The collapse of cod in Eastern Canada: the evidence from tagging data

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We examined the history of exploitation of three cod populations in Eastern Canada since 1954 as estimated from tag return data from 122 tagging experiments. We found very high rates of exploitation in the late 1980s and early 1990s that are consistent with the hypothesis that these populations collapsed because of overfishing. The estimates were made with a new method that incorporates the data in the year of tagging which are often ignored.

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Introduction

By 1993, the six major cod stocks in Eastern Canada had collapsed to the point where a complete moratorium on fishing was declared. The cause of this collapse has been vigorously debated. It has been claimed that the primary cause of the collapse was environmental: climate change, seal predation, or changes in the ecosystem (Lear and Parsons, 1993; Mann and Drinkwater, 1994). Others have compiled extensive evidence that this collapse can be attributed to overfishing alone (Hutchings and Myers, 1994; Myers and Cadigan, 1995a,b; Myers *et al.*, in press, b).

We examined historic tagging data to reconstruct fishing mortality on three of these stocks: southern Labrador/north-east Newfoundland (North-west Atlantic Fisheries Organization (NAFO) Div. 2J3KL), St Pierre Bank (NAFO Div. 3Ps), and northern Gulf of St Lawrence (NAFO Div. 3Pn4RS). For completeness, we also examined the limited data available from northern Labrador (NAFO Div. 2GH). Our goal was to determine whether fishing mortality alone is sufficient to explain the collapse of these stocks. We further wished to determine if fishing mortality varied among components, i.e. substocks, of the populations. In a previous analysis, Myers *et al.* (in press, a) examined a small

portion of these data (14 tagging experiments) to determine if inshore populations of cod existed. They found high fishing mortality on these inshore components.

The exploitation rate, u, is defined as the fraction of the stock present at the start of a time period that is caught during that time period. The exploitation rate for a group of tagged fish in the year of tagging is $u = R'/N'$ where R' is the number of tagged fish caught and N' is the number of tagged fish available to be caught. If the fish are tagged before the fishing season begins and if the fish mix thoroughly throughout the population then the exploitation rate of the tagged fish is an estimate of the exploitation rate in the whole population. Typically, we do not know R' and N' but, rather, we have observed values R and N. R is the number of tags recovered from the fishers. It is less than R' because not all recaptured fish with tags are reported. N is the number of tagged fish released. It is greater than N' because some tagged fish experience tag-induced mortality, initial tag loss or chronic tag loss. Therefore, to estimate exploitation rate from a single year of data it is necessary to convert N and R to estimates of N' and R'. Double tagging experiments and holding pen studies can be used to estimate shedding rates and tag-induced mortality. Reporting rate can be estimated using a high-reward tag study, port sampling, or planted tags

(see Pollock *et al.*, 1991). If these studies are not conducted then it is not possible to analyze a single year's tag returns. If batches of tagged fish are released in two or more consecutive years then it is possible to estimate survival rate provided that the chronic tag shedding rate is known and the different tagged batches of fish have the same behaviour (movement patterns) (Brownie *et al.*, 1985). That is, reporting rate need not be known nor constant and initial tag-induced mortality and initial tag loss need not be known.

The cod tagging studies around Newfoundland were designed when stock structure and movements were not well known. Consequently, the studies were not designed for estimating mortality rates. We develop here new methods which may be useful for analyzing a variety of historic databases, like those of the Newfoundland cod.

In the model, the returns of tags from a single tagged batch of fish were followed over a number of years. It was assumed that fishing mortality and the tag reporting rate were unknown but constant from year to year over the period considered. The natural mortality rate was assumed known. These assumptions allowed us to estimate the availability of tags and the exploitation rate. Because the necessary assumptions are quite strong, we carefully considered the robustness of the method to failures of assumptions.

An interesting feature of the model is that tag returns from the first year of the study (the year of tagging) can be utilized even if the tagging took place during the fishing season rather than prior to the start of the season. These data are usually ignored. This allowed us to compare availability of tags (and thus, indirectly, reporting rates) within and among regions for different time periods. A traditional analysis, in contrast, would consist of regressing the logarithm of the number of tag returns versus the year of recovery starting with the second year of recovery. If there is no chronic tag shedding the slope of the regression line would be an estimate of the survival rate.

The tagging experiments

We examined 122 separate tagging experiments conducted from 1954–1990 (Fig. 1). An experiment refers to a single release of fish in a relatively small area (typically within 20 nautical miles) over a period of a week. We limited our analysis to fish 50 cm (i.e. approximately 6 years old) or longer at the time of release and the numbers stated below are thus subsets of the total number of fish tagged. In 1954 and 1955, there were 13 tagging experiments (Templeman, 1974). About half of the tags were internal tags and half were external tags made of vinylite or celluloid (Templeman, 1963). For the 1950s data, the median number of fish released per experiment that we analyzed was 880 and the median number of returns was 213. Between 1962 and 1966, and

after 1977, the tagging experiments we examined were conducted using Petersen disk tags attached posterior or anterior to the dorsal fins (Templeman, 1977; Lear, 1984). For the 1960s data, the median number of fish released per experiment was 672 and the median number of returns was 191. For the data after 1978, the median number of releases per experiment was 978 and the median number of returns was 105. Taggart *et al.* (1995) provide a summary of the historical tagging data in the Newfoundland region.

Cod were captured for tagging by baited hooks, traps, or trawls of short duration; only fish in excellent condition were released. Each tagging episode typically took a week. Each tagging is identified by an experiment number which consists of the last two digits of the year of release and a two digit sequential identifier. The data we used are given in Myers *et al.* (1995); a subset for NAFO Div. 3K is given in Appendix 1. We used all available data, but there were periods in which no tagging was carried out.

For 2J3KL cod, we used returns up to and including 1991, when a moratorium was declared on all fishing in the region. For the other regions, the moratorium came the next year, so we used data up to and including 1992 for these.

The model

We modified existing tagging models to reflect the details of the tagging experiments and the nature of the fishery. First, we used models that did not assume that the commercial catch is known because of possible misreporting. In this way our models resembled band return models (see Pollock, 1991). Second, our model assumed that fishing mortality occurs during a short period of time in the middle of each year. This assumption is known as "Pope's approximation" in models of commercial catch-at-age data, and is a very good approximation for these data (Mertz and Myers, in press). It also allows our results to be compared directly to the results from the analysis of commercial catch-at-age data. Third, we assumed that natural mortality is known. We assumed that instantaneous natural mortality was 0.2 yr^{-1} to make our results comparable to the analysis of commercial catch-at-age data. We will examine this assumption below. Fourth, we considered experiments where more than one type of tag was used with different loss rates. Fifth, we developed a correction for the fact that, in different experiments, tags were put on at different times of the year.

We classified tags by tag type, k. Let the reporting rate (the probability that a tag on a fish that is caught by a fisher is reported) be λ. Let the finite exploitation rate, i.e. the proportion of fish present at the beginning of the year that are caught, be u, and let the proportion of fish with tags of type k that die naturally or lose their tags
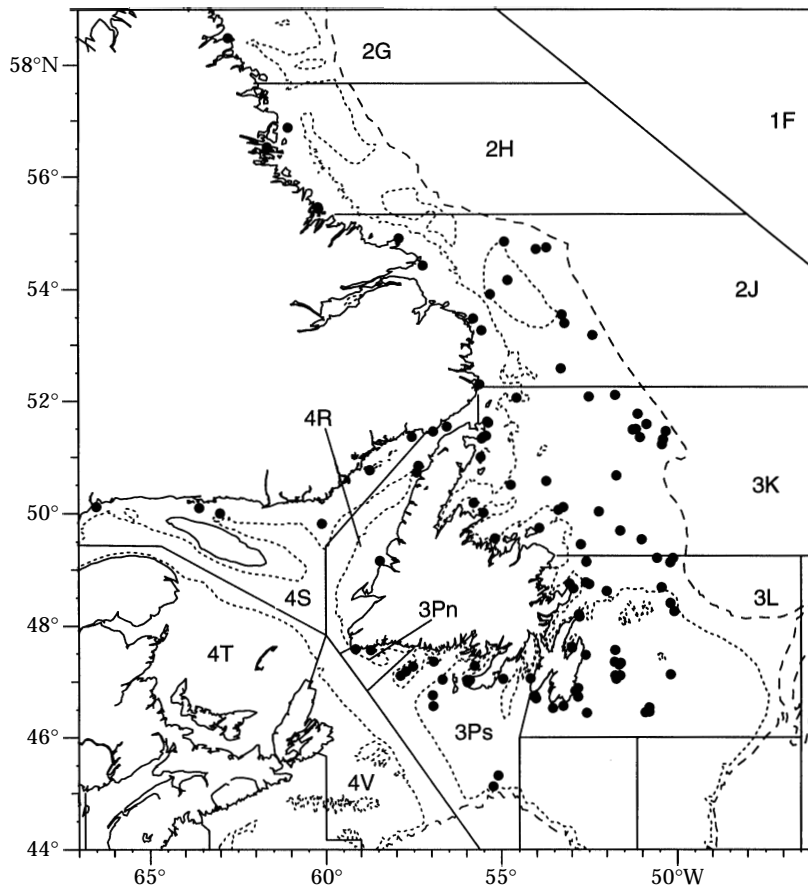
Figure 1. Locations of tagging experiments and the NAFO divisions used to define management regions and populations. The dotted line is the 200 m isobath and the dashed line is the 1000 m isobath.

each year, be v_k (notation is given in Table 1). Assume N_k tags of type k are put on just before the fishing season, and that the fishing season is short so that natural mortality and tag shedding can be assumed to occur only between the periods of fishing. If λ, u, and v_k do not vary over time then the expected tag returns for the first three years will be

Year 1	Year 2	Year 3[1]
$N_k u \lambda$	$N_k(1-u)(1-v_k)u\lambda$	$N_k(1-u)^2(1-v_k)^2 u\lambda$

(1)

If v_k is known then it is possible to estimate u and λ in the above example.

We first develop the corrections needed for tag shedding. If the instantaneous rate of tag shedding is constant, the probability that a fish retains its type k tag at time t after release is

$$Q_k(t) = \rho_k e^{-\varphi_k t}$$

where $\rho_k = Q_k(0)$ is the probability of initial tag retention, and φ_k is the instantaneous shedding rate for tag type k.

Immediately after tagging, a proportion $(1-\rho_k)$ of the fish with tags of type k lose their tags. Additionally, we assumed that a proportion, q, of the fish die immediately from tagging. We also assumed that natural mortality occurs continuously throughout the year, but that fishing occurs only once at mid-year.

We considered tagging experiments that occur any time during the year. We thus needed to modify the model to include the returns during the year of tagging. We did this by assuming that the seasonal pattern of exploitation during the year of tagging was the same as it would be for subsequent years. Let t_T be the fraction of the year between the tagging and the end of the calendar year, and let $\alpha(t_T)$ be the proportion of the tags that are returned in subsequent years during that fraction of the calendar year before t_T. Suppose the finite exploitation rate is u and the natural mortality is M, assumed constant for all years. Define $\theta_k = (1-q)\rho_k\lambda$.

Table 1. Parameter notation. Note that some parameters may depend upon tag type k.

Parameter	Definition
y	subscript: year (y=0 represents the year of tagging)
t_T	fraction of year between the tagging and the end of the calendar year
$\alpha(t_T)$	the average fraction of the catch taken in the part of the calendar year before t_T
$h(u,\alpha(t_T))$	fraction of the fishing that occurs before t_T if the exploitation rate is u
k	subscript: tag type (1=reference tag)
q	proportion of fish that die immediately due to tagging
ρ	proportion of fish that retain their tags immediately after tagging
G(t)	probability of tag retention at time t, conditional on initial tag retention
$Q_k(t)$	$=\rho_k e^{\varphi_k}$; proportion of fish that retain their tags at time t
φ_k	instantaneous rate of tag shedding of tag type k
λ	reporting rate
θ_k	$=(1-q)\rho_k\lambda$; proportion of tags that are potentially available to be recovered, namely those that initially survive tagging, are initially retained, and will be reported if captured
M	instantaneous natural mortality per year (yr^{-1})
v_k	finite natural mortality plus tag shedding rate of tag type k
u	finite exploitation rate
$R_{y,k}$	observed tag returns in year y of the tag type k
N	number tagged
N*	effective number of tagged fish for years greater than the initial year

Note that $1-\theta_k$ represents the proportion of tags that disappear immediately from our view, i.e. the Type I losses identified by Beverton and Holt (1957). If $t_T \le \frac{1}{2}$, the expected number of tags returned in the initial year of tagging, i.e. year ''0'', is

$$E(R_{0k})=N_k\theta_k u(1-h(u,\alpha(t_T))) \qquad (2)$$

where $h(u,\alpha(t_T))$ is the fraction of the fishing that occurs before time t_T if the exploitation rate is u; this term is derived in Appendix 2. If $t_T>\frac{1}{2}$, then we need to correct for the tag loss and natural mortality that occurs before midyear. Then the expected number of tags returned in the initial year of tagging is

$$E(R_{0k})=N_k\theta_k u(1-h(u,\alpha(t_T)))e^{-(M+\varphi_k)(t_T-\frac{1}{2})} \qquad (3)$$

The number of fish that are alive and retain their tags at the beginning of the fishing season, assumed to be midyear, in the year after the tagging year is

$$N_k(1-q)\rho_k(1-u(1-h(u,\alpha(t_T))))e^{-(M+\varphi_k)(t_T+\frac{1}{2})}$$

We let v_k represent the proportion of fish with type k tags that die naturally each year or lose their tags, i.e. $v_k=1-e^{-(M+\varphi_k)}$. Our definition of v differs from Ricker's (1975) notation because his v included only natural mortality.

The *effective number of fish tagged* can now be calculated as

$$N^*_k=N_k\theta_k (1-u(1-h(u,\alpha(t_T)))) (1-v_k)^{(t_T+\frac{1}{2})}$$

The expected number of tags returned in year y is

$$E(R_{yk})=N^*_k[(1-u)(1-v_k)]^{y-1}u \qquad (4)$$

An analysis of relative tag shedding, using the methods of Barrowman and Myers (in press), gave relative estimates of θ_k for each tag type (estimates of relative loss rates, $\varphi_1-\varphi_k$, were also obtained). For example, for the 1950s data, if we let the external plastic tags be the reference type, k=1, we estimated θ_2/θ_1, where k=2 is the internal tag type (Appendix 1). Significant differences were found only between the internal and external tags used in the 1950s experiments. The θ for external tags was found to be 1.49 (s.e.=0.09) times that for internal tags, and the φ for external tags was found to be 0.09 (s.e.=0.02) greater than that for internal tags. For the Petersen disk tags, the φ was found to be 0.02 (s.e.=0.02) greater than that for internal tags. We assumed that the tag shedding rate (φ) for internal tags was 0, so that the estimated differences in φ provide estimates of absolute shedding rate.

Estimation

We estimated two parameters for each experiment: θ_1 (reporting rate × initial tag retention × initial tag survival for the reference tag type), and u (finite exploitation rate).

The observed tag returns were modelled as independent Poisson random variables with expectations having the form in Equation (4). The log likelihood for our model is thus

$$\ell = \sum_{k=1}^{K} \sum_{y=0}^{Y} r_{yk} \log E(R_{yk}) - E(R_{yk}) - \log r_{yk}!$$

where r_{yk} is the observed number of tags of type k returned in year y, and Y is the total number of years of tag returns used (generally, 5 years). Maximum likelihood estimation is then straightforward. We maximized the log-likelihood using the Broyden-Fletcher-Goldfarb-Shanno positive definite secant update algorithm (Dennis and Schnabel, 1983). Asymptotic standard errors and correlations of the estimates were calculated from the inverse of the Hessian matrix evaluated at the maximum likelihood estimates (Cox and Hinkley, 1974).

We first discuss the base case in which we examined the data from the year of tagging plus the five years of recoveries after the year in which the tagging took place. (For the most recent experiments there were not always 5 years of data available.) We chose this time because the double tagging experiments could not be extrapolated beyond this and tag loss could have changed after this period (Barrowman and Myers, in press). Furthermore, it is unlikely that fishing mortality would remain reasonably constant for more than 5 years.

The fishing mortalities estimated from tagging are compared with those estimated from virtual population analyses (VPA) which are compiled in Myers *et al.* (1995).

Results

We considered 140 tagging experiments between 1954 and 1990, of which there were 127 which had more than 70 releases of tags of the appropriate type in the regions we considered. Two experiments, 8301 and 8402, had very few returns, apparently because of high mortality associated with freezing conditions during tagging. These two experiments were not included in the analysis. Three other experiments between 1989 and 1990 were not used because of low returns. Of the remaining 122 experiments, the estimates of θ and the exploitation rate were within the feasible range for cases with only 4 exceptions. These four exceptions are plotted as stars in Fig. 2. The inclusion of the few questionable cases had no effect on our overall results.

The pattern of results is similar for all areas (Fig. 2). Estimates of θ were higher in the 1950s and 1960s than in the 1980s in all regions. Fishing mortality in all regions appeared to be $0.5 \, \text{yr}^{-1}$ or higher in all regions in the 1960s. It drastically increased in the late 1980s and early 1990s. This is consistent with the hypothesis that these populations collapsed because of overfishing. During this time period the estimate of fishing mortality was at or above $1.0 \, \text{yr}^{-1}$. The fishing mortality we estimate from the tagging is generally higher than that estimated from the VPA (Fig. 2).

Robustness and violations of model assumptions

We examined the robustness of our estimates to violations of model assumptions (reviewed by Pollock *et al.*, 1991; Myers *et al.*, in press, a). Where possible we tested the robustness of our conclusions by altering the model assumptions, re-estimating all parameters, and calculating the average percentage change in the estimates.

We let the data itself set the bounds on the limits of robustness tests. For example, during the 1960s there was a very high return rate of tags. This sets clear limits on the amount of tag loss and the portion of fish that die because of tagging.

The assumptions for the model are:

(1) *Natural mortality and tag shedding rate are known and constant.* Small changes in the assumed level of natural mortality or tag shedding rate results in an approximately proportional change in the estimate of fishing mortality over all experiments. A change in the assumption of natural mortality from 0.2 to 0.1 or 0.5 does not change the basic results of the model (Fig. 3). Under the assumption that natural mortality is 0.1, the estimates of fishing mortality are reduced by approximately 0.1. The θs in this case are reasonable, i.e. all estimates are within the limits between 0 and 1. Under the assumption that natural mortality is 0.5, a large fraction of the θs are estimated at the constraint of 1. Clearly, such a high natural mortality is not generally consistent with this data. Note that even if natural mortality was 0.5 for the late 1980s and early 1990s then the estimated fishing mortality is still very high. That is, when the fishing mortality was estimated under the assumption that natural mortality equals 0.2, most of the estimates of fishing mortality in the later years were above 1; this is still the case under the assumption that natural mortality is 0.5.

(2) *Long term mortality rates are not influenced by tagging.* Tagging may increase the catchability of fish in gill nets only because tags may become entangled. Since only large, fully recruited cod are considered in this paper, the difference in susceptibility to gill nets of cod with and without tags is probably small. In addition, gill nets generally account for only 10% of the catch (up to 30% in the most recent years) so this effect is probably small (Hutchings and Myers, 1994). Mortality may be increased because of infections induced by the tagging; however, these also appear to be small (Templeman and Fleming, 1962). If mortality is increased by tagging our estimates will be positively biased.

(3) *The number of years used to estimate exploitation is unimportant.* If four years of data after the year of release were used the mean percentage change in exploitation rate was small: 2.3%. Similar small changes occurred if other time frames were selected.

(4) *The year of the tag recovery is correctly tabulated.* Misreportings was probably minor since we only used tags in which the location and gear type of the tag was also reported, and there were follow-up letter or telephone interviews of any suspicious tags by the original investigators. Any such tabulation errors that wrongly report tags being caught in years after they actually were result in a negative bias in the estimated exploitation rate (Pollock *et al.*, 1991).

(5) *The fate of each tagged fish is independent of the fate of other tagged fish, e.g. tagged animals mix through the population.* Violations of this assumption will not bias the estimates but will result in the standard errors being underestimated (Pollock *et al.*, 1991). For this reason, we will examine groups of experiments instead of
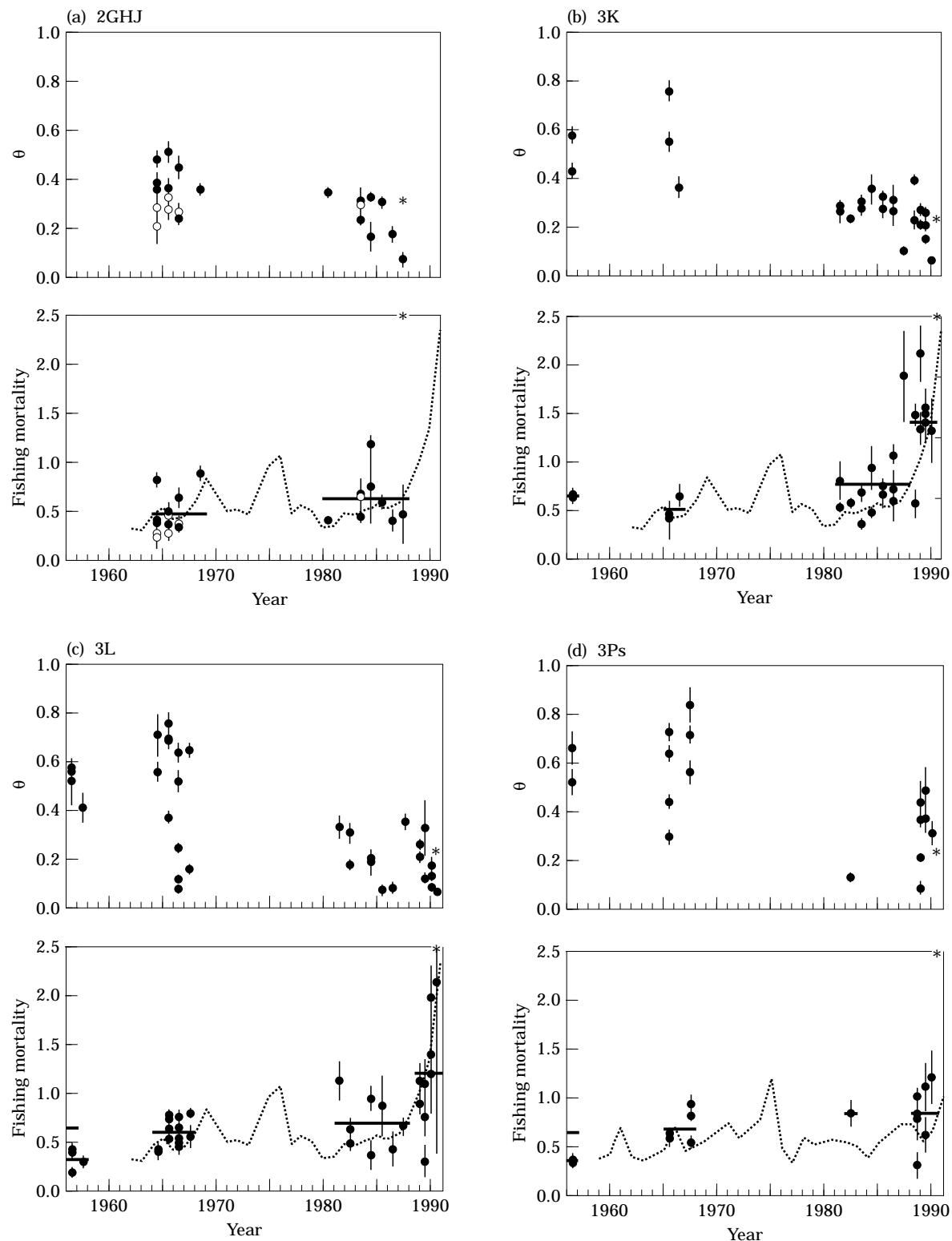
Figure 2. Estimates and s.e.s of fishing mortality and θ (i.e. proportion of tags that are potentially available to be recovered, namely those that initially survive tagging, are initially retained, and will be reported if captured) by NAFO management region. Each point represents a separate experiment, i.e. release, and is plotted at the midpoint of the period from which tag recoveries were obtained. The dotted line on the bottom panel is the fully recruited fishing mortality estimated from the virtual population analysis for the whole population for ages 7 to 9. Estimates in 2G and 2H (Fig. 2a) are given by open circles. The mean estimated fishing mortality, is given by a horizontal solid line for the 1950s, 1960s, 1978–1987, and after 1987. Estimates of exploitation rate greater than 1 occurred in four cases; these are denoted by stars and assigned an estimated fishing mortality of 2.5. Figure 2e over page.
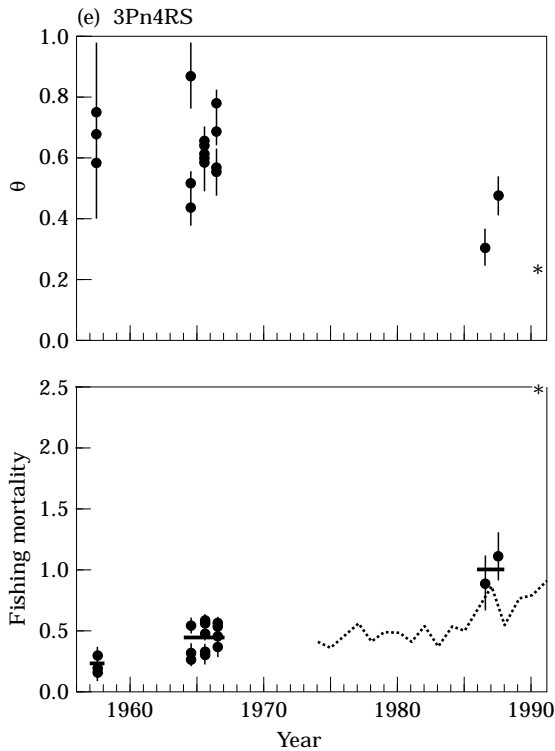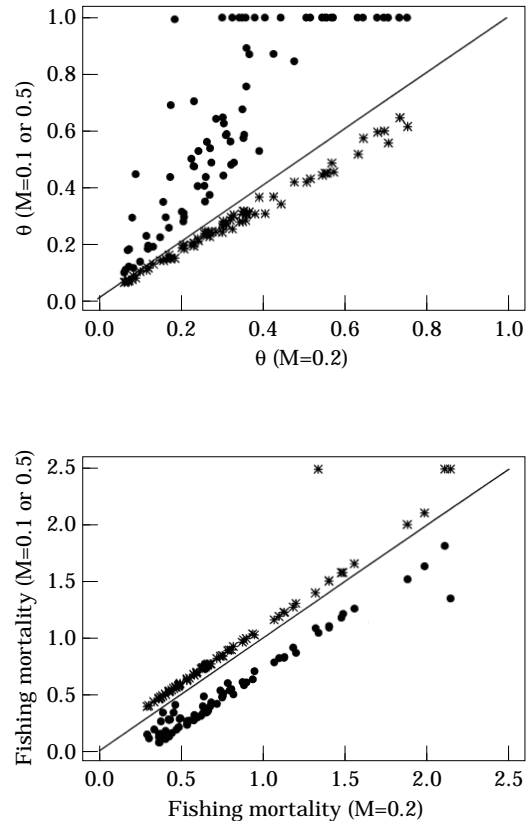
(e) 3Pn4RS

Figure 2. Continued.

Figure 3. Estimates of θ and fishing mortality of the base model with natural mortality assumed to be 0.2 versus estimates under the assumption that natural mortality is equal to 0.5 (●) and 0.1 (*). For three estimates made under the assumption that natural mortality is equal to 0.1, the estimates of fishing mortality were greater than 2.5; these were constrained to equal 2.5. Data are for 2J3KL releases. The diagonal line is the one-to-one reference line.

single releases when possible. Thus, we will estimate the exploitation rate for the tagged component of the population rather than for the population as a whole. We fully expect that exploitation will not be constant for all components of the population, i.e. some may be more exploited than others. The exploitation rate for the population as a whole should lie within the range of the estimates for any one time period.

(6) *All tagged fish have the same annual mortality and recovery probabilities.* The variability of the effect was reduced by using only fish which were of an adult size, i.e. over 50 cm. Nichols *et al.* (1982) and Pollock and Raveling (1982) found that no biases resulted due to heterogeneous recovery rates. They also found that if mortality rates varied, e.g. different fishing mortalities among a group of tagged fish, the fishing mortalities and exploitation rates would be positively biased. They also found that this bias should be reduced if the recovery period is long, e.g. several years, and mortality is low. Given the relatively high mortality, long recovery period, and that relatively discrete groups of tagged cod are examined, this positive bias should be small.

(7) *Mortality and recovery probabilities are constant for five years.* The only period covered by the tagging in which there is evidence of large changes in fishing mortality is the late 1980s and early 1990s when it increased (Myers and Cadigan, 1995a,b). This would

tend to give an underestimate of the fishing mortality because as fishing mortality increases over time, the rate of return of tagged fish stays high (suggestive of low mortality) for a while due to increasing catch rate of tagged fish. Thus, accounting for this effect may increase the already very high estimates of fishing mortality during this period.

(8) *Exploitation occurs during a short period in the middle of the calendar year and our model for the recoveries in the first year is correct.* We used Pope's approximation that is widely used in the analysis of catch-at-age data. Mertz and Myers (in press) investigated the accuracy of the approximation, and found it to be excellent for the 2J3KL cod. The exploitation patterns of the other populations are similar. We used an alternative model to check this assumption and the model for year ''0'', by making estimates without the year ''0'' data. We fitted the model
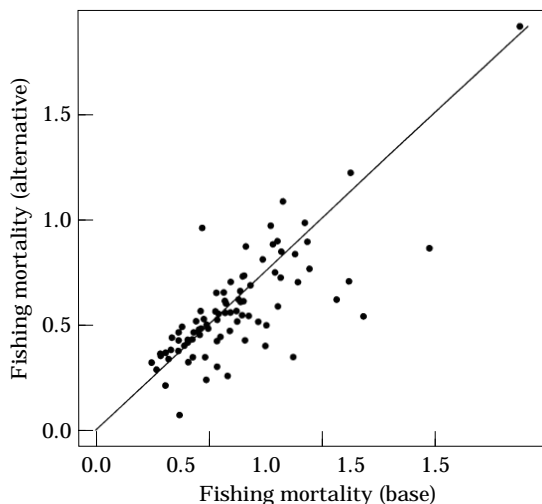
Figure 4. Estimates of fishing mortality from the alternative generalized linear model for recoveries after the year of tagging versus the estimates from the base model. In both cases natural mortality was assumed to be 0.2. In the generalized linear model the data from the year of tagging were not used. Each point represents an experiment. The diagonal line is the one-to-one reference line.

$$E(R_{y,k}) = e^{\beta_0 - \beta_1 y}$$

for years 1 to 5 using the generalized linear model with a log link and a Poisson error assumption (McCullagh and Nelder, 1989). β_0 and β_1 are regression parameters. β_1 is the total rate of disappearance and includes natural and fishing mortality and tag loss. We did not use the 1950s tagging data because of the complications caused by multiple tag types. We used the data up to 1989 for the robustness tests. Fishing mortality was estimated by subtracting the assumed natural mortality rate, 0.2, and the previously estimated instantaneous tag loss rate, φ from the estimate of total mortality disappearance β_1. Slightly fewer of the estimates from the alternative model were below (39) the original estimates than above (45) (Fig. 4). However, the mean difference between the alternative estimates and the base estimates was slightly negative (−0.045). We conclude that our results do not critically depend upon the assumptions of the pattern of exploitation or our model for recoveries in the first year.

We also conclude that our results are robust to violations of the model assumptions.

Discussion

The collapse of cod in Eastern Canada

Our analysis clearly shows very high fishing mortality in the late 1980s and early 1990s. This high fishing mortality is much higher than these populations can

sustain (Hutchings and Myers, 1994). It has been suggested that the collapse of the largest of these populations, Labrador/north-east Newfoundland, was caused by an increase in natural mortality in the spring of 1991 caused by cold water. Hutchings and Myers (1994) argued against this hypothesis. They showed that the components of the population were drastically reduced before this time, that fishing effort had greatly increased in the late 1980s, and that the ocean was not cold on a century time scale. Furthermore, Myers and Cadigan (1995a,b) showed that the methods used to derive the conclusions of high natural mortality were not statistically valid. Although we did not directly estimate natural mortality, our results clearly support the hypothesis that the populations collapsed because of overfishing. First, our results clearly show that fishing mortalities were very high before the supposed increase in natural mortality in 1991. Second, the same pattern of high fishing mortality occurred in all regions. St Pierre Bank and the Gulf of St Lawrence are very different oceanographic regimes compared to the Labrador shelf (Thompson *et al.*, 1988); there is no known oceanographic influence that would cause high natural mortality to all three stocks. These patterns of high fishing mortality also provide evidence against the hypothesis of migration appearing as increased natural mortality in any one region.

Our results show that fishing did not occur uniformly throughout the populations in the 2J3KL regions; fishing mortality was higher in the more northern part of the management area in the late 1980s. In particular, the 3K estimates are higher than the 3L estimates. This is consistent with the observation that the fish disappeared from this region first (Hutchings and Myers, 1994). Our estimates of higher fishing mortality north of the Grand Banks (e.g. NAFO Div. 3K) than on the northern Grand Banks (i.e. NAFO Div. 3L) in the late 1980s suggest that the reduction of fish in NAFO Div. 3K was caused by overfishing. Thus, our results are consistent with those of Hutchings and Myers (1993) and Lilly (1994) and are not consistent with the hypothesis that the fish moved south in the late 1980s from the northern regions as claimed by deYoung and Rose (1993), because, if they had, then the fishing mortality of those fish would have been similar to those tagged in 3L. To check further the hypothesis that cod moved south more than usual during the late 1980s and early 1990s, the proportion of recoveries from cod tagged in 3K that were recovered on offshore banks to the south of the region should be examined. There were nine tagging experiments between 1985 and 1989; a median of 3.9% of the recoveries occurred on offshore banks south of 3K (the range was 0.8–11.9%). The median percentage of cod tagged in 3K between 1979 and 1984 that were recovered to the south was greater, i.e. a median of 6.9%. We conclude that the tagging data provided no

support for the migration hypothesis, but is consistent with the hypothesis that the cod north of 3L were eliminated by overfishing.

The estimates of the fishing mortality in recent years were generally higher than those estimated from VPA. The simplest explanation for this is that the VPA is negatively biased because of under-reporting of commercial catches, which is known to be a large problem in this region (Angel *et al.*, 1994; Myers *et al.*, in press, a). Furthermore, the estimates of fishing mortality from VPA are negatively biased in the most recent years even if commercial catch-at-age is known without error because of known statistical biases (Myers and Cadigan, 1995a).

Was fishing mortality alone responsible for the collapse of the cod stocks in Eastern Canada? We believe the answer is yes, and that the process of collapse deserves to be studied with care. The following senario is developed in Myers *et al.* (in press, b). First, recruitment as estimated from research surveys was not below average for the cohorts that should have contributed to the fishery in the year of collapse. Second, high fishing mortality was possible because population abundance was overestimated while fishing mortality was underestimated, thus leading to quotas that were too high. The overcapacity in the fishing fleet allowed for very high fishing mortality as the populations declined. Third, as this decline occurred, fishing mortality and in turn discarding of juveniles increased. This reduced the number of fish entering the fishery until the populations were reduced to the point of commercial extinction. Fourth, the extremely low levels of spawners have inhibited the recovery of the population (Myers and Barrowman, 1994). The analysis of the tagging data provides important support for these conclusions.

The use of improved tagging models for the assessment of marine fish populations

Tagging studies allow estimates to be made that cannot be made using VPA. That is, mortality on subcomponents of the population can be estimated from tagging. Tagging studies also allow estimates of fishing mortality which will have different biases than the known bias of fishing mortality estimated from VPA (Myers and Cadigan, 1995a,b). The use of tagging to estimate exploitation rate should be given more consideration in the assessment of marine demersal populations. The method used here makes use of data from the year of tagging, but requires at least two years of data.

Our method can be used to estimate θ, the proportion of tags that are potentially available to be recovered, namely those that initially survive tagging, are initially retained, and will be reported if captured. This parameter can be compared readily among experiments. For example, θ decreased since the 1960s probably because

there was much less hand processing of the fish during later periods (i.e. fewer fish were hand split and salted), the tag reward became less valuable than in previous years, curiosity about the tags has declined, and trawls were used during this period to obtain some of the fish for tagging, which may have resulted in higher mortality associated with tagging.

It may be possible to improve estimates of exploitation rate by estimating a common θ for several populations; we will investigate this possibility in future papers.

Acknowledgements

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Appendix 1

Tag release, recapture, parameter estimates × 100, and their standard errors for NAFO Div. 3K. The notation is as follows: exp refers to the experiment number whose first two digits represent the year when tagging occurred; date refers to the month/day when tagging occurred; $\hat{\theta}$ is the estimate of the product of initial survival, initial tag retention, and reporting rate, and s.e. is the estimated standard error of $\hat{\theta}$; $\hat{F}$ is the fishing mortality rate, and s.e. is the estimated standard error of $\hat{F}$, rls refers to the number of fish released; bf and af refer to the recapture numbers of fish after the initial tagging year before and after the tagging calendar date respectively; y0, y1, . . ., y5 refer to the recaptures during the initial tagging year, the first post-tagging year, . . ., the fifth post-tagging year. Experiments during the 1950s used internal tags. The later experiments listed in the table used Petersen disc tags. Estimates of exploitation rate greater than 1 occurred in two cases; these are denoted by stars and assigned an estimated fishing mortality of 2.5.

exp	date	$\hat{\theta}$	s.e.	$\hat{F}$	s.e.	rls	bf	af	y0	y1	y2	y3	y4	y5
5403	8/2	43	3	66	7	398	50	8	24	30	17	9	2	1
5404	8/11	57	4	64	6	400	54	17	43	39	24	11	0	1
6317	10/25	76	4	47	4	1008	446	5	0	263	98	71	38	11
6318	11/11	55	4	43	5	1008	295	2	3	173	79	51	17	17
6406	5/17	36	4	66	12	336	29	16	29	34	10	6	4	1
7901	2/25	29	2	54	5	1775	27	142	183	75	35	23	13	12
7902	3/9	26	5	81	19	184	2	13	22	8	4	1	0	1
8002	3/15	24	1	58	5	2417	24	150	230	68	42	26	18	9
8102	3/14	28	3	69	10	572	4	52	62	33	12	5	1	2
8105	3/25	30	3	37	6	1292	34	118	81	73	35	20	13	7
8204	3/24	36	3	48	5	1145	23	119	131	71	29	19	14	8
8211	9/27	36	6	94	22	127	30	0	2	25	3	2	0	2
8302	3/23	32	2	75	8	937	19	63	135	43	18	17	4	4
8305	9/6	27	4	67	13	312	51	8	1	39	16	3	1	1
8403	6/5	31	2	107	8	1432	33	73	234	72	20	19	2	4
8404	9/29	31	6	72	19	143	23	0	8	14	4	3	3	0
8405	10/9	27	6	60	20	129	20	2	1	15	5	1	1	1
8502	6/9	24	2	250*	—	934	23	20	173	27	6	5	2	3
8503	6/14	10	2	188	46	525	4	9	31	14	0	1	0	0
8606	6/13	40	2	148	11	1037	32	52	244	63	23	3	3	2
8607	6/19	23	4	58	15	284	11	11	15	17	8	2	3	0
8701	2/11	21	2	211	28	772	6	16	106	17	4	2	0	—
8704	6/20	27	2	134	17	570	11	17	93	22	5	7	1	—
8705	6/21	24	3	250*	—	440	12	17	74	20	7	4	1	—
8801	2/17	15	1	149	20	990	6	15	90	15	9	3	—	—
8806	6/13	26	2	156	20	657	9	15	106	22	13	2	—	—
8807	6/16	21	2	141	24	482	6	20	54	25	4	1	—	—
8901	2/8	7	1	132	33	840	1	8	31	8	3	—	—	—

Appendix 2: Correction for year of tagging

We have assumed that the fishery takes place during a relatively short period of time in the middle of the year. Although this is a good approximation for these fisheries, a correction is needed for the year the tags were placed on the fish because the time of year when tags were applied was variable. Let u be the annual exploitation rate and let N_0 be the number of fish at the beginning of the year. Suppose that, on average, a fraction $\alpha(t_T)$ of the catch is taken in the part of the calendar year before the date of tagging (referred to as the first part of the year). For simplicity of notation, let $\alpha = \alpha(t_T)$.

We need to know the fraction, h, of the fishing that takes place in the first part of the year. The catch in the first part of the year is $N_0 uh$, leaving a population $N_0(1 - uh)$. The catch during the second part of the year is then $N_0(1 - uh)u(1 - h)$. Hence the fraction of the total catch taken during the first part of the year is

$$\alpha = \frac{N_0 uh}{N_0 uh + N_0(1 - uh)u(1 - h)} \tag{5}$$

Thus

$$\alpha uh^2 - (\alpha u + 1)h + \alpha = 0 \tag{6}$$

This equation is solved for h and we write $h = h(u, \alpha)$, to emphasize that h is a function of u and α. The equation has two roots, but only one lies within the interval (0, 1):

$$h(u,\alpha) = \frac{(\alpha u + 1) - \sqrt{(\alpha u + 1)^2 - 4\alpha^2 u}}{2\alpha u} \tag{7}$$