

Inshore exploitation of Newfoundland Atlantic cod (*Gadus morhua*) since 1948 as estimated from mark-recapture data

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Abstract: We use tagging studies to estimate fishing mortality (F) of inshore populations of Atlantic cod (*Gadus morhua*) around Newfoundland. New methods have been developed for this analysis that allow fishing mortalities and reporting rates to be estimated for different sectors of a fishery, e.g., inshore fixed gear and offshore trawlers. We find that the fishing mortalities on inshore components of the cod stocks have been high since 1948, when the estimated fishing mortality was greater than 0.5. Since then the fishing mortality has increased, and in recent years has been much greater than the population can sustain. There is a critical need to define inshore stocks and to institute conservation measures specific to inshore populations.

Résumé : Nous utilisons des études de marquage afin d'estimer la mortalité par pêche (F) des populations côtières de morue franche (*Gadus morhua*) autour de Terre-Neuve. Pour notre analyse, nous avons développé de nouvelles méthodes qui permettent l'estimation des taux de mortalité par pêche et des taux de déclaration des prises pour les différents secteurs d'une pêche, p.ex., pour la pêche côtière aux engins fixes et pour les chalutiers hauturiers. Nous trouvons que les taux de mortalité par pêche dans les composantes côtières des stocks de morue sont élevés depuis 1948, alors que le taux estimatif de mortalité par pêche était supérieur à 0,5. Depuis ce temps, la mortalité par pêche a augmenté et, dans les dernières années, elle a été de beaucoup supérieure à ce que la population peut supporter. Il est impératif de définir les stocks côtiers et d'instaurer des mesures de conservation visant de façon spécifique les populations des eaux côtières.

[Traduit par la Rédaction]

Introduction

Fisheries are often managed under the assumption that breeding populations are large and generally follow the management units that are convenient to administer. However, if a "stock" is actually composed of many independent or semi-independent populations, then it is easy to overexploit or eliminate the subpopulations that are more easily fished (Clark 1990). This is perhaps the most difficult problem in the management of exploited populations. Here we analyze tagging data from 1948 to 1991 to estimate the exploitation of subpopulations of Atlantic cod (*Gadus morhua*) around Newfoundland. We examine inshore stock components because there is strong evidence that they have been historically subject to overexploitation (Templeman 1966; Hutchings and Myers 1994, 1995).

We develop new methods that allow us to separate fishing mortality into different components, e.g., inshore and offshore mortality. Our methods are similar to Brownie "band return" models (Brownie and Pollock 1985; Pollock 1991) in that they do not assume that the commercial catch is known. This is important because we will attempt to estimate the ex-

ploitation rate on subpopulations, and it is impossible to obtain commercial catches separated in an appropriate fashion. Pollock et al. (1991) were the first to point out that band return models can be used to apportion exploitation rate among different user groups although we are unaware of any such analysis.

It is clear that the stock structure of cod around Newfoundland is complex. There is evidence of four types of subpopulations: (1) bay stocks, i.e., subpopulations that spawn and overwinter in deep bays such as Trinity Bay and Placentia Bay (Nielsen 1895; Hutchings et al. 1993; Smedbol and Wroblewski 1997), (2) headland stocks, i.e., subpopulations that overwinter in the deep water off headlands such as Cape Bonavista (Templeman 1966), (3) offshore migrants that overwinter on the edge of the continental shelf and migrate inshore to feed in the summer (Lear 1984), and (4) offshore residents that do not migrate inshore (Lear 1984). We examine data on groups of cod that may be a mixture of the first three types of subpopulations, the fourth being excluded because we examine tagging that only occurred inshore.

A simple example

Initially we consider a simple case with a fishery in which exploitation takes place over a short period, e.g., the inshore cod trap fishery in 2J3KL lasts for approximately 3 mo. Let the reporting rate (the probability that a tag on a captured fish is reported) be λ . Let the finite exploitation rate, i.e., the proportion of fish caught, be u , and let the proportion of fish that die naturally or lose their tags each year be v (notation

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Table 1. Notation.

Parameter	Definition
s	Subscript: fishing stage (1 = offshore, 2 = inshore)
y	Subscript: year
k	Subscript: tag type (1 = reference tag)
q	Proportion of fish that die immediately from 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
$Q(t)$	$= \rho G(t)$; 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	$= (1 - q)\rho\lambda$; proportion of tags potentially available to be recovered, namely those that survive the tagging, are initially retained, and will be reported if captured
θ_{sk}	Value of θ for fishing stage s and tag type k
M	Instantaneous natural mortality per year
r_0	Recoveries during the late fall immediately after tagging
v	Finite natural mortality plus tag shedding rate
u_s	Finite exploitation rate for fishing stage s
F_s	Fishing mortality for fishing stage s
r_{syk}	Observed tag returns from fishing stage s in year y of tag type k
r_{s0k}	Observed tag returns from fishing stage s until end of year for fall tag release
t_F	Fraction of year between tagging and the next June
N_k	Number tagged with tag type k
N_{sk}^*	$= (N_k\theta_{sk} - r_{s0k})e^{-(M + \phi_k)t_F}$; effective number of fish released for fishing stage s with tags of type k at the start of the first fishing season after tagging

is given in Table 1). Assume that N tags are applied 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 do not vary over time, then the expected tag returns for the first three years will be as follows:

$$\begin{array}{ccc} \text{Year 1} & \text{Year 2} & \text{Year 3} \\ \hline Nu\lambda & N(1-u)(1-v)u\lambda & N(1-u)^2(1-v)^2u\lambda \end{array}$$

If v is known, then it is possible to estimate u and λ in the above example. For example, dividing the observed number of tag returns in the second year by the number in the first year is an estimate of

$$\frac{N(1-u)(1-v)u\lambda}{Nu\lambda} = (1-u)(1-v)$$

and if v is known, then u can be estimated. The observed number of returns in year 3 can then be equated with the expected number and the equation solved for the remaining unknown, λ . It is simple to write down the likelihood equation for the parameters λ and u given the observed returns and obtain maximum likelihood estimates of the parameters. This formulation is similar to the basic catch equations for tagging data described by Beverton and Holt (1957) and Ricker (1958).

This model is also similar to bird banding return models (Brownie and Pollock 1985; Pollock 1991) in that there is no assumption that the catch is known. The models differ in that in band return models the total survival is usually estimated, while our model concentrates on estimating the exploitation

rate with the assumption that natural mortality is known. Another difference in our approach is that we usually have only one year of tagging, while in banding models, tagging is typically carried out for a number of years in the same location. Our exploitation rate, u , is the same as the annual kill probability, K , in band return models, and our λ has the same interpretation as in band return rates.

In most applications of mark-recapture, the tagged animals are assumed to mix through the population. We will not make that assumption here because we are interested in exploitation rates of subpopulations or components of a larger population that cannot easily be identified. Thus, our estimates of exploitation rate will be those for components of the population.

The model used in this paper (Table 2) is an elaboration of the simple model which takes into account tag shedding, returns during the end of the year after tagging, fishing in inshore and offshore sectors, and different tag types. The sections that follow explain these details.

Tag shedding and a correction for the first year

In the above example, we considered natural mortality and tag shedding together in one parameter, v , which was assumed constant. In general, we represent the probability that a fish retains its tag at time t after release as

$$Q(t) = \rho G(t)$$

where $G(t)$ is the probability of tag retention at time t conditional on initial tag retention, with $G(0) = 1$, so that $\rho = Q(0)$

Table 2. Expected returns of tag type k for the model used in this paper (for notation, see Table 1).

	Effective number of fish released	×	Probability of capture in year y
Offshore	$(N_k\theta_{1k} - r_{10k})e^{-(M+\phi_k)t_F}$	×	$[(1-u_1)(1-u_2)(1-v_k)]^{y-1}u_1$
Inshore	$(N_k\theta_{2k} - r_{20k})e^{-(M+\phi_k)t_F}$	×	$[(1-u_1)(1-u_2)(1-v_k)]^{y-1}(1-u_1)u_2$

is the probability of initial tag retention. If the instantaneous rate of tag shedding is constant, then $G(t)$ can be expressed as $e^{-\phi t}$, i.e.,

$$Q(t) = \rho e^{-\phi t}.$$

As noted above, we assume that immediately after tagging, we expect a proportion $(1-\rho)$ of the fish to lose their tags. Additionally, we assume that a proportion, q , of the fish die immediately from tagging. If the tagging took place in the late fall, recoveries may take place before the next year. We also assume that natural mortality occurs continuously throughout the year, but that fishing occurs only at one time at midyear.

To account for these losses prior to the first fishing season, we need to adjust N . The number of fish that are alive and retain their tags at the beginning of the first fishing season after tagging is

$$\left(N(1-q)\rho - \frac{r_0}{\lambda}\right)e^{-(M+\phi)t_F}$$

where r_0 is the number of tagged fish recovered during the late fall immediately after tagging, t_F is the fraction of year between the tagging and the next June, and M is the natural mortality, which is assumed constant for all years. Recall that v represents the proportion of fish that die naturally each year or lose their tags, i.e., $v = 1 - e^{-(M+\phi)}$. Note that our definition of v differs from Ricker's (1975) notation because his v included only natural mortality. If the reporting rate is λ , then at most

$$N^* = \left(N(1-q)\rho - \frac{r_0}{\lambda}\right)(1-v)^{t_F}\lambda$$

tags will subsequently be returned. We refer to N^* as the *effective number of fish released* because it corresponds to the number released just before the fishing season in an idealized experiment where there is no initial tagging mortality, no initial tag shedding, no natural mortality or shedding between the time of tagging and the first fishing season, and all tags are reported. Letting $\theta = (1-q)\rho\lambda$, we can write

$$N^* = (N\theta - r_0)(1-v)^{t_F}.$$

Note that $1-\theta$ represents the proportion of tags that disappear immediately from our view, i.e., the Type I losses identified by Beverton and Holt (1957).

The Type II losses identified by Beverton and Holt (1957) are natural mortality, fishing mortality, and tag loss. If natural mortality and fishing mortality are constant, then the proportion of fish (after adjusting for initial losses) that survive and retain their tags at the beginning of the y th fishing season is

$$[(1-u)(1-v)]^{y-1}.$$

During the y th fishing season, a proportion u of these fish will be caught and reported. Therefore, the expected number of tags returned in year y is

$$E(R_y) = N^*[(1-u)(1-v)]^{y-1}u.$$

A model for sequential fishing

Suppose fishing takes place each year in two nonoverlapping stages ($s = 1, 2$) with exploitation rates u_1 and u_2 . Then the proportion of fish (after adjusting for initial losses) that will survive and retain their tags at the beginning of the first stage of the y th fishing season is

$$[(1-u_1)(1-u_2)(1-v)]^{y-1}.$$

Similarly, at the beginning of the second stage of the y th fishing season, the proportion is

$$[(1-u_1)(1-u_2)(1-v)]^{y-1}(1-u_1).$$

A model that varies with tag type and fishing gear

Our model is based on the sequential fishing model described above. The two stages of fishing we consider are the offshore fishery ($s = 1$), which occurs first, and the inshore fishery ($s = 2$), which occurs after the offshore fishery. The number of fish tagged is adjusted as described above, i.e., the number of fish tagged, N , is adjusted to N^* , the effective number of released fish at the start of the first fishing season after tagging. Returned tags are classified as coming from the inshore or offshore fishery based on the fishing gear type used.

Additionally, we classify tags by tag type, k . We assume that all tags are released simultaneously. Suppose that N_k tags of type k were released and that, for fall experiments, r_{s0k} of these were returned from stage s prior to the end of the year of tagging. Let the instantaneous shedding rate for tag type k be ϕ_k . Let θ depend on both tag type and on the fishery (inshore or offshore), i.e., for fishery s and tag type k , let $\theta = \theta_{sk}$.

The expected returns of tag type k from the offshore fishery in year y is

$$E(R_{1yk}) = N_{1k}^*[(1-u_1)(1-u_2)(1-v_k)]^{y-1}u_1$$

and from the inshore fishery is

$$E(R_{2yk}) = N_{2k}^*[(1-u_1)(1-u_2)(1-v_k)]^{y-1}(1-u_1)u_2$$

where $v_k = 1 - e^{-(M+\phi_k)}$ and $N_{sk}^* = (N_k\theta_{sk} - r_{s0k})e^{-(M+\phi_k)t_F}$.

In the above analysis, we again assume that the fishing mortality occurs during a short period of time each year. This

assumption is known as "Pope's approximation" in models of commercial catch-at-age data and is an excellent approximation to the Newfoundland cod data (Mertz and Myers 1996).

Unfortunately, we generally cannot simultaneously estimate all of the θ_{sk} parameters and the exploitation rates. To circumvent this problem, we assume that the effects of tag type, k , and fishing stage, s , enter into θ_{sk} multiplicatively. This allows us to consider separately the effects of tag type and fishing stage. To study the effects of tag type, an analysis of relative tag shedding, using the methods of Barrowman and Myers (1996), gave estimates of θ_{sk} relative to a reference tag type, $k = 1$, for each tag type, k , averaged over both fishing stages. For example, for the 1950's data, we let the external plastic tags be the reference type. 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.

We can obtain information on the ratio of θ inshore to offshore from several sources. Assuming that the mortality associated with tagging and initial tag shedding is the same inshore and offshore, this is equivalent to examining the ratio of reporting rates inshore and offshore. There is reason to believe that the offshore reporting rate is quite low. In an experiment on English trawlers in which tags were secretly placed on cod caught at sea, Margetts (1963) found that only one third of the tags were subsequently reported by the fish-

Table 3. Base case settings.

Tag type	Parameters	
	Inshore θ	ϕ
External plastic	θ_{21}	0.09
Internal	$0.67\theta_{21}$	0
Disc	θ_{21}	0.02

Note: For the base case, $M = 0.2$, the first 5 yrs of tag return data are used, and we set the ratio of θ offshore to inshore = 1/3. The settings for inshore θ and for ϕ are given. θ_{21} is the parameter directly estimated in the model.

where r_{syk} is the observed number of tags of type k returned from fishing stage s , in year y , K is the total number of different tag types, and Y is the total number of years of tag returns used. Maximum likelihood estimation is then straightforward. We maximize the log likelihood using the BFGS 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 (Cox and Hinkley 1974).

Data

During late spring and early summer, there is an inshore migration of cod that winters on the edge of the banks (Tom

Table 4. Tag releases and returns (years refer to years in which fish were recaptured during the same year as tagging, yr0, up to the sixth year posttagging, yr6).

Expr.	Year	Month	Day	Area	Tag	Released	Shore	yr0	yr1	yr2	yr3	yr4	yr5	yr6
4802	1948	10	20	3Lj	Internal	286	In	15	29	12	4	5	1	1
5406	1954	10	15	3Lq	Internal	400	Off	1	5	6	3	0	1	0
					External plastic	482	In	2	35	19	7	2	6	1
							Off	4	17	12	10	1	1	0
							In	0	62	31	12	4	2	0
5408	1954	11	10	3Lj	Internal	792	Off	1	18	11	4	1	0	0
					External plastic	965	In	0	78	28	25	6	2	2
							Off	0	32	27	12	5	3	3
							In	2	101	63	31	14	12	2
6208	1962	10	11	3Lb	Disc	336	Off	0	12	16	12	3	0	0
							In	3	48	29	6	4	6	5
6210	1962	11	10	3Lc	Disc	1008	Off	0	33	36	19	7	5	6
							In	0	133	76	19	10	9	2
6315	1963	10	6	3Lj	Disc	1008	Off	0	68	18	12	7	4	0
							In	49	297	59	25	11	4	2
6316	1963	10	18	3Lj	Disc	1008	Off	0	89	34	7	4	4	1
							In	27	232	63	33	9	5	4
6317	1963	10	25	3Ki	Disc	1008	Off	0	39	28	9	3	2	2
							In	0	224	70	62	35	9	20
6318	1963	11	11	3Kd	Disc	1008	Off	0	59	30	11	2	2	1
							In	3	112	49	40	15	15	8
6319	1963	11	6	3Lq	Disc	1008	Off	2	58	20	14	5	1	1
							In	9	240	82	48	13	8	4
6414	1964	10	18	3La	Disc	1008	Off	3	75	36	18	10	6	0
							In	13	142	39	38	10	12	3
6416	1964	11	20	3Lc	Disc	672	Off	0	50	24	17	10	4	1
							In	0	73	30	13	4	3	2
6505	1965	11	25	3Lj	Disc	1007	Off	0	67	45	17	7	6	1
							In	70	206	51	18	7	2	2
7905	1979	10	19	3Lf	Disc	193	Off	0	3	3	0	0	0	0
					t-bar	163	In	2	32	7	1	0	0	1
							Off	0	2	2	1	1	0	0
							In	1	19	10	4	2	3	0
8102	1981	3	14	3Ki	Disc	572	Off	0	4	5	2	2	1	2
					t-bar	560	In	0	58	28	10	3	0	0
							Off	0	3	4	8	1	7	1
							In	0	16	24	5	3	1	1
8405	1984	10	9	3Kd	Disc	129	Off	1	8	3	0	0	0	0
					t-bar	130	In	0	7	1	1	1	1	0
							Off	0	13	6	1	2	0	0
							In	1	5	2	0	0	0	0
9004	1990	3	24	3Lb	Disc	259	Off	0	0	1	—	—	—	—
					t-bar	174	In	0	32	10	—	—	—	—
							Off	0	0	1	—	—	—	—
							In	0	18	7	—	—	—	—
9101	1991	1	20	3Lb	t-bar	199	Off	0	0	—	—	—	—	—
							In	0	79	—	—	—	—	—

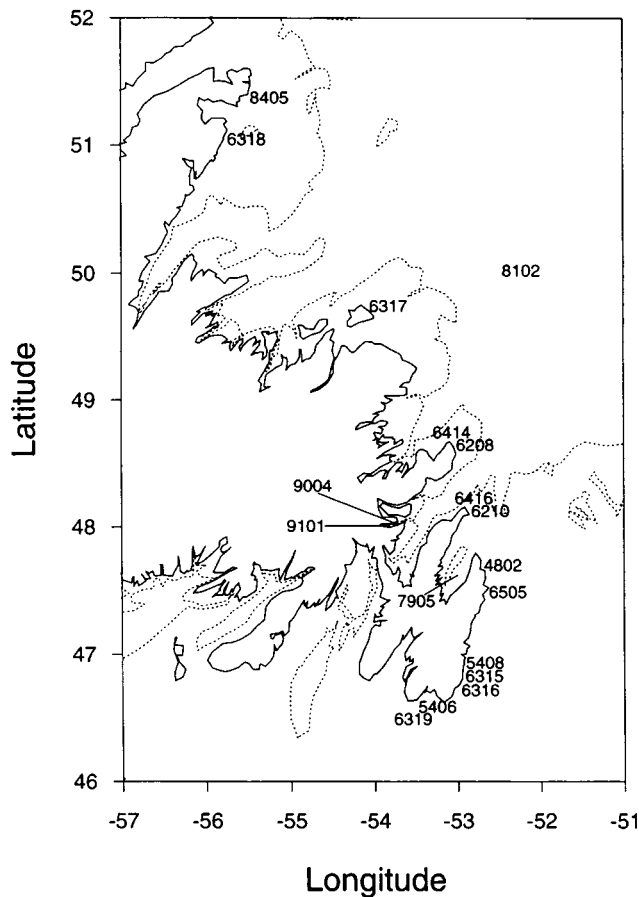
made of vinylite or celluloid with widths from 4.8 to 9.5 mm and with lengths from 20 mm to 76 mm were also used; these tags were attached by a variety of methods described in Templeman (1963). These different varieties were also put on in equal frequencies. We will consider only external tags attached to the dorsal fin because these appear to have had higher retention rates.

Between 1962 and 1965, tagging experiments were con-

ducted using Petersen disk tags (Templeman 1977). Most of these tags were attached to the dorsal fins, but 12% were attached to the preopercular bone. We will analyze only the dorsal fin taggings. Some tags had "danglers" attached. These taggings were carried out by the same technicians using very similar methods throughout the study. These inshore tagging studies covered most of the region.

In the taggings after 1977, the tags were 2.5-cm Petersen

Fig. 1. Locations of inshore taggings examined. The tagging experiment is identified by a number that begins with the last two digits of the year of tagging (see Table 4). The broken line is the 200-m isobath.



disks attached through the posterior of the first dorsal fin, with or without a dangler (Lear 1984). Some fish were tagged using 1.5-cm spaghetti anchor t-bar tags attached through the base of the first dorsal, but we will not consider these results here to keep the models from becoming overly complicated. The results were similar when they were included.

We will limit our analysis to fish 50 cm or longer at the time of release. Cod were captured by baited hooks or trawls of short duration (Fig. 1); only fish in excellent condition were released. Each tagging episode typically took at least a week, so not all tags were placed on one group of fish.

We will consider two gear types: inshore gear comprising traps, baited hooks, jiggers, and gill nets, and offshore gear comprising trawlers. The reason for this breakdown is that reporting rates should be similar when fishermen handle fish individually. This division into gear types is a good approximation of fish caught close to shore and away from shore. There are exceptions to this rule, e.g., some gill nets are used in areas considerable distances from shore (Hutchings and Myers 1994), but such exceptions constitute only a very small fraction of the data (less than 2%). The inshore and offshore tag returns are compiled in Table 4. The offshore catch tended to precede the inshore catch (Fig. 2). This justifies our assumption that the offshore catch occurs first.

In our base case (Table 3), we will examine the 5 yr of recoveries from the beginning of the first new year after the tagging took place. We chose this time because the double tagging experiments could not be extrapolated beyond this (Barrowman and Myers 1996), and tag loss could have changed subsequently. Furthermore, it is unlikely that fishing mortality would remain reasonably constant for more than 5 yr. We will test the robustness of our results by making estimates over 4 and 6 yr.

Results

For each tagging experiment in Table 4, we extracted the observed returns and fit a sequence of models to the data (Table 5). We will begin with a base assumption (Table 3) and test the robustness of the conclusions by varying these assumptions. With our base assumptions, we estimate relatively high rates of exploitation for all time periods.

The proportion of tags that do not immediately disappear from view because of death caused by tagging, initial tag loss, and nonreporting, θ , is high in the 1950's and 1960's experiments, approximately 70% for externally tagged fish in the 1950's and over 75% in the 1960's. These high rates are a result of careful tagging and relatively high rewards for the tags. In the 1980's, the estimated inshore θ is much lower under our base assumption. Possibly, tag loss was higher during that period. Estimates of the inshore reporting rates obtained from interviews with fishermen were approximately 72% (Lear and Rice 1987), much lower than would be compatible with our estimates here. We suspect that the offshore reporting rate is much less than we have used in the base case; the estimates that assume that the ratio of the θ 's was 0.2 were more reasonable, i.e., the estimate of the θ_0 is between 0.25 and 0.76.

In 1990 and 1991, there were inshore taggings in Trinity Bay in January or March (experiments 9004 and 9101). We use only 2 yr of recoveries for the 1990 release and one for the 1991 because of the cod fishing moratorium in 1992. The recovery rate of the 1990 experiment was much lower than for 1991 (Table 4). For the 1991 tagging experiment, there was only 1 yr of recovery, so we cannot use our model; nevertheless, some estimates are possible. Of the 476 cod larger than 50 cm tagged in Trinity Bay with Petersen disk tags in January, 212 tags were recovered in Trinity Bay and surrounding bays during the summer of 1991. Independent experiments show that approximately 13% of tagged cod die immediately from tagging during this period and that inshore reporting rate of tags is approximately 72% (Lear and Rice 1987). If the instantaneous natural mortality is 0.2, then approximately 294 fish were actually caught of the approximately 375 alive in the summer of 1991. This represents an exploitation rate of 78%, or an instantaneous fishing mortality of 1.54-yr^{-1} (shown on Fig. 3).

Our results on fishing mortality must be interpreted in light of probable stock structure mentioned in the introduction. Three of the taggings (experiments 7905, 9004, and 9101) were carried out deep inside bays and probably represent primarily bay stocks. Most of the rest of the taggings probably represent a combination of headland, bay, and offshore migrants. The fishing mortality estimated from these experiments should be viewed as that experienced by such

Fig. 2. Seasonal cycles of the inshore and offshore returns for three representative experiments.

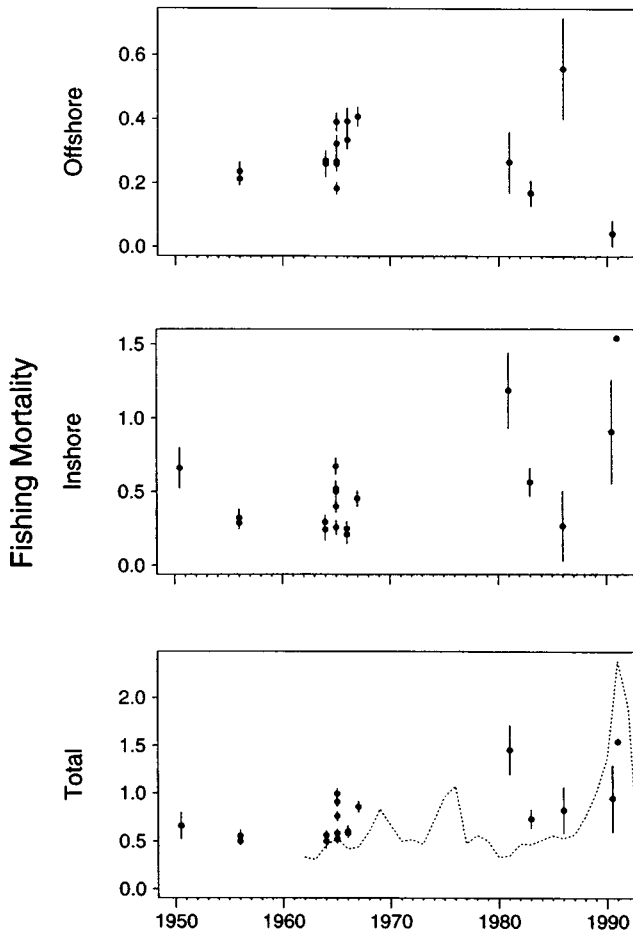
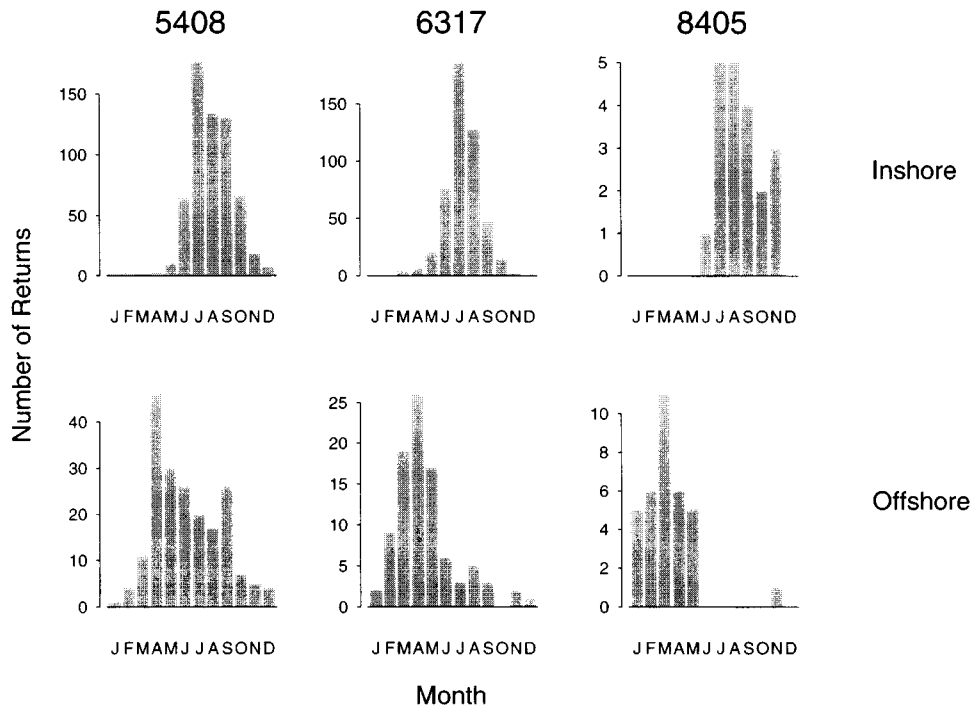


Fig. 3. Inshore, offshore, and total estimated mortality, with standard errors, from each tagging versus the midpoint of the period used to estimate mortality for the $M = 0.1$ case listed in Table 5, i.e., same as the base case (Table 3) except $M = 0.1$. There is no standard error for the 1991 estimate because only 1-yr returns were used in the estimate. The broken line on the bottom panel is the fully recruited fishing mortality estimated from the sequential population analysis for the whole population.

a mixture of fish. One of our taggings (experiment 8405) probably consisted almost entirely of offshore migrants; this group of fish had relatively low inshore fishing mortality and the highest offshore fishing mortality of any group of fish tagged. In contrast, experiment 8102 was not tagged close to shore (Fig. 1), and yet this group of fish was almost entirely exploited by the inshore fishery.

Robustness and violations of model assumptions

We will examine the robustness of our estimates to violations of model assumptions (reviewed by Pollock et al. 1991).

(1) *Natural mortality is 0.2.* The results of our robustness analysis show very small changes in the estimates of the fishing mortality over the range of assumptions we tested (Table 5). Using the alternative assumption that natural mortality is 0.1, we estimate a higher fishing mortality by about 10%. This usually resulted in a lower θ in the 1960's, which appears to be more reasonable because it is extremely unlikely that θ could be close to 1. For this to occur the product

Table 5. Parameter estimates $\times 100$ (with standard errors) under various conditions.

Condition	Parameter	Experiment						
		4802	5406	5408	6208	6210	6315	6316
Base case	θ_{21}	31 (4.2)	80 (7.5)	83 (6)	100 (—)	85 (6.5)	98 (5)	100 (—)
	F_1		20 (2.9)	17 (1.9)	22 (3.7)	23 (2.6)	30 (2.5)	36 (2.7)
	F_2		26 (4.2)	23 (2.8)	22 (3.3)	24 (3.2)	59 (4.8)	46 (3.6)
	F_{total}	56 (14)	46 (6.2)	40 (4.2)	44 (6)	46 (5)	89 (5.6)	82 (5.2)
$m = 0.1$	θ_{21}	27 (3.2)	64 (5.2)	65 (3.9)	88 (9.7)	69 (4.6)	86 (4.3)	89 (4.7)
	F_1		23 (3)	21 (2)	26 (4.2)	27 (2.6)	32 (2.7)	39 (2.8)
	F_2		32 (4.5)	29 (3)	24 (4.8)	29 (3.4)	67 (5)	52 (4.3)
	F_{total}	66 (14)	56 (6.1)	50 (4.2)	50 (7.7)	56 (5)	99 (5.6)	91 (5.4)
4 yr	θ_{21}	32 (5)	76 (7.5)	83 (7.1)	100 (—)	82 (6.8)	95 (4.9)	100 (5.5)
	F_1		22 (3.4)	17 (2.2)	24 (4.3)	24 (2.9)	31 (2.7)	37 (2.9)
	F_2		29 (5.1)	22 (3.3)	22 (3.5)	25 (3.8)	64 (5.4)	49 (4.7)
	F_{total}	53 (16)	51 (7.5)	40 (5.1)	47 (6.8)	49 (6.1)	95 (6.3)	86 (6.2)
6 yr	θ_{21}	32 (4.2)	77 (6.6)	82 (5.4)	100 (—)	88 (6.4)	98 (5)	100 (—)
	F_1		21 (2.8)	18 (1.8)	20 (3.2)	23 (2.4)	30 (2.5)	34 (2.5)
	F_2		28 (4.1)	23 (2.6)	21 (3)	22 (2.8)	59 (4.6)	44 (3.4)
	F_{total}	54 (12)	49 (5.7)	41 (3.8)	41 (5.3)	45 (4.4)	89 (5.3)	78 (4.8)
Disc $\phi = 0.1$, internal $\phi = 0.1$	θ_{21}	37 (6.3)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)
	F_1		16 (2.4)	15 (1.5)	21 (3.5)	20 (2.2)	27 (2.3)	32 (2.6)
	F_2		21 (2.3)	19 (1.4)	23 (3.3)	20 (1.9)	57 (4.1)	45 (3.5)
	F_{total}	46 (14)	37 (4)	34 (2.5)	44 (5.6)	40 (3.6)	85 (5.3)	78 (5)
Ratio of θ offshore to inshore = 0.2	θ_{21}		100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)
	F_1		26 (3.4)	23 (2.2)	28 (4.1)	29 (2.9)	36 (2.7)	42 (2.8)
	F_2		22 (2.5)	20 (1.6)	23 (3.3)	21 (2)	57 (4.1)	46 (3.5)
	F_{total}		48 (5.2)	43 (3.4)	51 (6.4)	51 (4.3)	94 (5.4)	87 (5.2)
Ratio of θ offshore to inshore = 0.5	θ_{21}		67 (5.9)	69 (4.8)	91 (11)	70 (5)	84 (3.9)	84 (4.2)
	F_1		15 (2.4)	14 (1.6)	17 (3.4)	18 (2.1)	23 (2.1)	28 (2.3)
	F_2		30 (4.7)	26 (3.1)	23 (5.1)	28 (3.6)	67 (5)	53 (4.4)
	F_{total}		46 (6.2)	40 (4.2)	40 (7.7)	46 (5)	89 (5.6)	81 (5.4)

Note: In cases where parameter constraints were applied, standard errors could not be computed and are represented as (—). The parameter θ_{21} is the product of initial survival after tagging, initial tag retention, and reporting rate for the reference tag type in the inshore fishery. The parameters F_1 and F_2 are the offshore and inshore fishing mortalities, respectively (derived from the exploitation rates u_1 and u_2 estimated in the model). The estimate of total fishing mortality, $F_{\text{total}} = F_1 + F_2$, is also given. The first set of estimates represents the base case (Table 3), while the other sets of estimates are deviations from the base case.

of initial survival probability after tagging, tag retention, and reporting probability would have to be 1, which is unlikely.

(2) *Mortality and reporting rates are constant over the estimation period.* Fishing mortality increased in the late 1980's and early 1990's (Myers and Cadigan 1995a, 1995b). An increase in fishing mortality over time would tend to negatively bias the estimated 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, we may underestimate fishing mortality during this period. Other changes in mortality and reporting rates are likely to be smaller and may increase or decrease any one estimate, but should not systematically bias our results.

(3) *The tag shedding rate is known.* If the tag shedding

rate was increased from 0.02 to 0.1 for the Petersen tags, then the estimated exploitation rate was usually decreased by less than 10%. Note that this tag shedding rate is clearly too high for the 1960's data because three of the θ 's are estimated to be greater than 1, which is impossible.

(4) *Mortality rates are not influenced by tagging.* Experiments on mortality of tagged fish obtained from trawls and held for 2 wk indicate that mortality under these conditions is less than 13% (Lear and Rice 1987). These estimates are probably positively biased because some of the fish died when their tags snagged in the nets covering the tank. Furthermore, mortality associated with trawling fish from around 200 m is probably greater than that for fish obtained in shallower water. In any case, our estimates indicate that natural mortality plus tag-induced mortality could not be much

Table 5 (concluded).

Experiment									
6317	6318	6319	6414	6416	6505	7905	8102	8405	9004
100 (6.3)	88 (7.1)	96 (5.4)	100 (—)	99 (8.8)	97 (5.5)	38 (6.3)	32 (3.8)	49 (12)	24 (5.6)
16 (1.7)	22 (2.6)	23 (2.2)	29 (2.6)	33 (4.1)	37 (2.9)	26 (9.3)	15 (3.7)	50 (16)	3.9 (3.9)
33 (3.4)	20 (3)	43 (3.9)	22 (2)	17 (2.9)	39 (3.9)	110 (25)	48 (8.6)	23 (11)	81 (34)
48 (4.3)	43 (5)	66 (4.8)	51 (4.1)	50 (6.3)	76 (5.5)	130 (26)	63 (9.8)	73 (24)	85 (35)
81 (4.5)	70 (4.8)	82 (4.4)	86 (5.3)	82 (6.5)	85 (4.6)	34 (5.6)	28 (3.1)	42 (10)	22 (4.5)
18 (1.9)	27 (2.7)	26 (2.3)	33 (2.8)	39 (4.1)	41 (3)	26 (9.6)	17 (4)	56 (16)	4.2 (4.2)
40 (3.5)	26 (3.2)	50 (4)	25 (2.8)	21 (3.2)	45 (4.2)	120 (25)	56 (8.9)	27 (12)	91 (34)
58 (4.3)	53 (5)	76 (4.8)	58 (4.8)	60 (6.3)	86 (5.5)	140 (26)	73 (9.7)	83 (24)	95 (35)
100 (—)	83 (7.2)	96 (5.6)	100 (7.2)	98 (9.7)	95 (5.4)	38 (6.3)	33 (4.2)	46 (11)	24 (5.6)
15 (1.8)	25 (3.2)	23 (2.3)	32 (3.3)	33 (4.8)	38 (3.1)	25 (9.3)	13 (3.6)	63 (20)	3.9 (3.9)
32 (2.5)	23 (3.6)	43 (4.3)	23 (3.2)	17 (3.4)	42 (4.5)	110 (25)	45 (9.4)	29 (15)	81 (34)
47 (3.7)	48 (6.2)	66 (5.5)	55 (5.9)	51 (7.5)	80 (6.3)	130 (26)	58 (11)	92 (30)	85 (35)
100 (—)	89 (6.8)	97 (5.3)	100 (—)	98 (8.3)	98 (5.4)	40 (6.5)	34 (3.9)	49 (12)	24 (5.6)
13 (1.4)	21 (2.3)	23 (2.1)	30 (2.6)	33 (3.8)	37 (2.8)	22 (8.1)	16 (3.6)	51 (15)	3.9 (3.9)
30 (2.2)	20 (2.6)	42 (3.6)	22 (2)	17 (2.7)	38 (3.7)	88 (20)	44 (7.6)	24 (11)	81 (34)
43 (3)	41 (4.3)	65 (4.4)	52 (3.9)	50 (5.7)	75 (5.2)	110 (21)	60 (8.7)	75 (23)	85 (35)
100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	41 (6.9)	37 (4.6)	56 (15)	26 (7)
14 (1.6)	20 (2.2)	21 (2)	27 (2.4)	31 (3.5)	34 (2.8)	25 (9.1)	14 (3.5)	45 (16)	3.6 (3.7)
33 (2.4)	18 (1.7)	41 (3.1)	22 (2)	17 (2.1)	37 (3.2)	100 (25)	42 (8.4)	20 (11)	73 (35)
47 (3.3)	38 (3.4)	62 (4.2)	50 (3.8)	49 (4.9)	71 (5)	130 (26)	55 (9.8)	65 (24)	77 (36)
100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	100 (—)	45 (8.9)	39 (5.2)	74 (19)	25 (6.2)
20 (2)	29 (2.9)	29 (2.4)	36 (2.8)	42 (4.1)	44 (3.1)	38 (12)	22 (4.8)	57 (18)	6.3 (6.1)
34 (2.5)	19 (1.9)	42 (3.1)	23 (2)	18 (2.2)	38 (3.2)	97 (25)	42 (8.2)	16 (8.4)	79 (34)
54 (3.7)	48 (4.1)	71 (4.5)	59 (4.2)	60 (5.5)	82 (5.2)	130 (26)	63 (9.8)	73 (24)	85 (35)
87 (5.1)	71 (5.4)	82 (4.2)	84 (5.5)	75 (6.4)	79 (4.1)	34 (5.2)	29 (3.2)	37 (8.6)	23 (5.4)
12 (1.4)	18 (2.2)	18 (1.7)	23 (2.4)	29 (3.6)	29 (2.5)	18 (7.1)	11 (2.9)	43 (14)	2.6 (2.7)
37 (3.6)	25 (3.4)	49 (4.1)	25 (3.1)	22 (3.5)	47 (4.3)	120 (25)	52 (8.9)	30 (14)	82 (35)
48 (4.3)	43 (5)	66 (4.8)	48 (4.8)	50 (6.3)	76 (5.5)	130 (26)	63 (9.8)	73 (24)	85 (35)

greater than 0.1. It is possible that fish tagged with Petersen disks have a higher probability of becoming entangled in gill nets, and thus suffering higher fishing mortality. We do not believe that this is an important problem because gill nets deliver a relatively small proportion of the returns (approximately 10%), and similar estimates of fishing mortality were obtained when we examined the fishing mortality from tags that are not likely to increase catchability (internal tags or t-bar tags).

(5) *The ratio of θ inshore and offshore is known.* If the ratio of θ offshore to inshore is changed, then the largest change occurs in the ratio of inshore to offshore mortality; there is relatively little change in the overall exploitation rate. If the ratio is reduced to 0.2, then the estimated offshore mortality generally increases; however, this results in a θ greater than 1 for the 1960's. A more moderate reduction produces reasonable results.

(6) *The year of the tag recovery is correctly tabulated.* Some tags may be reported from fish caught in previous years. This type of misreporting is probably small, since we

only used tags in which the location and gear type of the tag were also reported, and there were followup telephone interviews of any suspicious tags. Any such tabulation errors will result in a negative bias in the estimated exploitation rate (Pollock et al. 1991).

(7) *The fate of each tagged fish is independent of the fate of other tagged fish.* Violations of this assumption will not bias the estimates but will result in standard errors being underestimated (Pollock et al. 1991).

(8) *All tagged fish have the same annual mortality and recovery probabilities.* Heterogeneity of survival and recovery rates is almost certain to occur for a variety of reasons, e.g., tagged fish may be from more than one subpopulation. Nichols et al. (1982) and Pollock and Raveling (1982) found, using simulations, that if recovery rates were heterogeneous, e.g., we combined more than one type of tag type in the 1950's and 1960's, then no biases resulted. They also found that if mortality rates varied, e.g., different fishing mortalities among a group of tagged fish, the estimated 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 fact that relatively discrete groups of tagged cod are examined, this positive bias should be small.

It is possible to compare our estimates of fishing mortality with those obtained from sequential population analysis (SPA; Fig 3). In these comparisons, we assumed that natural mortality was 0.1 instead of the usual 0.2. A lower natural mortality than the usual assumption of 0.2 for such a slow-growing northern population is consistent with estimates of natural mortality derived from evolutionary models (Myers and Doyle 1983).

The fishing mortality we estimate from the inshore tagging is generally higher than that estimated by SPA (Bishop et al. 1994; Myers and Cadigan 1995a, 1995b). This remains true if we use an estimate of 0.2 for natural mortality (Table 5). There are two reasonable explanations for the higher inshore fishing mortality. First, the exploitation rate for fish that remain inshore for most or all of the year could be much higher than that of offshore components, some of which may not migrate inshore at all. Second, the fishing mortality estimated from the SPA will be much less if there has been underreporting of commercial catches. We believe that both factors are important. Myers et al. (1996a) examined estimates of fishing mortality from tagging data from mainly offshore stock components and found only that they gave higher estimates of fishing mortality than the SPA, but not as high as estimated here. Myers et al. (1997) tested fishing mortality estimated from SPA with those estimated directly from research surveys. Although they found evidence of large misreporting and discarding for young cod, the bias in the estimates of fishing mortality for older cod was present, but not large. Taken together, this evidence indicates a higher fishing mortality on inshore stock components than on offshore stock components.

The θ 's for the 1980's and 1990's experiments were generally much lower. There are several reasons for this. First, there was much less hand processing of the fish during this period, i.e., fewer fish were hand split and salted. Second, the tag reward was much less than in previous years because the rewards had not kept up with inflation. Third, 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.

Conclusion

Do inshore stocks exist?

Cod in the 2J3KL region have been managed on the assumption that they are a single stock. We believe that there is overwhelming evidence that inshore stock components exist. Based on tagging, morphometric, and meristic data, several researchers have concluded that northern cod comprise several substocks (e.g., Graham 1923; Thompson 1943; Templeman 1974, 1977). The existence of significant spatial and temporal variability in spawning location and spawning time, respectively, is consistent with the hypothesis that northern cod are not panmictic (Hutchings et al. 1993; Myers et al. 1993). Spatial variation in spawning location may be responsible for the spatial variability in recruitment documented in research surveys (Mertz and Myers 1994). Evidence of the

existence of inshore stocks is further supported by evidence of inshore spawning locations (Neilsen 1895; Graham 1923; Hutchings et al. 1993; Wroblewski et al. 1994; Smedbol and Wroblewski 1997) and by recently documented differences in microsatellite DNA between cod overwintering in Trinity Bay and cod overwintering on the northern Grand Banks (Ruzzante et al. 1996).

Additional evidence of temporal differences in spawning time between inshore and offshore cod has been documented by studies of larval cod abundance in inshore waters. Methven and Bajdik (1994) indicated that 0-group cod collected inshore may originate from both offshore and coastal spawning populations. They observed two periods of high abundance of 0-group cod (August–September and October–November) at a single sampling site in southern Trinity bay and suggested that these cod may be progeny of (spatially or temporally) discrete inshore spawning events. In addition, Pinsent and Methven (1997), concluded that recently settled 0-group cod collected in coastal locations of southern Trinity Bay, Newfoundland, during autumn and early winter likely had a nearshore (Trinity Bay) origin based on spawning times calculated from otolith microstructure and local water temperatures.

Can an inshore fishery exert high fishing mortality?

Our analysis indicates that exploitation rates on inshore stock components of Atlantic cod have been very high at least since the late 1940's. Our high estimates of inshore fishing mortality are consistent with the hypothesis that inshore subpopulations of cod around Newfoundland have been greatly reduced or possibly eliminated. Quantitative analyses have clearly demonstrated that populations have very low probability of growing under such high levels of fishing mortality (Hutchings and Myers 1994).

We believe that the inshore fishery has effected very high mortality rates on these inshore subpopulations. This is evident in our estimates of inshore fishing mortality, but is also supported from other sources. The first tagging experiments in the Newfoundland region were carried out by Thompson (1943) in the 1930's. Although the type of tags used caused high mortality rates and had relatively low retention (Templeman and Fleming 1962) and, therefore, could not be used in our analysis, Thompson's results are consistent with a high fishing mortality rate on inshore subpopulations during the 1930's. Twelve percent of the fish tagged inshore were returned in the first year after tagging, and only 3.025% were returned later. Given the high tag-induced mortality, the low tag retention rate, and an unknown reporting rate, it seems likely that the exploitation rate must have been higher than 25% for 12% of the tags to be returned the first year.

Support for the hypothesis that inshore stock components have been overexploited can be seen in the drastic decline in catch per unit effort from inshore fixed gear, e.g., cod traps and gill nets. Hutchings and Myers (1995) showed that catch per cod trap declined from over 200 tonnes per trap to 50 tonnes per trap between 1938 and 1945 in Labrador. Templeman (1966) showed that catch per man declined for northern cod between 1956 and 1964; however, this decline was concurrent with an increase in fishing effort offshore by foreign trawlers and inshore by improved gill nets (Hutchings and Myers 1995).

Hutchings and Myers (1994) showed that catch per cod trap and catch per gill net declined between 1987 and 1991 in all inshore areas in the 2J3KL region. These declines in catch rates, derived from sociological data on purchase slips, have been confirmed from interviews and logbooks from individual fishers (J.A. Hutchings, unpublished data). The decline in the gillnet catch rates occurred first inshore and then further offshore. This pattern is consistent with the hypothesis that inshore subpopulations were reduced before subpopulations that migrated to a lesser extent inshore (Hutchings and Myers 1995).

Our analysis of the 1991 tagging in Trinity Bay bears on the causes of the recent collapse of the northern cod stock. It has been suggested that the collapse was caused by an increase in natural mortality in 1991 (discussed in Myers and Cadigan 1995b). Our analyses demonstrate that the fish from this stock component in 1991 did not suffer extraordinary natural mortality and that the fishing mortality on them was very high in 1991. We conclude from the results of Hutchings and Myers (1994), Myers and Cadigan (1995b), Hutchings (1996), and Myers et al. (1996a, 1996b, 1997) that the collapse of northern cod was caused by overfishing.

The population dynamics of overexploitation of a mixed fishery with one component more catchable than the other are well understood. The population that is more catchable will be overfished or eliminated entirely (Clark 1990). That is, the offshore components of the population will allow exploitation of the inshore components to continue even when the inshore components are reduced to a very low level. The challenge in fisheries management is to devise a management policy that can effectively protect inshore subpopulations from overexploitation. Until recently, this fishery has been managed with virtually no limits on inshore fishing effort; this policy should be changed in the future.

Future tagging experiments

In the past, monitoring the inshore subpopulations and fishing mortality has not been possible. The inshore region is difficult to sample using traditional trawl or acoustic surveys because of its rough bottom, deep canyons, and large area. The resumption of an inshore tagging program would allow estimates of inshore fishing mortality to be obtained. If tagging were carried out over several years in the same location, it would be possible to use Brownie models, which allow many of the model assumptions to be tested.

Clearly, tagging can give reliable estimates of fishing mortality on stock components. Several points need to be considered in future experiments. (1) Double tagging experiments should be carried out to estimate tag loss. (2) At most, two types of tags should be applied. (If more than two types are used, it is difficult to achieve sufficiently large sample sizes to make valid comparisons of tag types.) (3) A portion of the tagged fish should be kept for at least a week after tagging in an aquarium or field cage to determine immediate death due to tagging. (4) Methods for tagging should be kept as constant as possible using only trained, closely supervised crews; otherwise, there can be considerable variation in tag return rates among and within experiments. (5) Taggings should be repeated in the same region in more than one year to test model assumptions using methods similar to the Brownie models. (6) Tag rewards should be sufficiently high

to assure high probability of a tag being returned. (7) Some high rewards for tags, to encourage near 100% reporting of tags if they are detected, should be used so that reporting rate for standard tags can be estimated (Henny and Burnham 1976). If these conditions are met, it should be possible to use mark-recapture methods such as the ones developed here to estimate exploitation rates.

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