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Estimates of cod mortality in the Newfoundland Region from tagging data

by

R. A. Myers, N. J. Barrowman, and J. M. Hoenig
Science Branch
Department of Fisheries and Oceans
P.O. Box 5667
St. John's NF A1C 5X1

ABSTRACT

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

RESUME

Nous avons étudié, à partir des données obtenues de 122 expériences de marquage, l'exploitation de trois populations de morue de l'est du Canada depuis 1954 . Nous avons déterminé des taux d'exploitation très élevés pour la fin des années 1980 et le début des années 1990 qui appuient l'hypothèse d'un effondrement de ces populations causé par la surpêche. Les estimations sont obtenues à l'aide d'une nouvelle méthode qui tient compte des données de l'année de marquage, qui sont souvent délaissées.

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. 1995b).

We examine historic tagging data to reconstruct fishing mortality on three of these stocks: Southern Labrador/Northeast Newfoundland (Northwest 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 examine the limited data available from Northern Labrador (NAFO Div. 2GH). Our goal is to determine whether fishing mortality alone is sufficient to explain the collapse of these stocks. We further wish to determine if fishing mortality varied among components, i.e., substocks, of the populations. In a previous analysis, Myers et al. (1996) 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 $u = \frac{R'}{N'}$ 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 were 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 chronic tag shedding rate is known and the different tagged batches have the same behaviour (movement patterns) (Brownie et al. 1985). That is, reporting rate need not be known nor constant and 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 new methods which may be useful for analyzing a variety of historic databases, like the Newfoundland cod ones.

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

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 allows 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 examine 122 separate tagging experiments conducted from 1954 to 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 limit 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 1950's data, the median number of fish released per experiment 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 1960's 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 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 use data up to and including 1992 for these regions.

The Model

We modify existing tagging models to reflect the details of the tagging experiments and the nature of the fishery. First, we use models that do not assume the commercial catch is known because of possible misreporting. In this way our models resemble band return models (see Pollock 1991). Second, our model assumes that the 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 1996). This assumption will also allow our results to be directly compared to the results from the analysis of commercial catch-at-age data. Third, we assume that natural mortality is known. We assume that instantaneous natural mortality is 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 consider experiments where more than one type of tag was used with different loss rates. Fifth, we develop a correction for the fact that in different experiments, tags were put on at different times of the year.

We classify 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 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
$N_k u\lambda$	$N_k(1-u)(1-v_k)u\lambda$	$N_k(1-u)^2(1-v_k)^2u\lambda$

(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

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

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 assume that a proportion, q, of the fish die immediately from tagging. We also assume that natural mortality occurs continuously throughout the year, but that fishing occurs only at one time at mid-year.

We consider tagging experiments that occur any time during the year. We thus need to modify the model to include the returns during the year of tagging. We do this by assuming the seasonal pattern of exploitation during the year of tagging is the same as it is for subsequent years. Let t_T be the fraction of 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 $\theta_k = (1-q)\rho_k\lambda$. 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 $t_T \leq \frac{1}{2}$, the expected number of tags returned in the initial year of tagging, i.e., year "0", is

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

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

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

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

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

We let v_k represent the proportion of fish with type k tags that die naturally each year or lose their tags, i.e., $v_k = 1 - e^{-(M+\phi_k)}$. 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

$$E(R_{yk}) = N_k^*\,[(1-u)(1-v_k)]^{y-1}\,u. \tag{4}$$

An analysis of relative tag shedding, using the methods of Barrowman and Myers (in prep), gave relative estimates of θ_k for each tag type (estimates of relative loss rates, $\phi_1 - \phi_k$, were also obtained). For example, for the 1950's 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 (Table 1). Significant differences were found only between the internal and external tags used in the 1950's experiments. The θ for external tags was found to be 1.49 (SE=0.09) times that for internal tags, and the ϕ for external tags was found to be 0.09 (SE=0.02) greater than that for internal tags. For the Petersen disk tags, the ϕ was found to be 0.02 (SE=0.02) greater than that for internal tags. We assume that the tag shedding rate (ϕ) for internal tags is 0, so that the estimated differences in ϕ provide estimates of absolute shedding rate.

Estimation

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

The observed tag returns are modeled as independent Poisson random variables with expectations having the form in (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 maximize 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 are 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 weren't 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 prep). 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. (1995a).

Results

We considered 140 taggings 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 1950's and 1960's than in the 1980's in all regions. Fishing mortality in all regions appeared to be 0.5 yr^{-1} or higher in all regions in the 1960's. It drastically increased in the late 1980's and early 1990's. 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 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 examine the robustness of our estimates to violations of model assumptions (reviewed by Pollock et al. 1991, Myers et al. 1996). Where possible we tested the robustness of our conclusions by altering the model assumptions, reestimating all parameters, and calculating the average percent change in the estimates.

We let the data itself set the bounds on the limits of robustness tests. For example, during the 1960's 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 θ's 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 the θ's 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 1980's and early 1990's 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 assumption that natural mortality is 0.5.

(2) Long term mortality rates are not influenced by tagging. — Tagging may increase the catchability of fish only in gill nets because tags may become entangled. Since only large, fully recruited cod are considered in this paper, the difference in susceptibility to gillnets of cod with and without tags is probably small. Also, 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 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. — Misreporting is probably small 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 result in tags being reported to be 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 single releases when possible. Thus, we will estimate 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 the 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 1980's and early 1990's when it increased (Myers and Cadigan 1995 a,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 (1996) 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 fit the model

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

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 1950's tagging because of the complications caused by multiple tag types. We use the data up to 1989 for the robustness tests. Fishing mortality was estimated by subtracting off 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 less 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 our results do not critically depend upon the assumptions of the pattern of exploitation or our model for recoveries in the first year.

We 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 1980's and early 1990's. 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/Northeast 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 1980's, and the ocean was not cold on a century time scale. Furthermore, Myers and Cadigan (1995b) showed that the methods used to derive the conclusions of high natural mortality were not statistically valid. Although we do 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 than the Labrador shelf (Thompson et al. 1988); there is no known oceanographic influence that would cause high natural mortality to all three stocks.

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 1980's. 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 1980's suggest 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 1980's from the northern regions as claimed by deYoung and Rose (1993) because if they had then the fishing mortality on those fish would have been similar to those tagged in 3L. A further check on the hypothesis that cod moved south more than usual during the late 1980's and early 1990's is to examine the proportion of recoveries from cod tagged in 3K that were recovered on offshore banks to the south of the region. There were 9 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% to 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. 1995b). 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 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. (1995b). 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, the high fishing mortality was possible because population abundance was overestimated and the 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 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. 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). 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 is readily compared among experiments. For example, θ decreased since the 1960's probably because there was much less hand processing of the fish during later periods (i.e., much less of the fish was hand split and salted), the tag reward was much 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 a 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.

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References

Angel, J.R., D.L. Burke, R.N. O'Boyle, F.G. Peacock, M. Sinclair, and K.C.T. Zwanenburg. 1994. Report of the workshop on Scotia-Fundy groundfish management from 1977 to 1993. Can. Tech. Rep. Fish. Aquat. Sci. 1979. 175 p.

Barrowman, N.J., and R.A. Myers. in prep. Estimates of tag shedding using Petersen and spaghetti tags in Atlantic cod, (*Gadus morhua*), using double taggings.

Beverton, R.J.H., and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fishery Invest. Ser. 2. no. 19. 533 p.

Brownie, C., D.R. Anderson, K.P. Burnham, and D.S. Robson. 1985. Statistical inference from band recovery data: a handbook. U.S. Fish and Wildlife Service Resource Publication 156.

Cox, D.R., and D.V. Hinkley. 1974. Theoretical statistics. Chapman and Hall, London, J.K. 210 p.

Dennis, J.E., and R.B. Schnabel. 1983. Numerical methods for unconstrained optimization and nonlinear equations. Prentice-Hall, Englewood Cliffs. 378 p.

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

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

Lear, W.H. 1984. Discrimination of the stock complex of Atlantic cod (*Gadus morhua*) off southern Labrador and eastern Newfoundland, as inferred from tagging studies. J. Northwest Atl. Fish. Sci. 5: 143-159.

Lear, W.H., and L.S. Parsons. 1993. History and management of the fishery for northern cod in NAFO Divisions 2J, 3K and 3L. In: Parsons, L.S., Lear, W.H. (eds.) Perspectives on Canadian marine fisheries management. Can. Bull. Fish. Aquat. Sci. No. 226, p. 55-89.

Lilly, G.R. 1994. Predation by Atlantic cod on capelin on the southern Labrador and northeast Newfoundland shelves during a period of changing distributions. ICES Mar. Sci. Symposium 198:600-611..

Mann, K.H., and K.F. Drinkwater. 1994. Environmental influences on fish and shellfish production in the Northwest Atlantic. Environ. Rev. 2: 16-32

McCullagh, P., and Nelder, J.A. 1989. Generalized linear models. Chapman and Hall, London, 511 pp.

Mertz, G. and R. A. Myers. 1996. An extended cohort analysis: incorporating the effect of seasonal catches. Can. J. Fish. Aquat. Sci.

Myers, R. A., and N. J. Barrowman. 1994. Is fish recruitment related to spawner abundance? ICES C.M.1994/G:37.

Myers, R.A., N.J. Barrowman, and J.A. Hutchings. 1996. Inshore exploitation of Newfoundland cod since 1948 as estimated from mark-recapture data. Can. J. Fish. Aquat. Sci. in press.

Myers, R. A., J. Bridson, and N. J. Barrowman. 1995a. Summary of worldwide stock and recruitment data. Can. Tech. Rep. Fish. Aquat. Sci. 2024: iv + 327p.

Myers, R.A., and N.G. Cadigan. 1995a. The statistical analysis of catch-at-age data with correlated errors. Can. J. Fish. Aquat. Sci. *in press.*

Myers, R.A., and N.G. Cadigan. 1995b. Was an increase in natural mortality responsible for the collapse of northern cod? Can. J. Fish. Aquat. Sci. *in press.*

Myers, R.A., Hutchings, J.A., Barrowman, N.J. 1995b. Why do fish stocks collapse. Ecological Applications. in press.

Nichols, J.D., S.L. Stokes, J. E. Hines, and M. J. Conroy. 1982. Additional comments on the assumptions of homogeneous survival rates in modern bird banding estimation models. J. Wildl. Manage. 46: 953-962.

Pollock, K.H. 1991. Modeling capture, recapture, and removal statistics for estimation of demographic parameters for fish and wildlife populations: past, present, and future. J. Am. Stat. Ass. 86: 225-238.

Pollock, K.H., J.M. Hoenig, and C.M. Jones. 1991. Estimation of fishing and natural mortality when a tagging study is combined with a creel survey or port sampling. Am Fish. Soc. Symp. 12:423-434.

Pollock, K.H. and D.G. Raveling. 1982. Assumptions of modern band-recovery models with emphasis on heterogeneous survival rates. J. Wildl. Manage. 46: 88-98.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191, 382p.

Taggart, C.T., P. Penney, N. Barrowman, and C. George. 1995. The 1954-1993 Newfoundland cod-tagging data base: statistical summaries and spatial-temporal distributions. Can. Tech. Rep. Fish. Aquat. Sci. 2042.

Templeman, W. 1963. Comparison of returns from different tags and methods of attachment used in cod tagging in the Newfoundland area, 1954 and 1955. ICNAF Spec. Pub. 4: 272-287.

Templeman, W. 1974. Migrations and intermingling of Atlantic cod, (*Gadus morhua*), stocks of the Newfoundland area. J. Fish. Res. Bd. Canada. 31: 1073-1092.

Templeman, W. 1977. Migration and intermingling of stocks of Atlantic cod, *Gadus morhua*, of the Newfoundland and adjacent areas from tagging in 1962-66. ICNAF Res. Bull. 14: 5-50.

Templeman, W. and A.M. Fleming. 1962. Cod tagging in the Newfoundland area during 1947 and 1948. J. Fish. Res. Bd. Canada. 19:445-487.

Thompson, K.R., R.H. Loucks and R.W. Trites. 1988. Sea surface temperature variability in the shelf-slope region of the northwest Atlantic. Atmos.-Ocean, 26, 282-299.

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
$Q_k(t)$	$= \rho_k e^{\phi_k}$; 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 tag type k
N	number tagged
N^*	effective number of tagged fish for years greater than the initial year

Appendix 1: Mark-recapture data, and parameter estimators × 100 and their standard errors. 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; area, lat and lon refer to the NAFO subarea, latitude and longitude where tagging occurred; $\hat{\theta}$ is the estimate of the product of initial survival, initial tag retention, and reporting rate, and SE is the estimated standard error of $\hat{\theta}$; $\hat{F}$ is the fishing mortality rate, and SE is the estimated standard error of $\hat{F}$; tag refers to the tag type used, for which i, p, t, dg represent internal, external plastic, t-bar and Peterson disc respectively; 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, . . ., y10 refer to the recaptures during the initial tagging year, the first post-tagging year,. . ., the tenth post-tagging year.

exp	date	area	lat	lon	$\hat{\theta}$	SE	$\hat{F}$	SE	tag	rls	bf	af	y0	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10
5401	4/22	3PSa	47.1	57.9	66	7	33	5	i	398	10	30	32	16	15	10	4	0	1	0	1	1	0
									p	480	47	71	48	57	35	25	9	3	2	0	0	0	0
5402	5/20	3PSe	46.6	56.9	51	5	37	6	i	399	6	40	24	18	16	3	4	5	2	2	0	0	3
									p	462	15	77	51	64	21	12	3	2	2	1	1	0	0
5403	8/ 2	3Kd	51.4	55.5	43	3	66	7	i	398	50	8	24	30	17	9	2	1	2	1	0	0	0
5404	8/11	3Kh	50	55.5	57	4	64	6	i	400	54	17	43	39	24	11	0	1	1	1	0	0	0
									p	482	84	15	62	53	26	16	3	7	1	1	1	1	0
5405	9/24	3La	46.6	53	52	10	19	5	i	800	95	10	8	34	34	27	6	7	2	1	0	2	2
									p	964	137	16	16	57	38	40	16	9	5	1	1	1	1
5406	10/15	3Lq	46.6	53.2	56	5	43	6	i	400	73	3	3	40	25	10	2	7	1	2	1	0	1
									p	482	136	6	4	79	43	22	5	3	0	3	2	1	0
5407	10/19	3PSc	46.7	54	65	7	35	6	i	400	88	3	4	44	22	17	13	2	4	1	0	1	1
									p	474	132	6	2	79	37	24	7	5	7	2	0	1	1
5408	11/10	3Lj	46.9	52.8	56	4	36	4	i	792	161	5	1	96	39	29	7	2	4	4	1	1	0
									p	965	273	3	2	133	90	43	20	15	5	3	1	2	1
5501	7/ 6	4Ra	51.4	56.9	58	6	30	6	i	300	25	27	12	25	5	9	9	2	0	2	1	0	0
									p	412	29	44	38	44	19	7	9	3	3	0	1	0	2
5502	9/16	4Ra	50.7	57.4	75	23	20	9	i	299	59	6	3	27	7	16	6	6	1	2	0	0	1
									p	412	83	6	2	43	26	24	5	3	1	0	0	0	0
5503	9/27	4Ra	51.3	56.6	66	28	17	10	i	299	52	8	3	21	13	9	11	7	3	1	1	0	2
									p	411	59	7	3	34	17	16	3	2	2	1	1	0	1
5504	9/30	3Lr	46.5	50.8	41	6	30	7	i	499	63	11	0	35	23	9	4	3	3	1	1	0	0
									p	536	83	16	1	54	24	14	6	4	1	0	1	1	1

exp	date	area	lat	lon	$\hat{\theta}$	SE	$\hat{F}$	SE	tag	rls	bf	af	y0	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10
5505	9/11	3Nc	44.9	50	31	7	36	13	i	200	16	9	6	9	10	3	0	2	0	0	2	0	0
									p	148	16	2	3	7	6	2	1	0	1	1	0	0	0
6201	7/28	2Jm	53.5	55.8	48	3	62	8	dg	672	116	21	78	98	38	15	6	2	4	1	1	2	0
6202	8/ 3	2Hd	55.5	60.2	29	6	29	9	dg	640	68	11	3	46	14	15	10	3	3	1	0	0	0
6203	8/ 4	2Ha	56.5	61.6	21	7	25	13	dg	607	42	6	1	24	14	13	5	1	0	0	0	0	0
6204	8/18	4Ra	51.6	55.4	51	4	54	6	dg	671	150	20	35	100	56	23	10	3	4	2	0	0	0
6205	9/12	2Je	53.9	55.3	35	4	38	6	dg	943	135	14	28	78	37	26	16	7	2	1	2	0	0
6206	9/25	2Ji	52	54.6	38	4	41	7	dg	640	123	8	8	70	34	18	11	5	3	4	1	1	0
6207	9/29	4Ra	51.5	56.5	87	11	27	5	dg	672	268	8	2	115	76	46	25	14	14	2	4	5	0
6208	10/11	3Lb	48.7	52.9	71	9	39	8	dg	336	126	3	3	60	45	18	7	6	5	1	0	0	0
6209	10/24	4Sv	49.8	60.1	43	6	32	7	dg	672	145	3	1	71	38	27	11	8	7	2	3	1	1
6210	11/10	3Lc	48.2	52.8	56	4	43	5	dg	1008	312	8	1	166	112	38	17	14	8	5	2	1	0
6301	1/16	3PSh	45.3	55.1	30	3	58	8	dg	640	2	58	64	40	11	9	2	2	0	0	0	0	0
6302	3/14	4Rd	47.6	59.2	58	3	60	4	dg	1344	90	176	222	170	71	33	21	6	2	3	1	1	0
6303	4/ 4	3PSe	47.4	56.9	72	4	63	5	dg	1008	74	166	239	139	72	34	14	7	1	0	1	0	0
6304	3/21	3PN	47.6	58.7	61	4	57	6	dg	672	66	81	100	92	43	22	9	3	0	1	1	0	0
6305	4/ 1	3PSa	47.2	57.7	63	3	64	5	dg	1008	62	151	202	141	59	28	13	4	2	4	0	1	0
6306	5/ 7	3PSe	46.8	57	44	3	57	6	dg	1008	54	106	106	110	55	22	4	4	1	1	0	0	0
6307	7/ 6	3Lr	46.5	50.8	37	3	54	6	dg	1008	79	73	86	93	41	21	7	7	1	1	0	1	0
6308	8/ 5	2Jm	53.5	55.8	51	4	50	6	dg	671	116	26	46	90	38	36	6	4	2	0	0	0	0
6309	8/12	2Ja	54.9	57.9	36	4	37	6	dg	1008	142	34	15	97	50	32	6	8	4	4	2	0	0
6310	8/17	2Hd	55.4	60.2	28	5	47	12	dg	336	45	5	1	29	20	5	0	3	0	0	0	0	0
6311	8/23	2Ha	56.5	61.6	33	6	29	6	dg	672	66	10	2	49	28	18	6	6	0	0	0	0	0
6312	9/12	4Sx	50	63	59	11	31	9	dg	336	84	6	0	52	22	14	10	5	3	2	0	0	0
6313	9/17	4Sw	50.8	58.7	64	6	33	5	dg	1008	299	19	3	172	82	39	33	17	9	4	3	3	0
6314	9/28	4Sw	51.4	57.5	65	4	46	5	dg	1008	356	13	0	226	99	59	18	13	9	1	1	3	0
6315	10/ 6	3Lj	46.8	52.9	74	3	79	5	dg	1008	411	35	49	365	77	37	18	9	2	2	3	0	0
6316	10/18	3Lj	46.7	52.8	68	3	74	5	dg	1008	398	21	27	321	97	40	13	9	5	1	0	0	0
6317	10/25	3Ki	49.7	53.9	76	4	47	4	dg	1008	446	5	0	263	96	71	38	11	22	4	5	1	1
6318	11/11	3Kd	51	55.6	55	4	43	5	dg	1008	295	2	3	173	79	51	17	17	9	3	1	0	0
6319	11/ 6	3Lq	46.5	53.5	70	3	64	5	dg	1006	405	7	11	298	102	62	18	9	5	0	2	1	0
6401	4/16	3Ld	48.3	50.1	12	2	65	14	dg	672	6	17	28	16	7	3	3	0	0	0	0	0	0
6402	4/25	3Nb	45.7	48.4	19	3	34	10	dg	671	6	35	27	19	14	7	6	0	0	0	0	1	0
6403	4/26	3Lg	47.1	51.6	24	2	76	8	dg	1008	10	51	111	42	16	7	6	3	1	1	0	0	0
6404	5/10	2Jf	53.5	53.3	23	2	65	6	dg	1008	50	50	54	71	23	10	6	1	0	0	0	0	0

exp	date	area	lat	lon	$\hat{\theta}$	SE	$\hat{F}$	SE	tag	rls	bf	af	y0	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10
6405	5/15	2Jn	52.6	53.3	25	3	63	10	dg	672	38	26	41	43	16	4	7	2	3	0	0	0	0
6406	5/17	3Kc	51.3	51.1	36	4	66	12	dg	336	29	16	29	34	10	6	4	1	2	0	0	0	0
6407	5/20	3Ld	48.4	50.2	8	2	54	16	dg	672	7	11	15	9	6	3	2	0	0	1	0	0	0
6408	7/ 8	3Md	46.9	44.8					dg	608	12	15	82	22	7	7	1	0	0	0	0	0	0
6409	7/22	2Jd	54.4	57.2	45	5	34	6	dg	1008	144	33	13	109	70	29	17	6	1	0	1	0	0
6410	8/ 5	2Ge	58.5	62.8	27	3	38	7	dg	1008	111	14	0	64	68	10	10	2	1	0	0	0	0
6411	9/10	4Ra	50.8	57.3	68	5	53	5	dg	672	200	29	41	147	70	22	19	6	5	3	1	0	0
6412	9/30	4Sy	50.1	63.6	55	8	37	9	dg	336	79	5	0	51	26	20	4	4	1	1	1	0	0
6413	10/ 6	4Sz	50.1	66.5	57	4	46	5	dg	1008	234	28	52	161	75	49	15	13	13	3	3	1	0
6414	10/18	3La	48.8	53.1	64	4	46	5	dg	1008	316	13	16	217	75	56	20	19	3	2	0	0	0
6415	11/ 8	4Rc	49.2	58.5	78	5	57	5	dg	672	298	8	2	201	94	38	20	4	3	3	1	0	0
6416	11/20	3Lc	46.2	52.8	52	4	49	6	dg	672	184	1	0	123	54	30	14	7	3	5	4	0	0
6501	5/ 4	3La	46.4	52.6	16	2	55	11	dg	672	9	23	34	22	6	7	5	0	1	0	0	0	0
6502	9/15	3PSc	46.7	54.1	71	3	81	5	dg	1007	313	37	72	321	90	30	15	5	1	2	0	0	0
6503	9/21	3PSc	47	55	83	7	54	7	dg	336	143	16	4	113	39	15	10	5	1	2	0	0	0
6504	10/25	3PSb	47	55.9	56	5	93	10	dg	336	119	2	2	103	26	8	3	2	0	1	0	0	0
6505	11/25	3Lj	47.5	52.6	65	3	80	5	dg	1007	347	9	70	273	96	35	14	9	3	1	0	0	0
6601	4/21	2Jc	54.9	54.9	36	2	89	8	dg	976	40	68	130	82	38	8	3	1	1	0	0	0	0
7801	2/26	2Jn	52.1	51.6	35	2	41	3	dg	2990	86	301	259	172	79	57	35	19	8	14	2	2	2
									t	779	22	38	25	21	12	12	7	5	2	0	1	0	0
7901	2/25	3Kc	51.6	50.9	29	2	54	5	dg	1775	27	142	183	75	35	23	13	12	10	2	0	1	1
									t	1779	43	133	131	74	39	38	12	6	12	6	0	1	0
7902	3/ 9	3Kf	49.5	51	26	5	81	19	dg	184	2	13	22	8	4	1	0	1	2	0	0	0	0
									t	318	5	13	16	9	4	3	0	1	0	2	0	0	0
7905	10/19	3Lf	47.6	53	33	5	113	20	dg	193	49	1	2	37	10	1	1	0	1	0	0	1	0
									t	163	52	1	1	28	12	5	3	3	0	1	1	0	0
8001	2/10	3PSe	47	56.7	13	2	63	13	dg	903	6	40	45	30	12	2	0	0	3	1	0	0	0
									t	1133	10	46	55	33	11	5	3	4	1	1	1	0	0
8002	3/15	3Kc	50.7	51.7	24	1	58	5	dg	2417	24	150	230	68	42	26	18	9	6	4	1	2	1
									t	2346	22	148	123	63	42	33	15	10	8	4	0	0	0
8003	3/27	3Ld	49.1	50.2	18	2	49	9	dg	914	10	40	55	19	14	11	5	2	1	0	1	1	0
									t	922	16	39	40	23	16	5	3	7	1	0	2	0	0
8004	6/17	3Lj	47	52.9					t	15	1	1	4	2	0	0	0	0	0	0	0	0	0
8006	10/ 9	3Lf	47.6	53	31	4	63	12	dg	313	62	1	4	32	22	6	3	0	0	0	0	1	0
									t	293	62	5	6	34	15	11	4	3	0	0	0	0	0
8101	1/22	3Lf	47.6	53					t	55	0	10	12	2	5	3	0	0	0	0	0	0	0

exp	date	area	lat	lon	$\hat{\theta}$	SE	$\hat{F}$	SE	tag	rls	bf	af	y0	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10
8102	3/14	3Ki	50	52.2	26	3	69	10	dg	572	4	52	62	33	12	5	1	2	0	0	3	0	0
									t	560	2	58	23	29	14	5	8	2	0	1	1	1	0
8103	3/18	2Jc	54.7	54	23	2	45	6	dg	1677	42	118	84	91	35	19	10	6	1	0	0	0	0
									t	1602	59	105	38	96	30	23	13	7	0	0	2	1	1
8104	3/24	2Jn	53.4	53.2	31	5	68	16	dg	194	6	17	22	13	4	0	4	0	1	0	0	0	1
									t	174	4	14	5	7	6	0	3	2	0	0	0	0	0
8105	3/25	3Kc	51.8	51.1	30	3	37	6	dg	1292	34	118	81	73	35	20	13	7	3	3	1	1	0
									t	1663	58	159	49	97	54	30	22	10	6	2	3	0	0
8109	8/20	2Ha	56.9	61.1	30	5	66	17	dg	189	34	3	3	22	7	7	0	0	0	1	1	0	0
									t	149	13	4	0	7	5	2	3	0	0	0	0	0	0
8201	3/12	3Lb	48.6	52	21	2	95	13	dg	644	2	33	68	24	5	3	0	2	0	0	1	0	0
									t	696	1	22	25	10	9	2	4	1	0	1	0	0	0
8202	3/16	2Jc	54.7	53.7	17	6	75	36	dg	75	1	3	5	2	1	1	0	0	0	0	0	0	0
									t	92	0	1	1	0	0	1	0	0	0	0	0	0	0
8203	3/20	2Jf	53.2	52.4	33	2	119	6	dg	1470	24	72	275	53	25	11	8	1	3	1	0	1	0
									t	1474	25	67	266	46	14	19	11	2	1	2	0	0	0
8204	3/24	3Kc	51.5	51.3	36	3	48	5	dg	1145	23	119	131	71	29	19	14	8	2	2	3	0	0
									t	1152	24	82	58	47	23	19	10	5	2	2	3	0	0
8206	3/27	3Ld	49.2	50.6	19	5	37	16	dg	282	7	9	14	4	5	3	4	0	0	0	0	0	0
									t	194	1	0	2	0	1	0	0	0	0	0	0	0	0
8209	9/20	3Ki	49.4	55.1					t	57	12	1	1	5	7	0	0	0	1	0	0	0	0
8211	9/27	3Kh	49.6	55.2	36	6	94	22	dg	127	30	0	2	25	3	2	0	2	0	0	0	0	0
									t	95	11	1	1	7	1	3	1	1	0	0	0	0	0
8301	3/19	3Ld	48.3	49.3					dg	928	6	9	7	4	3	6	3	0	0	0	0	0	
									t	930	1	11	4	3	7	1	0	2	0	0	0	0	
8302	3/23	3Kc	51.5	51.2	32	2	75	8	dg	937	19	63	135	43	18	17	4	4	2	1	2	0	
									t	959	36	81	54	49	40	25	9	2	3	1	1	0	
8303	3/25	2Jn	52.1	52.5	31	2	60	7	dg	1029	34	72	100	55	34	16	6	3	0	0	0	1	
									t	1816	62	130	97	86	66	27	14	7	3	2	0	0	
8304	5/19	3Ld	48.7	50.4	8	2	88	31	dg	272	1	4	11	3	0	1	1	0	0	0	0	0	
									t	537	5	12	15	9	7	0	2	0	0	0	0	0	
8305	9/ 6	3Kh	50.2	55.8	27	4	67	13	dg	312	51	8	1	39	16	3	1	1	0	0	0	0	
									t	186	22	4	0	9	9	6	3	0	0	0	0	0	
8306	9/24	3Kd	50.1	56					dg	7	1	0	2	1	0	0	0	0	0	0	0	0	
									t	86	17	2	0	9	5	4	0	1	0	0	0	0	
8401	5/27	3Lg	47	51.7	8	2	43	16	dg	477	7	8	9	9	3	1	1	2	0	0	0		
									t	478	9	1	6	6	1	2	1	1	0	0	0		
8402	6/ 2	3Ld	48.6	50.6					dg	231	2	3	1	2	1	2	0	1	0	0	0		
									t	241	1	2	0	0	2	0	1	0	0	0	0		
8403	6/ 5	3Ki	49.1	52.6	31	2	107	8	dg	1432	33	73	234	72	20	19	2	4	2	1	0		
									t	1459	59	81	105	85	38	17	3	5	1	0	0		
8404	9/29	3Kd	51.3	55.5	31	6	72	19	dg	143	23	0	6	14	4	3	3	0	0	0	0		
									t	83	14	1	0	7	8	1	0	0	0	0	0		

exp	date	area	lat	lon	$\hat{\theta}$	SE	$\hat{F}$	SE	tag	rls	bf	af	y0	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10
8405	10/ 9	3Kd	51.4	55.4	27	6	60	20	dg	129	20	2	1	15	5	1	1	1	0	0	0		
									t	130	27	3	1	19	8	1	2	1	0	1	0		
8406	9/30	4Ra	51.6	55.4	30	6	90	23	dg	132	24	0	7	12	10	0	0	1	0	0	1		
									t	157	25	0	0	10	10	4	0	3	0	0	0		
8407	11/11	2Je	54.2	54.8	18	3	41	11	dg	615	58	1	1	31	20	7	3	4	0	1	0		
									t	616	65	2	0	34	16	16	1	2	0	0	0		
8501	6/ 2	3Lh	47.1	50.2	35	4	66	10	dg	459	26	31	58	31	11	9	5	2	2	0			
									t	418	20	11	23	19	12	3	2	2	0	0			
8502	6/ 9	3Ki	49	52.6	24	2	250*		dg	934	23	20	173	27	6	5	2	3	2	1			
									t	956	29	32	65	35	20	6	5	3	0	0			
8503	6/14	3Ke	50.1	53.4	10	2	188	46	dg	525	4	9	31	14	0	1	0	0	0	0			
									t	326	3	3	9	3	1	1	1	0	0	0			
8504	7/17	2Jm	53.3	55.6	7	3	47	30	dg	177	1	5	2	5	1	1	0	0	0	0			
									t	182	3	1	4	1	2	1	0	0	0	0			
8505	7/28	2Jm	53.4	55.8	31	4	250*		dg	198	8	3	51	8	3	2	1	1	0	0			
									t	165	14	1	19	11	6	0	1	0	0	0			
8506	8/ 2	4Ra	52.3	55.6	47	6	113	19	dg	166	23	3	33	18	6	2	1	1	0	0			
									t	165	26	7	12	23	10	1	3	0	0	0			
8601	3/13	3PSa	47.3	57.5	21	1	101	9	dg	1453	31	52	139	61	17	9	3	3	0				
									t	1403	17	31	79	34	15	5	2	1	1				
8602	3/18	3PSh	45.1	55.2	9	3	31	13	dg	992	11	17	16	12	10	3	0	5	2				
									t	921	8	14	17	12	5	4	1	2	1				
8603	3/21	3Oa	45.2	54.4	21	5	29	10	dg	691	19	29	27	18	12	7	5	5	3				
									t	637	16	23	16	19	11	4	4	3	3				
8604	6/ 6	3Ld	48.6	50.5	9	5	37	28	dg	179	2	4	4	2	3	0	0	1	0				
									t	83	2	1	1	3	0	0	0	0	0				
8605	6/10	3Kc	51.4	50.9					t	69	5	2	0	6	1	1	0	0	0				
8606	6/13	3Ka	50.5	54.7	40	2	148	11	dg	1037	32	52	244	63	23	3	3	2	1				
									t	996	34	44	126	62	13	8	2	2	0				
8607	6/19	3Kf	49.7	51.6	23	4	58	15	dg	284	11	11	15	17	8	2	3	0	0				
									t	223	14	8	7	13	10	1	2	0	1				
8608	9/11	3PSc	46.7	54.1	37	3	83	9	dg	620	105	13	35	97	17	16	5	1	0				
									t	613	70	17	7	50	26	9	5	4	0				
8609	9/30	3PSc	47.1	54.2	44	9	78	22	dg	88	20	4	3	20	3	2	0	1	0				
									t	54	8	0	0	6	2	0	0	0	0				
8701	2/11	3Kc	51.3	50.4	21	2	211	26	dg	772	6	16	106	17	4	2	0						
									t	727	5	21	78	17	8	10	4						
8702	6/ 6	3Lg	47.1	51.6	21	2	113	16	dg	494	10	11	55	13	11	1	2						
									t	489	13	10	30	15	7	3	4						
8703	6/13	3Lb	48.7	52.5	26	2	90	11	dg	740	19	29	94	30	10	10	5						
									t	643	13	21	48	26	10	4	1						
8704	6/20	3Ke	50.1	53.2	27	2	134	17	dg	570	11	17	93	22	5	7	1						
									t	550	28	18	42	34	12	5	5						

exp	date	area	lat	lon	$\hat{\theta}$	SE	$\hat{F}$	SE	tag	rls	bf	af	y0	y1	y2	y3	y4	y5	y6	y7	y8	y9	y10
8705	6/21	3Ki	49.1	52.6	24	3	250*		dg	440	12	17	74	20	7	4	1						
									t	435	27	20	31	31	15	6	1						
8801	2/17	3Kc	51.2	50.4	15	1	149	20	dg	990	6	15	90	15	9	3							
									t	881	2	29	61	20	7	5							
8802	3/27	3Lb	48	53.6					dg	58	0	2	18	1	0	1							
									t	3	0	1	1	1	0	0							
8803	4/ 6	3Lg	47.3	51.8	12	2	110	26	dg	470	3	14	26	15	4	0							
									t	463	7	11	27	15	6	3							
8804	6/ 6	3Lr	46.5	50.9	33	11	31	16	dg	484	17	29	27	23	21	7							
									t	489	16	15	19	20	12	5							
8805	6/ 8	3Lg	47.6	51.8	12	2	76	20	dg	483	2	15	28	8	7	2							
									t	483	7	8	12	9	6	4							
8806	6/13	3Ke	50.6	53.7	26	2	156	20	dg	657	9	15	106	22	13	2							
									t	677	13	29	46	34	13	1							
8807	6/16	3Ki	49.4	52.7	21	2	141	24	dg	482	6	20	54	25	4	1							
									t	430	12	10	25	15	7	2							
8809	8/24	3PSc	47	56	37	6	111	25	dg	139	31	2	4	29	4	3	0						
									t	118	18	2	2	15	5	2	0						
8810	8/25	3PSb	47.3	55.8	49	9	62	18	dg	121	22	1	9	17	6	5	2						
									t	80	4	3	5	7	5	1	0						
8811	8/29	3PSe	47.3	56.2					dg	46	3	0	2	1	2	0	0						
									t	55	3	0	1	0	5	0	0						
8901	2/ 8	3Kc	51.5	50.3	7	1	132	33	dg	840	1	8	31	8	3								
									t	865	0	8	22	10	0								
8902	6/ 6	3Lb	48.8	52.6	9	1	199	59	dg	555	2	7	30	10	1								
									t	497	3	3	17	5	1								
8903	6/ 9	3Ki	49.3	52.9					dg	539	0	0	43	2	0								
									t	543	2	11	20	9	5								
8904	6/11	3Lg	47.3	51.6	14	2	141	34	dg	510	5	5	40	8	7								
									t	494	11	8	25	6	12								
8905	6/14	3Lg	47.3	51.7	17	3	120	41	dg	262	5	4	23	7	5								
									t	245	1	3	27	4	0								
8906	6/17	3Lb	46.8	52.6					t	1033	15	12	30	20	9								
8907	8/22	3PSe	47	56	31	5	120	27	dg	192	34	2	7	30	9	0							
									t	163	16	3	2	11	6	5							
8908	11/20	2Jf	53.8	52.9					dg	304	3	0	6	4	1								
									t	270	6	0	3	5	0								
9001	2/24	3Ld	49.2	50.1	7	1	214	176	dg	951	6	7	33	16									
									t	745	3	6	23	10									
9004	3/24	3Lb	46	53.7					dg	259	0	8	32	11									
									t	174	1	7	19	10									
9005	6/17	3Lc	49	51.4	24	2	250*		dg	898	10	10	170	25									
									t	869	24	16	80	39									
9101	1/20	3Lb	48	53.6					dg	476	2	2	215										
									t	199	0	4	79										
9102	3/15	3Ld	49.1	50.1					dg	1553	0	1	77										
									t	1547	3	0	69										

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_0uh, 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

$$\alpha = \frac{N_0uh}{N_0uh + N_0(1-uh)u(1-h)}. \tag{5}$$

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):

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

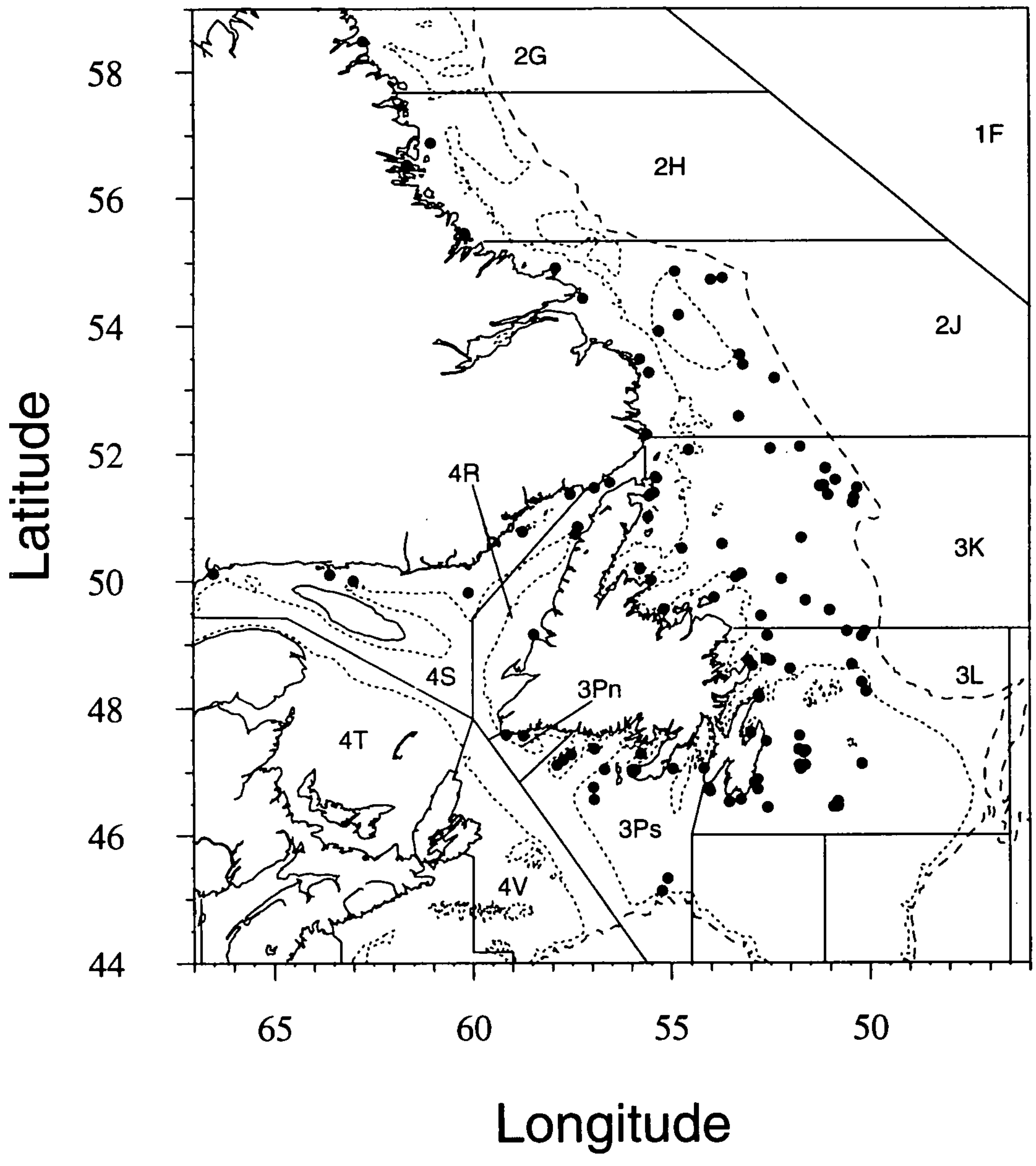


Fig. 1. Locations of tagging experiments and the NAFO divisions used to define management regions and populations. The dotted line is the 200 m isobath and the dashed line is the 1000 m isobath.

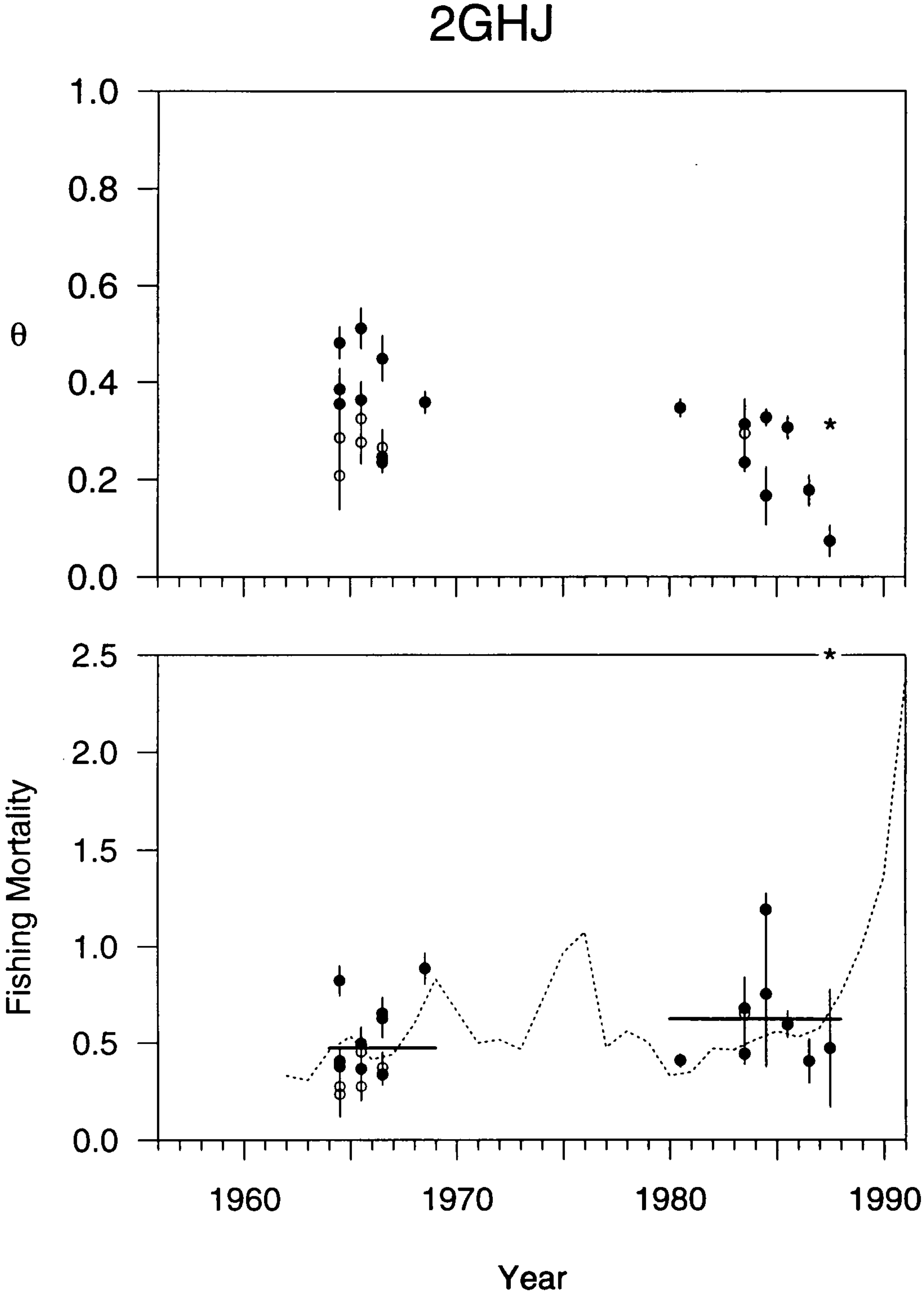
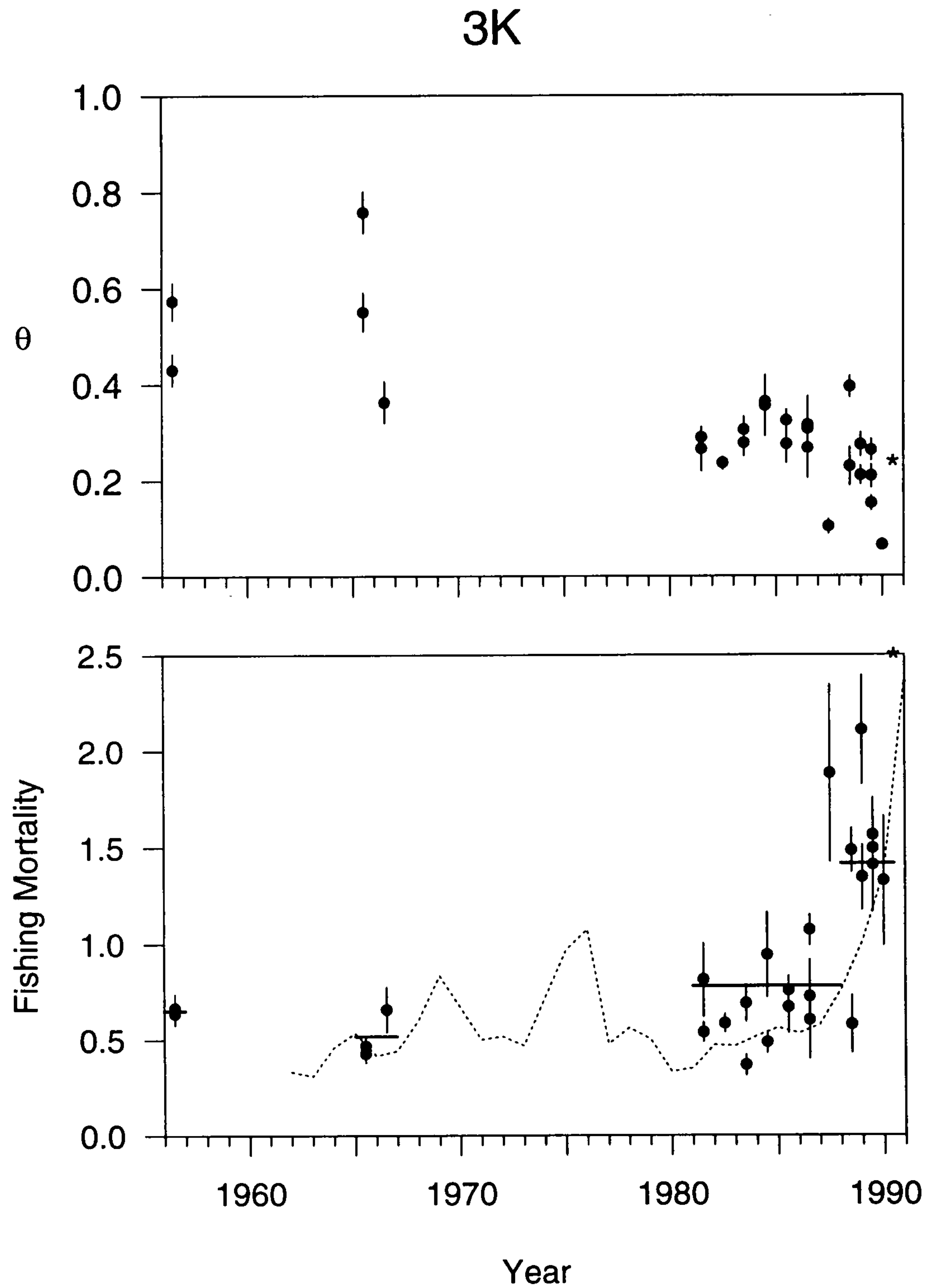
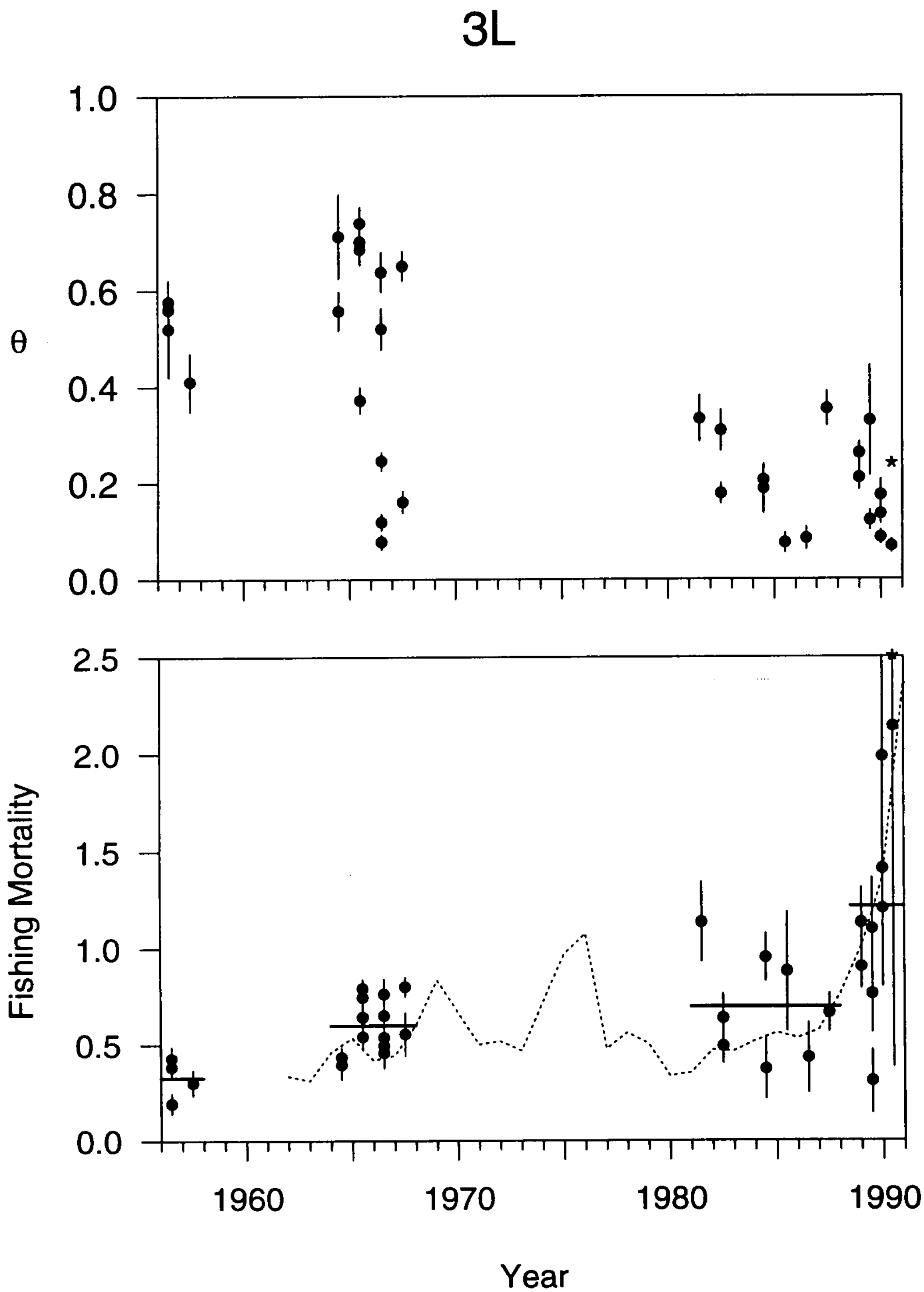


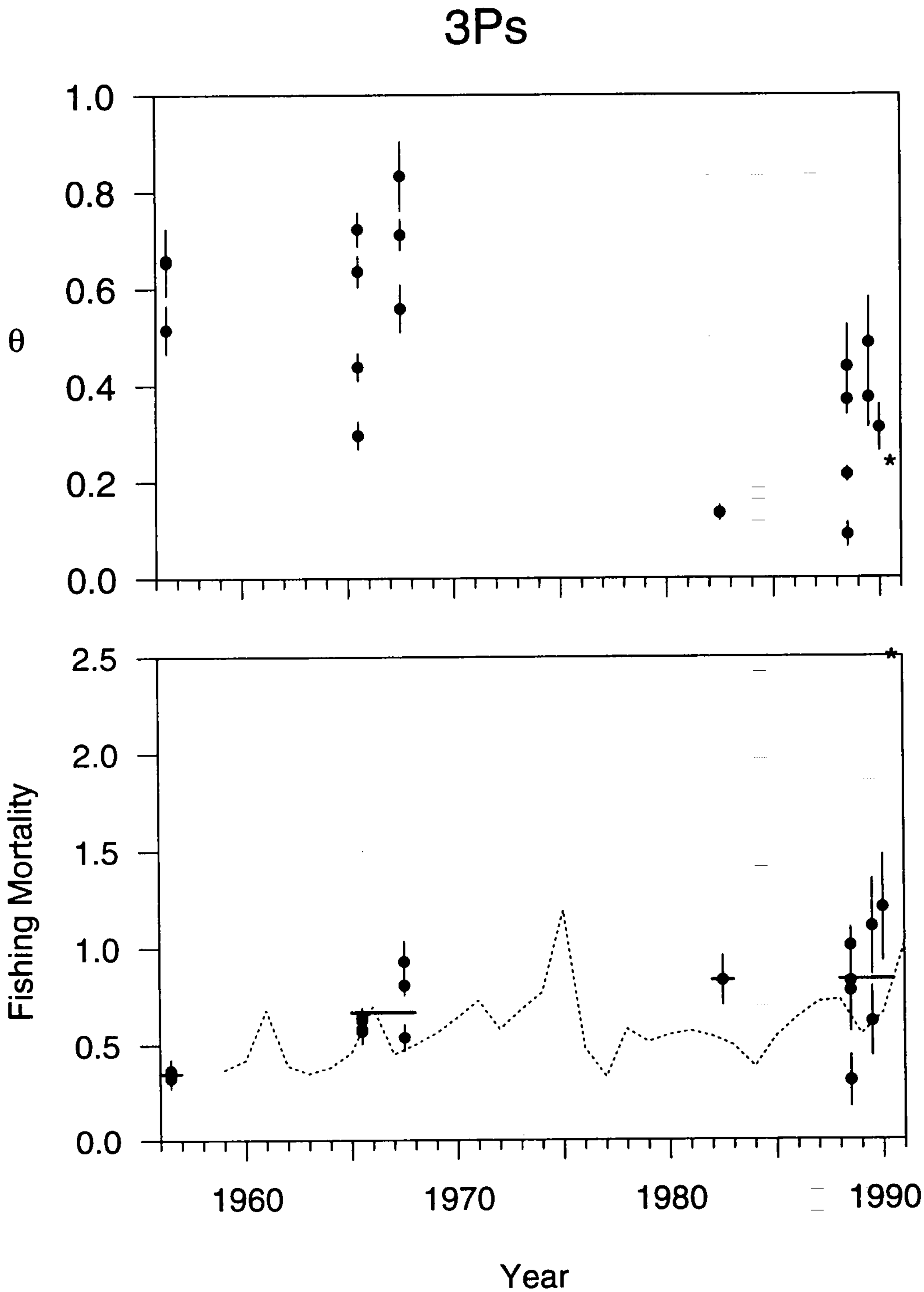
Fig. 2. Estimates and S.E.'s of fishing mortality and θ (i.e., proportion of tags that are potentially available to be recovered, namely those that initially survive tagging, are initially retained, and will be reported if captured) by NAFO management region. Each point represents a separate experiment, 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 1950's, 1960's, 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.


3K
1.0
0.8
0.6
0.4
0.2
0.0
θ
2.5
2.0
1.5
1.0
0.5
0.0
Fishing Mortality
1960
1970
1980
1990
Year
*

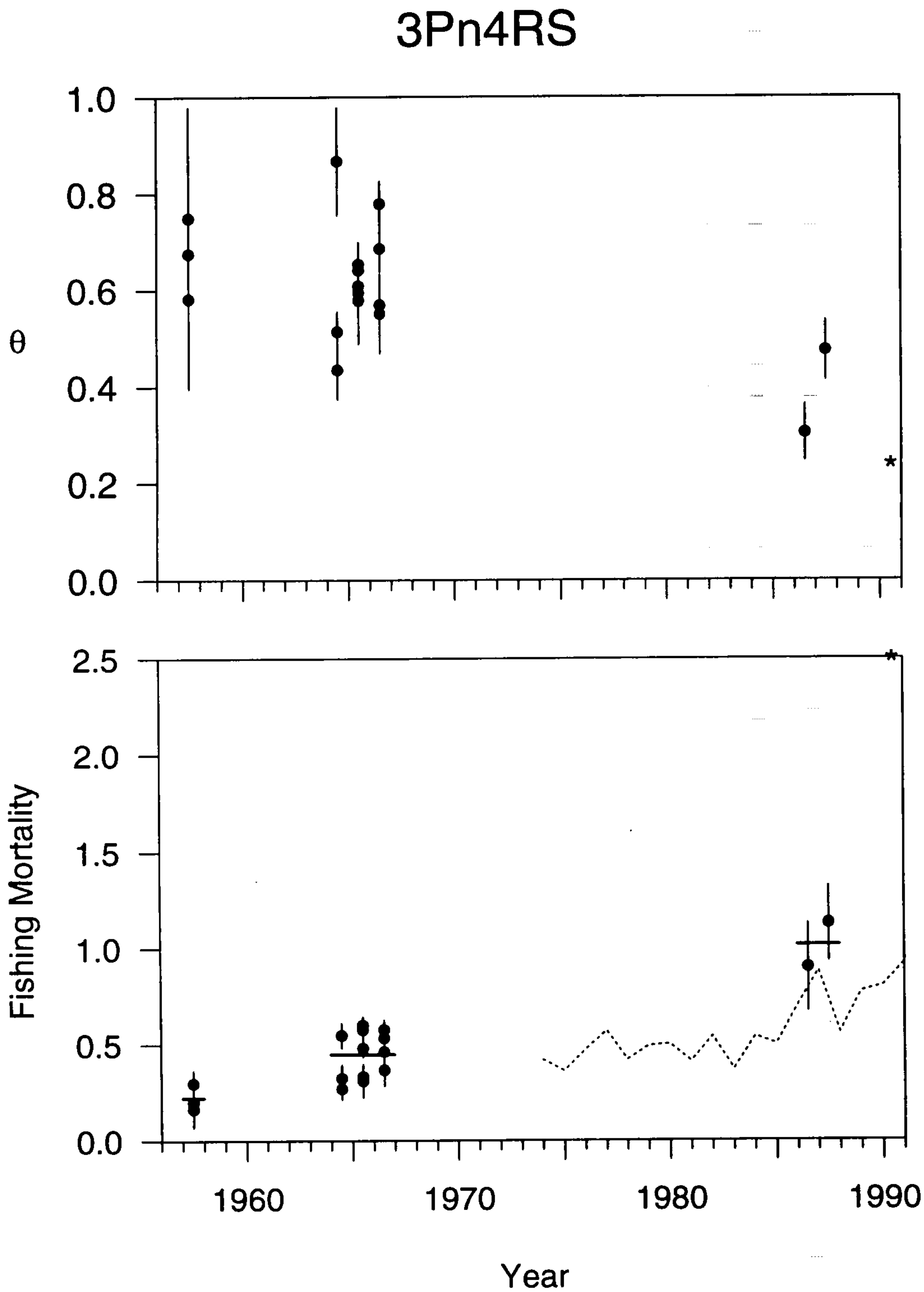
- fig2b -


3L
1.0
0.8
0.6
0.4
0.2
0.0
θ
2.5
2.0
1.5
1.0
0.5
0.0
Fishing Mortality
1960
1970
1980
1990
Year

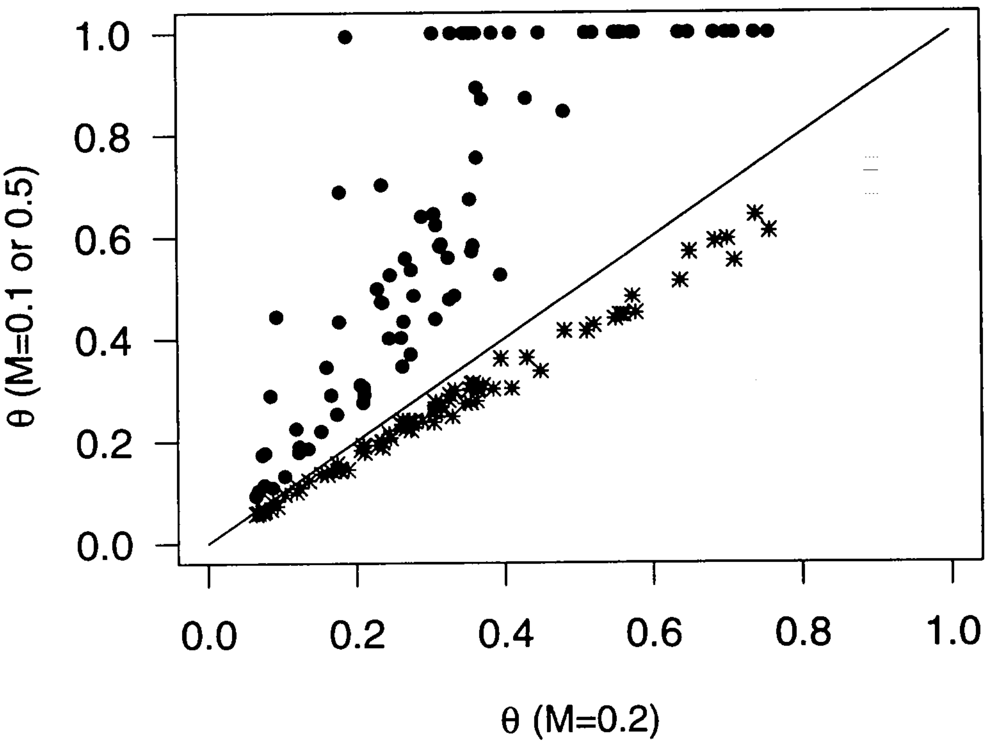
- fig2c -


3Ps
1.0
0.8
0.6
0.4
0.2
0.0
θ
2.5
2.0
1.5
1.0
0.5
0.0
Fishing Mortality
1960
1970
1980
1990
Year

- fig2d -


3Pn4RS
1.0
0.8
0.6
θ
0.4
0.2
0.0
2.5
2.0
1.5
Fishing Mortality
1.0
0.5
0.0
1960
1970
1980
1990
Year

- fig2e -



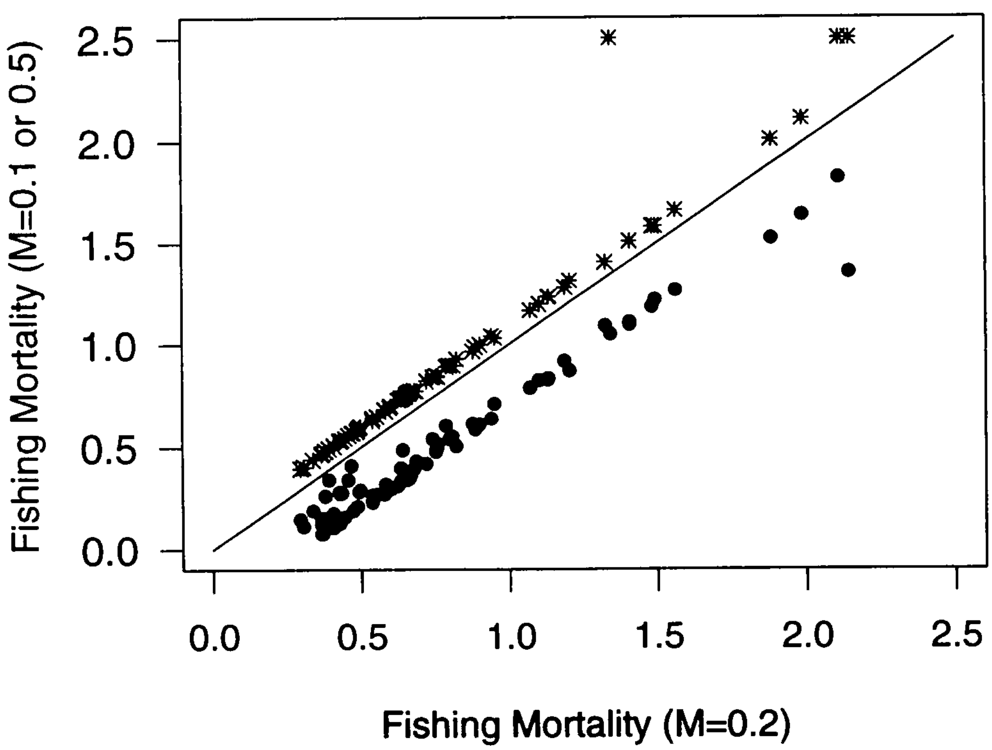


Fig. 3. Estimates of θ and fishing mortality of the base model with natural mortality assumed to be 0.2 versus estimates under the assumption that natural mortality is equal to 0.5 (•) and 0.1 (∗). For three estimates made under the assumption that natural mortality is equal to 0.1, the estimates of 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.

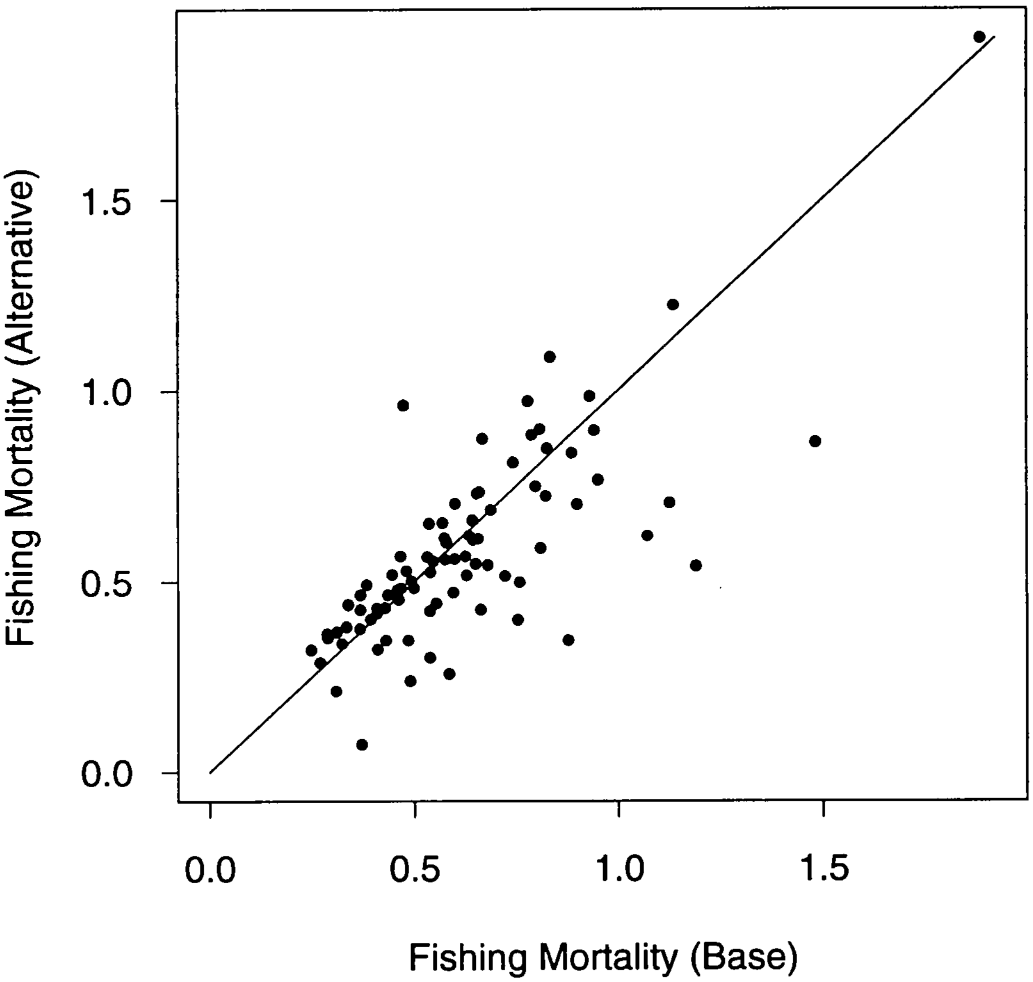


Fig. 4. Estimates of fishing mortality from the alternative generalized linear model for recoveries after the year of tagging versus the estimates from the base model. In both cases natural mortality was assumed to be 0.2. In the generalized linear model the data from the year of tagging was not used. Each point represents an experiment. The diagonal line is the one-to-one reference line.