.0138	0.1233	0.2315	0.1167
8	0.1800	0.1148	0.1605	0.1092
9	0.2980*	0.1133	0.0946	0.1060
10	0.3836*	0.1193	0.0301	0.1052
11	0.3207*	0.1307		
12	0.1405	0.1323		

appears to be entering a period of low abundance, so data may soon exist to distinguish more clearly between density-dependent and -independent explanations for these changes in k.

If interaction occurs among age groups of cod, then age i catchability may depend on total (3+) abundance rather than just age i abundance. Our approach to testing the density-dependence of catchability [i.e. using Equation (5) to substitute for catchability in the relationship between catch rate and abundance] does not permit tests of this possibility. Swain and Sinclair (1994) tested the density dependence of cod distribution in the southern Gulf using either age i abundance or total 3+ abundance. Results were similar using either abundance variable. This suggests that the age-specific comparisons reported here provide an adequate test for density-dependent catchability.

Our analysis depends on the assumptions of our SPA model. An alternate interpretation of our results is that the apparent trends in catchability reported here reflect errors in these assumptions rather than true changes in catchability. Errors in the values assumed for F of the oldest age group of each cohort and for M can generate spurious trends in SPA estimates of abundance (Bradford and Peterman, 1989). These spurious trends appear only in the recent portion of time series where some cohorts are incomplete. Because our results are similar using both the entire 1971–1991 time series and the "converged" portion of the time series, they cannot be explained by this effect alone. However, Lapointe *et al.* (1989) demonstrated that spurious time trends in abundance can be generated by SPA even when all cohorts are complete if errors in M are accompanied by trends in F. Apparent trends in catchability could also be spurious effects of time trends in M or in catch misreporting (Sinclair *et al.*, 1991). Discarding of undersized fish at sea is likely to be an important component of catch misreporting. We expect annual and density-dependent trends in discarding due to changes in gear and in size composition of the stock. Because of the discarding problem, trends in catch misreporting are likely to be greater for younger cod. Spurious effects of errors in M are also expected to be greater for younger age groups (e.g. Lapointe *et al.*, 1989). Thus, we expect that spurious trends in catchability should also be greater for younger cod. However, we did not find that apparent trends in catchability were generally greater for younger ages. For example, density-dependent trends in k were significant for older ages (5–7) but not for younger ages (Table 2). Nevertheless, simulation studies are needed to examine the extent to which errors in M and in catches may cause apparent trends or obscure real trends in the catchability of 4TVn cod.

Annual assessments of the 4TVn cod stock have usually used SPA "calibrated" or "tuned" using research survey and commercial otter-trawl catch rates (e.g. Hanson *et al.*, 1992). This calibration has assumed constant catchabilities to the survey and commercial fishery. Abundance estimates calculated in this way show a strong "retrospective" pattern for this stock in recent years. Sinclair *et al.* (1991) demonstrated that retrospective patterns can be generated by changes in the level of catch misreporting and by errors in M when there is a trend in F (though, in the latter case, retrospective effects were slight). The changes in catchability suggested by our results may also be a factor contributing to the retrospective pattern of the 4TVn stock.

In summary, we report apparent changes in catchability of 4TVn cod to both the otter-trawl fishery and the research survey. The changes in catchability to the fishery may be related to changes in fishing power and population characteristics (i.e. size at age). Those to the research survey may reflect density-dependent changes in availability. Systematic errors in the SPA (e.g. due to trends in M or in catch misreporting) may also contribute to these apparent trends in catchability. A better understanding of the mechanisms underlying these results will improve stock assessment. If these results are spurious effects of systematic errors in the SPA, then assessments based on relative indices of abundance, such as survey catch rates, may provide a better indication of population trends than SPA-generated abundance estimates. On the other hand, if these apparent changes in catchability are real, then variation in catch-rate indices do not accurately reflect variation in abundance and methods of SPA calibration that do not assume constant catchability are needed. In this case, functional relationships between catchability and population characteristics (e.g. abundance, size at age), fleet characteristics, and environmental conditions need to be identified.

Acknowledgements

We thank J. Allard for many helpful criticisms and suggestions, J. M. Hanson for helpful discussion, G. G. Thompson for a detailed and constructive review of the manuscript, and the associate editor and an anonymous referee for helpful comments.

References

Atchley, W. R., Gaskins, C. T., and Anderson, D. 1976. Statistical properties of ratios. I. Empirical results. Systematic Zoology, 25: 137–148.

Bradford, M. J., and Peterman, R. M. 1989. Incorrect parameter values used in virtual population analysis (VPA) generate spurious time trends in reconstructed abundances. *In* Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models, pp. 87–99. Ed. by R. J. Beamish and G. A. McFarlane. Canadian Special Publication on Fisheries and Aquatic Sciences, 108.

Carrothers, P. J. G. 1988. Scotia-Fundy groundfish survey trawls. Canadian Technical Report of Fisheries and Aquatic Sciences no. 1609. 27 pp.

Chouinard, G. A., Hanson, J. M., and Nielsen, G. A. 1992. Examination of the status of the southern Gulf of St Lawrence cod stock following the 1992 fall groundfish survey. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 92/105. 30 pp.

Chouinard, G. A., and Sinclair, A. F. 1987. Assessment of the 4TVn (Jan.-Apr.) cod stock for 1987. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 87/93. 48 pp.

Clay, D. 1991. Seasonal distribution of demersal fish (Osteichthyes) and skates (Chondrichthyes) in the Southeastern Gulf of St Lawrence. *In* The Gulf of St Lawrence: small ocean or big estuary?, pp. 241–259. Ed. by J.-C. Therriault. Canadian Special Publication on Fisheries and Aquatic Sciences no. 113.

Cook, R. M., and Armstrong, D. W. 1985. Changes in catchability of cod, haddock, and whiting associated with the Scottish seine-net fleet. Journal du Conseil International pour l'Exploration de la Mer, 42: 171–178.

Crecco, V., and Overholtz, W. J. 1990. Causes of density-dependent catchability for Georges Bank haddock *Melanogrammus aeglefinus*. Canadian Journal of Fisheries and Aquatic Sciences, 47: 385–394.

Garrod, D. J. 1964. Effective fishing effort and catchability coefficient. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 155: 66–70.

Gavaris, S. 1980. Use of the multiplicative model to estimate catch rate and effort from commercial data. Canadian Journal of Fisheries and Aquatic Sciences, 37: 2272–2275.

Gavaris, S. 1988. An adaptive framework for the estimation of population size. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 88/29. 12 pp.

Gordoa, A., and Hightower, J. E. 1991. Changes in catchability in a bottom-trawl fishery for Cape hake (*Merluccius capensis*). Canadian Journal of Fisheries and Aquatic Sciences, 48: 1887–1895.

Gulland, J. A. 1964. The reliability of catch per unit effort as a measure of abundance in North Sea trawl fisheries. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 155: 99–102.

Gulland, J. A. 1983. Fish stock assessment: a manual of basic methods. J. Wiley & Sons, New York. 223 pp.

Hanson, J. M., and Chouinard, G. A. 1992. Evidence that size-selective mortality affects growth of Atlantic cod (*Gadus morhua* L.) in the southern Gulf of St Lawrence. Journal of Fish Biology, 41: 31–41.

Hanson, J. M., Chouinard, G. A., Nielsen, G. A., and Currie, L. G. 1992. Stock status of the 4T-Vn (Jan.-Apr.) cod stock in 1992. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 92/55. 76 pp.

Houghton, R. G., and Flatman, S. 1980. The exploitation pattern, density-dependent catchability, and growth of cod, *Gadus morhua*, in the west-central North Sea. Journal du Conseil International pour l'Exploration de la Mer, 39: 271–287.

Hurlbut, T., and Clay, D. 1990. Protocols for research vessel cruises within the Gulf Region (demersal fish) (1970–1987). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2082. 143 pp.

Jean, Y. 1964. Seasonal distribution of cod (*Gadus morhua* L.) along the Canadian Atlantic coast in relation to water temperature. Journal of the Fisheries Research Board of Canada, 21: 429–460.

Kao, M. H., and Fletcher, G. L. 1988. Juvenile Atlantic cod (*Gadus morhua*) can be more freeze resistant than adults. Canadian Journal of Fisheries and Aquatic Sciences, 45: 902–905.

Lapointe, M. F., Peterman, R. M., and MacCall, A. D. 1989. Trends in fishing mortality rate along with errors in natural mortality rate can cause spurious time trends in fish stock abundances estimated by virtual population analysis (VPA). Canadian Journal of Fisheries and Aquatic Sciences, 46: 2129–2139.

MacCall, A. D. 1976. Density-dependence of catchability coefficient in the California sardine, *Sardinops sagax caerula*, purse-seine fishery. Marine Research Commission of California Cooperative Oceanic Fisheries Investigations Report, 18: 136–148.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. University of Washington Press, Seattle, Washington. 153 pp.

Martin, W. R., and Jean, Y. 1964. Winter cod tagging off Cape Breton and on onshore Nova Scotia banks. Journal of the Fisheries Research Board of Canada, 21: 215–238.

Nielsen, G. A. 1994. Comparison of the fishing efficiency of research vessels used in the southern Gulf of St Lawrence Groundfish Surveys from 1971 to 1992. Canadian Technical Report of Fisheries and Aquatic Sciences no. 1952. 56 pp.

Paloheimo, J. E., and Dickie, L. M. 1964. Abundance and fishing success. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 155: 152–163.

Paloheimo, J. E., and Kohler, A. C. 1968. Analysis of the southern Gulf of St Lawrence cod population. Journal of the Fisheries Research Board of Canada, 25: 555–578.

Pope, J. G. 1972. An investigation of the accuracy of virtual population analysis using cohort analysis. International Commission of Northwest Atlantic Fisheries Research Bulletin, 9: 65–74.

Pope, J. G., and Garrod, D. J. 1975. Sources of error in catch and effort quota regulations with particular reference to variation in the catchability coefficient. International Commission of Northwest Atlantic Fisheries Research Bulletin, 11: 17–30.

Rose, G. A., and Leggett, W. C. 1991. Effects of biomass-range interactions on catchability of migratory demersal fish by mobile fisheries: an example of Atlantic cod (*Gadus morhua*). Canadian Journal of Fisheries and Aquatic Sciences, 48: 843–848.

SAS Institute. 1990. SAS/STAT User's Guide, Version 6, fourth edn. SAS Institute Inc., Cary, North Carolina. 1686 pp.

Shepherd, J. G., and Nicholson, M. D. 1991. Multiplicative modelling of catch-at-age data, and its application to catch forecasts. Journal du Conseil International pour l'Exploration de la Mer, 47: 284–294.

Sinclair, A. 1992. Preliminary analysis of research survey and commercial indices for 4TVn cod up to 1992. Canadian Atlantic Fisheries Scientific Advisory Committee Research Document 92/100. 9 pp.

Sinclair, A. (ed.) 1993. Report on the assessments of groundfish stocks in the Canadian Northwest Atlantic, 4–14 May 1993. Canadian Technical Report of Fisheries and Aquatic Sciences no. 1946e. 200 pp.

Sinclair, A., Gascon, D., O'Boyle, R., Rivard, D., and Gavaris, S. 1991. Consistency of some Northwest Atlantic groundfish stock assessments. North Atlantic Fisheries Organization Scientific Council Studies, 16: 59–77.

Strain, P. M. 1988. Chemical oceanography in the Gulf of St Lawrence: geographic, physical oceanographic and geologic setting. *In* Chemical oceanography in the Gulf of St Lawrence, pp. 1–14. Ed. by P. M. Strain. Canadian Bulletin of Fisheries and Aquatic Sciences. 220 pp.

Swain, D. P. 1993. Age- and density-dependent bathymetric pattern of Atlantic cod (*Gadus morhua*) in the southern Gulf of St Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 50: 1255–1264.

Swain, D. P., and Wade, E. J. 1993. Density-dependent geographic distribution of Atlantic cod *Gadus morhua* in the southern Gulf of St Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 50: 725–733.

Swain, D. P., and Sinclair, A. F. 1994. Fish distribution and catchability: what is the appropriate measure of distribution? Canadian Journal of Fisheries and Aquatic Sciences, 51: 1046–1054.

Ulltang, O. 1980. Factors affecting the reaction of pelagic fish stocks to exploitation and requiring a new approach to assessment and management. Rapports et Procès-Verbaux des Réunions du Conseil International pour l'Exploration de la Mer, 177: 489–504.

Winters, G. H., and Wheeler, J. P. 1985. Interaction between stock area, stock abundance, and catchability coefficient. Canadian Journal of Fisheries and Aquatic Sciences, 42: 989–998.