Direct estimates of gear selectivity from multiple tagging experiments

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Abstract: A new method is introduced for estimating selectivity of fishing gear from tagging data in which data from many experiments are combined. Selectivity is modeled as a multiplicative function of length and experiment effects using a generalized linear model with a log link function and a binomial error structure. We apply this method to 137 tagging experiments on Atlantic cod (*Gadus morhua*) conducted from 1954 to 1991. We show that the selectivity of otter trawls changed from the 1960s to the 1980s; during the earlier period the maximum probability of capture occurred at 55 cm and declined for longer fish, whereas in recent years the maximum probability is at approximately 60 cm and remains constant for longer fish. We discuss how selectivity estimates can be used to improve stock assessments.

Résumé : Une nouvelle méthode est présentée pour estimer la sélectivité des engins de pêche à partir des données de marquage dans laquelle sont combinées les données de nombreuses expériences. La sélectivité est modélisée comme une fonction multiplicative de la longueur et des effets de l'expérience à l'aide d'un modèle linéaire généralisé comportant une fonction de liaison avec les journaux de pêche et une structure d'erreur binomiale. Nous appliquons cette méthode à 137 expériences de marquage de la morue franche (*Gadus morhua*) réalisées de 1954 à 1991. Nous montrons que la sélectivité des chaluts à panneaux a changé entre les années 1960 et les années 1980; durant la première de ces deux périodes, la probabilité maximale de capture survenait à 55 cm et diminuait pour les poissons plus longs, tandis qu'au cours de la période plus récente, la probabilité maximale de capture survenait à 60 cm et demeurait constante pour les poissons plus longs. Nous discutons de la façon dont les estimations de la sélectivité peuvent être utilisées pour améliorer les évaluations des stocks. [Traduit par la Rédaction]

Introduction

Determining the selectivity of fishing gear for fish of different sizes is a key component of fishery assessments. For example, during the late 1980s all Canadian stocks of Atlantic cod (*Gadus morhua*) were assessed using the assumption that the selectivity of the commercial fishing gear, primarily otter trawls, decreased at older ages (Myers and Cadigan 1995*b*). This assumption turned out not to hold up under statistical analysis (Myers and Cadigan 1995*b*) and resulted in the spawning biomass being overestimated. This overestimation of spawner abundance played a major role in the collapse of the cod stocks in Eastern Canada (Myers et al. 1997*a*).

The most direct method for estimating selectivity is to tag or mark a large number of fish and determine the proportion caught by the fishing gear in each size category. This is readily accomplished in small lakes (Hamley and Regier 1973); however, in large lakes and the ocean it is rare that enough tagged fish are released in a single tagging experiment to enable selectivity to be well determined. An exception is Anganuzzi et al. (1994) who estimated selectivity from two experiments in which over 55 000 fish were tagged.

The purpose of this paper is to present a simple method that allows selectivity of fishing gear to be estimated in a rigorous way using data from many separate tagging experiments. We make use of the theory of generalized linear models (McCullagh and Nelder 1989) and this allows us to perform the calculations using standard statistical software such as GLIM and SAS. A generalized linear model has three features: (*i*) a linear function of the explanatory variables, (*ii*) a link function (usually nonlinear) relating the expected value of a dependent variable to the linear combination of explanatory variables, and (*iii*) an error structure in the exponential family of statistical distributions. Common examples of generalized linear models are probit and logit models and log-linear (multiplicative) models.

We will briefly mention two alternative approaches to estimating selectivity. First, if the commercial catches are known by age and by year, then age-structured models such as virtual population analysis can be used to estimate selectivity of the commercial fishing gear. Statistical catch-at-age models can be formulated in a variety of ways; many formulations depend upon the selectivity of the independent survey or commercial catch rate series being known, at least for older ages. This may cause a fundamental indeterminacy in many formulations because the estimated selectivity of the gear that is being used to calibrate the VPA depends upon assumptions about the fishery (Myers and Cadigan 1995*a*, 1995*b*).

A second approach is to compare the catch rates of different sizes of fish in two or more gear types. This is known as indirect estimation of selectivity (Millar 1992). However, Millar (1995) recently showed that the functional form of selectivity from such a comparative approach cannot be determined from comparative catch data alone using two types of gear, e.g., two hook types. Furthermore, Millar and Holst (1996) showed that indirect methods of estimating selectivity cannot distinguish

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between models in which fishing power is constant with mesh size and models in which fishing power is assumed to be proportional to mesh size. It is possible to construct experiments in which two gear types can be directly compared, e.g., by constructing a trawl with two different types of cod ends (Hamley and Regier 1973; Millar 1992). Although these experiments are very valuable their results are limited, e.g., they only determine the selectivity of fish that enter the trawl, because small or larger fish may avoid entering the trawl by various avoidance behaviors (Millar 1992).

Methods

Consider a tagging experiment, i, in which $N_{i,l}$ fish of length l are tagged and released. We will examine tag returns for a relatively brief time after tagging, e.g., less than a year, in which growth and natural mortality should be minimal. The exploitation rate on the size group most vulnerable to gear type g in experiment i is $U_{i,g}$. The selectivity of gear type g is $S_{g,l}$, where the selectivity will be scaled so that the largest selectivity over all lengths will be 1. We construct a simple model in which the selectivity will be constant over several experiments. The expected value of the reported catch of tagged fish, $E[C_{i,g,l}]$, is

$$E[C_{i,g,l}] = N_{i,l}\, R_{i,g}\, U_{i,g}\, S_{g,l}$$

where $R_{i,g}$ is the product of the proportion of fish that survive tagging, the proportion of tags that are not lost (shed), and the proportion of recovered tags that is reported from experiment i in gear type g. $R_{i,g}$ is assumed to be constant over lengths of fish. Note that we have assumed that tagging mortality, natural mortality, tag loss, and tag reporting rate are independent of the length of fish for each gear type (but not necessarily constant from experiment to experiment). We have also assumed that natural mortality is small enough to be ignored during the analysis.

If the capture probability is the same for all fish of a given length, and the captures occur independently and at random, then the capture probability of a tagged fish will be

$$\pi_{i,g,l} = R_{i,g}\, U_{i,g}\, S_{g,l},$$

and the probability of observing $C_{i,g,l}$ recaptures is binomial:

$$\mathrm{Prob}(C_{i,g,l}) = \binom{N_{i,l}}{C_{i,g,l}} (\pi_{i,g,l})^{C_{i,g,l}} (1 - \pi_{i,g,l})^{N_{i,l} - C_{i,g,l}}.$$

The likelihood follows immediately from the above probabilities.

An overdispersed binomial model may be more appropriate if only a few schools of fish were tagged, and the fish in these schools were captured (Fryer 1991; Millar 1992). In this case overdispersion is easily modeled using a scale factor for the variances (McCullagh and Nelder 1989, p. 126).

The simplest model for the capture probabilities is a multiplicative model. Letting lowercase letters represent the log of a value, e.g., $s_{g,l} = \log(S_{g,l})$, we have

$$\log(\pi_{i,g,l}) = r_{i,g} + u_{i,g} + s_{g,l}\,.$$

Note that $r_{i,g}$ and $u_{i,g}$ are completely confounded in the above equation. This does not matter because we treat the sum, $r_{i,g} + u_{i,g}$, as a nuisance parameter and we do not require separate estimates of each. For the above model to make sense, $r_{i,g} + u_{i,g}$ and $s_{g,l}$ must be less than or equal to 0. In the data considered, all estimates were within the feasible range.

In the framework of a generalized linear model (McCullagh and Nelder 1989), the above equation predicts that the log of the proportion of tagged fish captured at a given length should have a binomial sampling error with a mean that is dependent upon $r_{i,g} + u_{i,g}$, which is a nuisance parameter, and $s_{g,l}$, which is the parameter of interest. Statistical tests and estimation were carried out using a binomial error assumption and a log link function. A length effect was estimated for each tagging experiment with length-class entered as factors in hierarchical tests. Differences in selectivity among length groups were tested using standard likelihood ratio tests and by looking at the deviance. The deviance, $d_{i,l,s}$, is defined to be twice the difference between the maximum likelihood achievable in a full model, in which there is one parameter fit per observation, and that achieved by the model under investigation. This procedure is similar to a standard analysis of variance method but is appropriate for binary data such as in a mark–recapture experiment.

The selectivities for each gear type estimated using this method are relative. We have standardized the data display so that the selectivity for the length-class with the maximum selectivity is equal to one for each gear type. There will be no standard error associated with this selectivity.

In the discussion, gear type g and length l are treated as factors, i.e., as "class" variables. We believe this is the best way to begin an analysis so that the estimated selectivity can be examined directly. This model formulation can be used to fit many continuous models as well. For example, Millar and Holst (1996) described how to estimate normal, gamma, and lognormal selectivity in the context of a model of indirect selection on gill nets; we will not repeat their formulation here because its application is straightforward.

There are several alternative definitions of generalized residuals for generalized linear models (McCullagh and Nelder 1989); we examine the Pearson residual, which is defined as

$$r_{\mathrm{P}} = \frac{y_k - \mu_k}{(V(\mu_k))^{1/2}}$$

and the deviance residual, which is defined as

$$r_{\mathrm{D}} = \mathrm{sign}(y_k - \mu_k)\, (d_k)^{1/2}$$

where y_k is the observed catch, μ_k is the predicted mean of the kth observation, $V(\mu_k)$ is the variance of the binomial for predicted mean, d_k is the deviance, and sign(x) is 1 if $x > 0$ and –1 if $x < 0$.

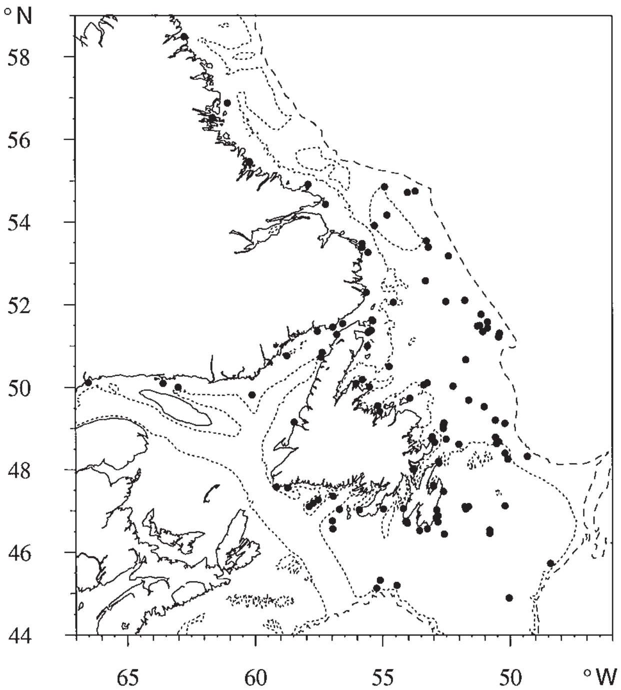
A brief description of the method of programming is given in the Appendix.

Data

We examined 137 tagging experiments conducted from 1954 to 1991 in which approximately 179 000 cod were tagged and released (Fig. 1). Cod were captured for tagging by baited hooks, traps, or trawls of short tow duration; only fish in excellent condition were released. Each tagging episode typically took a week. 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. Tag loss was initially approximately 10, and about 2% per year after that (Barrowman and Myers 1996).

In 1954 and 1955, there were 13 tagging experiments (Templeman 1974). About half of the tags were internal tags and half were external tags made of vinylite or celluloid (Templeman 1963). For the 1950s data, the median number of fish released per experiment we analyzed was 880 and the median number of returns was 213. Between 1962 and 1966, the tagging experiments we examined were conducted using Petersen disk tags attached posterior or anterior to the dorsal fins (Templeman 1977). Some tags had danglers attached. After 1978, fish were tagged with Petersen disk tags, with or without a dangler, or a 1.5-cm spaghetti tag with a t-bar anchor attached through the base of the first dorsal (Lear 1984). For the 1960s data, the median number of fish released per experiment was 672 and the median number of returns was 191. For the data after 1978, the median number of releases per experiment was

Fig. 1. Locations of tagging experiments. The dotted line is the 200-m isobath and the dashed line is the 1000-m isobath.



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. We used all available data, but there were periods in which no tagging was carried out.

We considered the six major fishing gear types used in the Newfoundland region for cod fishing: (*i*) cod traps with diamond mesh size usually of 89 mm (3.5 inches), (*ii*) otter bottom trawls usually with diamond mesh of 130 mm since 1974 (mesh sizes of 76 mm or smaller were used before 1957, at which time minimum mesh size increased to 114 mm) (Pinhorn and Halliday 1990), (*iii*) longlines, which are long lines of baited hooks (usually No. 15 Mustad J hooks) spread along the ocean floor, (*iv*) hand lines, a line with a weight and baited hook (usually No. 15 Mustad J hooks), (*v*) jiggers, which are lure-like hooks attached to a line that is moved up and down in a series of short movements to snag fish, and (*vi*) bottom gill nets that have a diamond mesh of 140 mm (larger meshes were previously used in the 1960s).

The type of gear used varied among fishermen. For example, small mesh liners are often illegally used to increase the catch rates of otter trawls (Palmer and Sinclair 1996). Our purpose here is to describe the selectivity of the gear actually used by fishermen.

We divided data into 5-cm length groups. For each commercial fishing gear investigated, we used data from experiments in which recaptures occurred in at least two length-classes.

Results

The first step in our analysis was to determine if tagging fish influences their catchability. We were particularly concerned that Petersen disk tags might affect the estimated selectivity of gill nets. To investigate this we analyzed data from the 50

Table 1. The deviance values and the respective degrees of freedom (df) for the six gear types for the two time periods as well as the difference in deviance (ΔDeviance) and difference in degrees of freedom (Δdf) between the models.

	1954–1966		1979–1990				
Gear	Deviance	df	Deviance	df	ΔDeviance	Δdf	*p*
Cod trap	415.9	404	374.2	485	7.5	7	0.37
Gill net	—	—	372.7	432	—	—	—
Handline	287.6	326	264.8	299	6.9	8	0.54
Jigger	295.3	360	193.2	268	5.7	8	0.68
Longline	386.9	399	303.0	343	6.9	8	0.54
Otter	424.4	434	533.7	560	45.2	8	10^{-7}

Note: *p* is the significance level for the test of the hypothesis that gear selectivity is the same for both time periods. For gill nets we only used data from fish tagged after 1978 with spaghetti tags.

experiments in which spaghetti and Petersen disk tags were both used. We found that the selectivity was significantly different between these two groups for gill nets (likelihood ratio test, $\chi^2 = 62.4$, df = 7, $p < 0.0001$), but not for the other fishing gear. The spaghetti tags are unlikely to become entangled in gill nets because they are soft and flexible, while it appears that Petersen disks, particularly those with danglers, have a greater chance of becoming entangled. Thus, we only analyzed gill-net selectivity for data after 1978 using the spaghetti tags. We combined data on all tag types for the analysis of other gear types.

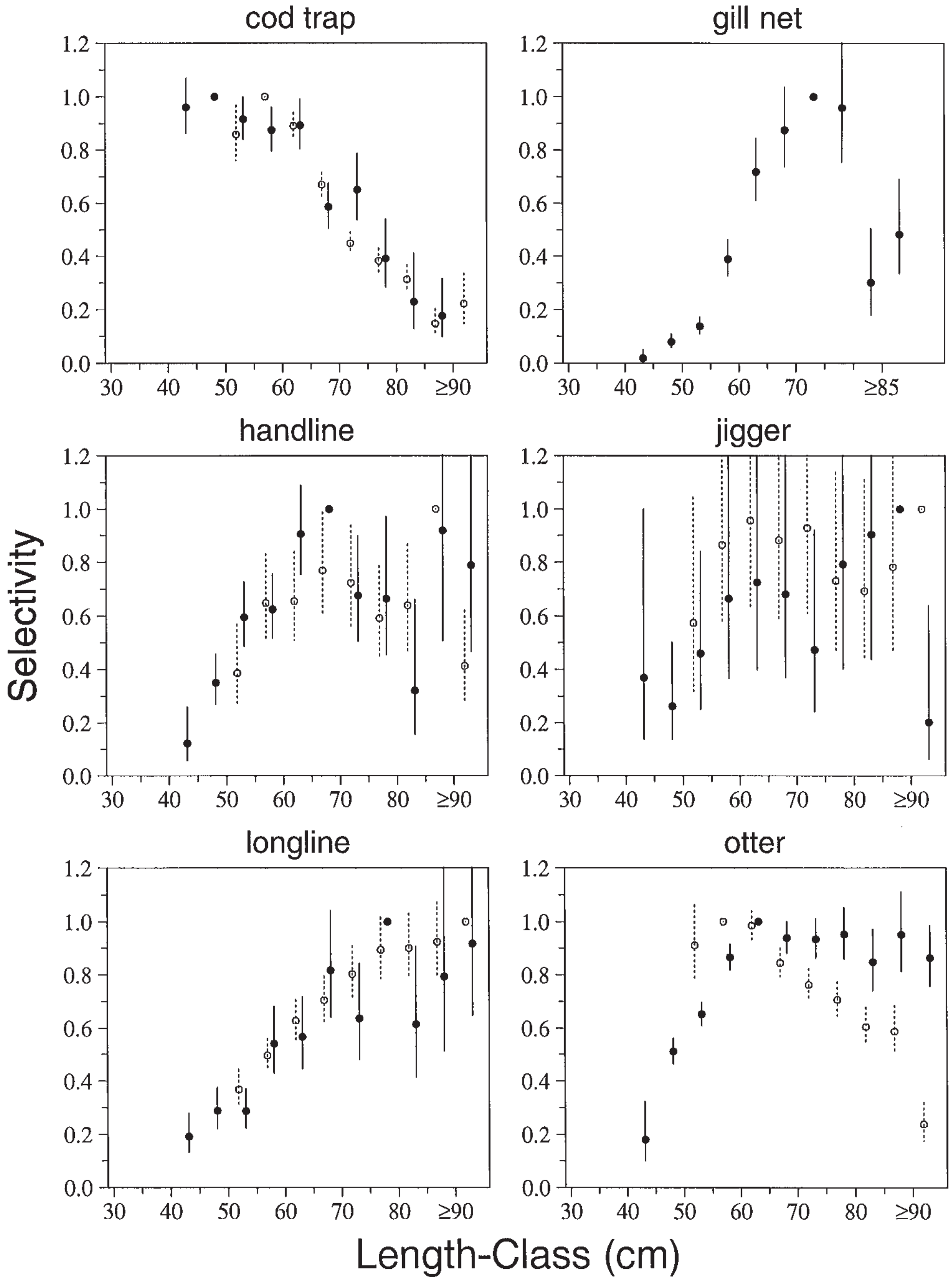
We initially analyzed the data on releases from 1954 to 1966 separately from the releases after 1977 (Table 1). We examined how the selectivity changed over time. For each of the gear types, we fit the models with separate selectivities for each time period and used a likelihood ratio test to determine if the hypothesis that they were equal could be rejected (last three columns in Table 1). The selectivity of otter trawls changed drastically from the pre-1969 data to the post-1977 data (likelihood ratio test, see Table 1); the selectivity for longer cod was less than for cod around 55 cm during the early period whereas in the latter period selectivity did not decline with increasing size (Fig. 2). During the early period most otter trawls were side, as opposed to stern, deployed. These older stern trawlers towed nets more slowly, the nets were smaller, vertical openings were lower, and smaller mesh was used. These factors evidently allowed larger cod to escape.

There was no significant decrease in the selectivity of cod at longer lengths for the post-1978 data. A linear relationship was fit to selectivity for lengths greater than 50 cm using the binomial errors assumed above and a factor for every experiment; the slope was not significant (likelihood ratio test, $\chi^2 = 1.4$, df = 1, $p = 0.094$).

There was no statistically significant difference between the selectivity of cod traps, line trawls, handlines, and jiggers between the two time periods.

In general the fits were good. There appeared to be very little evidence of overdispersion in our data; i.e., the observed variance of the data around the predicted means was usually less than that expected under the binomial assumption. A common method to adjust for overdispersion is to calculate a scale parameter to adjust the statistics, e.g., estimated standard errors (McCullagh and Nelder 1989). This scale parameter for the binomial is the square root of the deviance divided by the

Fig. 2. Estimates and standard errors of selectivity from 1954 to 1964 (open circles) and from 1979 to 1990 (solid circles) versus the length at tagging. The selectivity for each gear type is standardized so that the length-class with the maximum selectivity has selectivity equal to one. There will be no standard error associated with this selectivity. Data for fish longer than 90 cm have been pooled. For cod traps from 1979 to 1990 we combined all data over 85 cm because there were very few returns for cod longer than 85 cm. Gill-net selectivity is estimated from fish tagged after 1978 with spaghetti tags.



degrees of freedom. In our case, the scale parameter suggests that we had underdispersion, i.e., in all cases the deviance was less than the degrees of freedom (Table 1). However, the estimated capture probabilities were very small for many experiments and the asymptotic approximation used to determine underdispersion breaks down when the capture probabilities breaks are close to zero. Therefore, we do not feel that this is strong evidence of underdispersion. However, the likelihood ratio tests we used are more robust to the asymptotic assumption than are the tests for underdispersion (McCullagh and Nelder 1989).

We examined the χ^2 residuals and deviance residuals with respect to length of the fish and experiment. We examined changes of selectivity over time by plotting the residuals for each length-class and year (Fig. 3). There were some indications of slight differences in selectivity in different years, but these were not great, nor were they significant. The longer length-classes often showed all negative residuals; this was

Fig. 3. Deviance residuals for gill nets, otter trawls, longlines, and traps for the post-1978 data with respect to length and year of release.

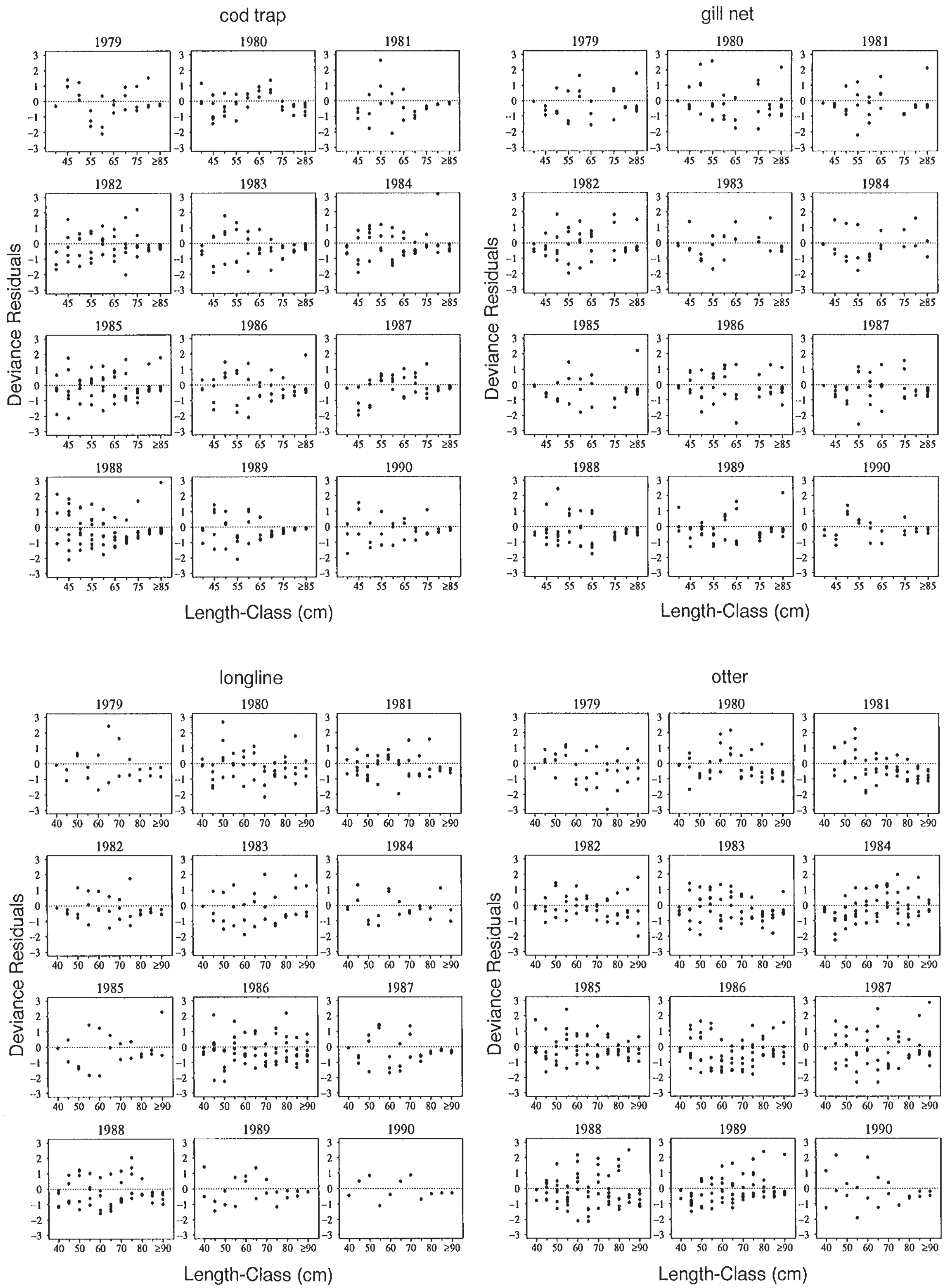
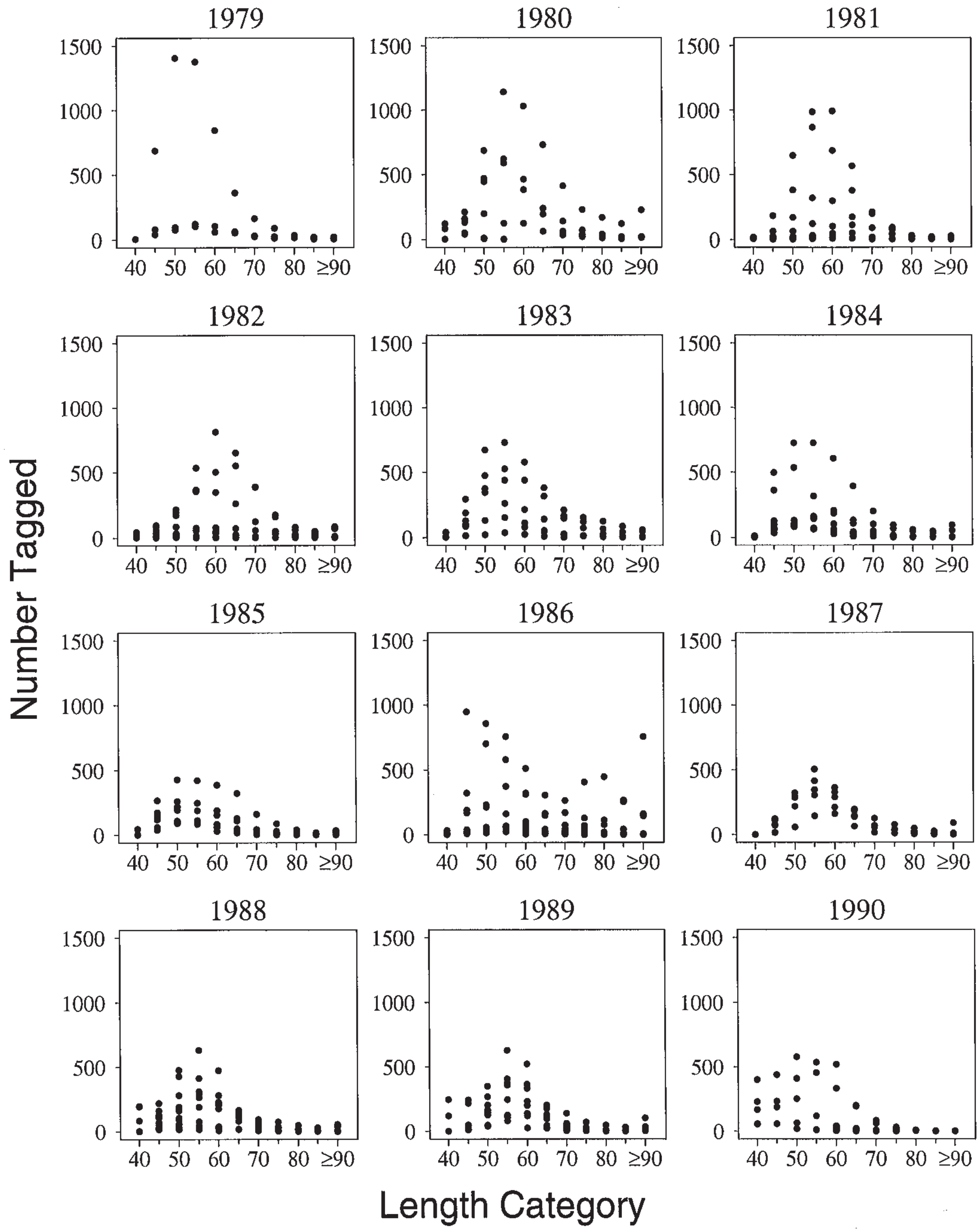


Fig. 4. Number of cod tagged and released during the period 1978–1990. Each point represents a different experiment or length-class.



usually because there were no returns in that length-class. This happened particularly in later years when there were very few longer fish available to be tagged (Fig. 4).

Robustness and violations of model assumptions

The most important limitation of our approach is that it is critically dependent upon the assumption that apart from differences in selectivity, tags are returned independently of the length of the fish. This assumption could be violated if smaller fish were discarded before they could be examined for tags or if smaller fish suffered higher mortality because of tagging.

The smallest size acceptable for plants salting fish was 45 cm, while plants processing cod for the fresh or frozen market accepted fish greater than 40 cm (Mercer and Brothers 1984). For this reason, we restricted our analysis to fish greater than 40 cm; however, we believe that the selectivity for the 40- to 45-cm length group was underestimated.

Fish will grow during the period between release and recapture. Although there is clearly substantial measurement error in the length data, it is possible to estimate the average growth during the period of release (Fig. 5). On average, the fish grew about 2 cm while at liberty and the amount of growth was not highly dependent on initial length (slope of regression of length at recapture on length at tagging = 0.98). In the range of sizes where catchability increases with length there will be a positive bias in the estimates of catchability and, likewise, where catchability decreases with length there will be a negative bias.

A limitation of our approach is that selective catch taken by one gear may change the availability of fish to be caught by other gear. This effect is minimal when the total fraction of tagged fish recovered is low; in practice one may need to limit the returns to 1 year, or even a fraction of the year. To investigate this possibility, we considered the returns from only the first 6 months after release and obtained similar results to that using a full year.

We also tried different criteria for selecting the data to analyze. We estimated the model parameters using the following selection criteria for experiments: (*i*) at least one fish was recaptured per experiment, (*ii*) recaptures occurred in at least four length categories, and (*iii*) recaptures occurred in at least six length categories. In no case were the estimates very different under these conditions.

Discussion

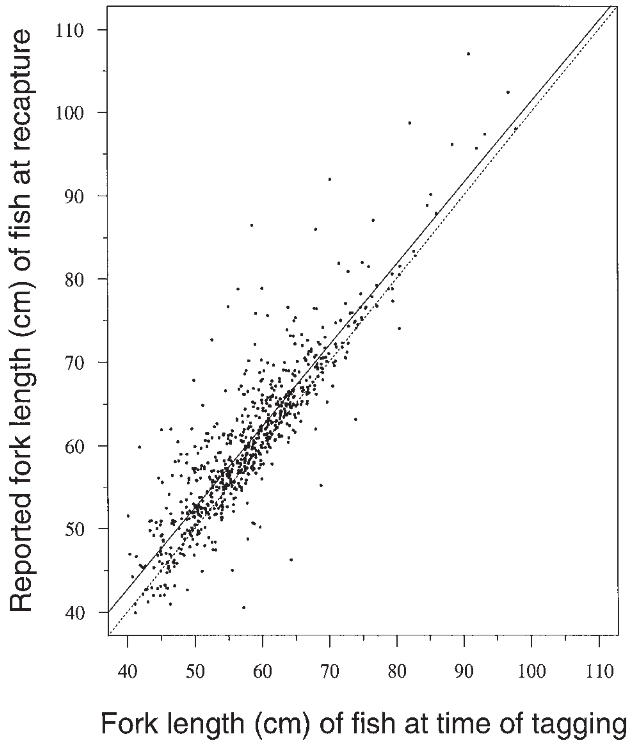
Our results show that selectivity of commercial fishing gear can be effectively estimated by combining results from many tagging experiments. Information on selectivity is crucial for the management of fish populations, and historical and ongoing tagging programs should be analyzed. For example, we detected large shifts to lower sizes in the gill-net selectivity that have occurred over the last 30 years. During this time, smaller mesh sizes were introduced in response to a reduction in the size of cod because of increased fishing pressure. Not all changes in selectivity were so simple: the functional form of otter trawl selectivity changed drastically over the same period.

We have shown that the assumption that the largest fish are much less vulnerable to otter trawls than fully vulnerable sizes is not valid in recent years. The selectivity of otter trawls in recent years in Newfoundland is almost constant with size for fish over 45 cm. This is very different from the assumptions used in Eastern Canada for many cod assessments (see Myers and Cadigan 1995*a*) in which the fishing mortality on the oldest age, e.g., 12, was assumed to be half of the average fishing mortality on ages 7–9 in each year. Myers and Cadigan (1995*a*) constructed a statistical model to test this assumption using the commercial catch-at-age data and research survey estimates of abundance and found that the best model fit was one in which the fishing mortality on the oldest ages did not decrease. Their statistical test was relatively weak and depended upon the assumption that the research survey selectivities were constant for older ages, an assumption that could not be tested.

Our analysis of the post-1979 otter trawl data is consistent with estimates of selectivity from experiments using paired tows, covered cod ends, and trouser trawls (reviewed by Halliday and White 1989). Halliday and White (1989) estimated that capture probability does not decrease at length for these experiments, and their selectivity was similar to the ones we estimated. This suggests that avoidance by cod over 40 cm of modern, fast-moving stern trawls does not depend upon length.

Our results differed from those obtained using most models of selectivity (Fryer 1992; Suuronen and Miller 1992; Millar 1992) and tagging (Cormack and Skalski 1992) in that we found no evidence of overdispersion. We believe that the

Fig. 5. The estimated length at recovery during the 1st year after release versus the length at release for the 1978–1990 data for fish greater than 40 cm. The solid line is the least squares regression ($y = 3.64 + 0.98x$, $R^2 = 0.80$). The one-to-one line is dotted.



reason for this is that it was rare for more than one tagged fish from a given experiment to be caught in the same deployment of the gear. The tagging usually took more than a week, so that more than one school of fish was tagged. This differs from selectivity experiments in which overdispersion can be created by the existence of individual schools of fish that the trawl encounters, or tagging experiments from hatcheries in which all releases in a given year may have the same tag type.

The chief limitation of our analysis is the questionable reliability of the estimates at smaller lengths. In particular, smaller fish were often discarded and these fish would not be examined for tags. Furthermore, illegal small mesh liners were sometimes used in trawls (Palmer and Sinclair 1996), and it is unlikely that fishermen would have returned small fish in these cases. We thus must view the estimates of selectivity below 45 cm as lower estimates.

Use of improved tagging models for assessment of marine fish populations

Tagging studies can be used to estimate gear selectivity by size, identify substocks and movement patterns, quantify movement rates, and estimate total mortality rate and exploitation rate by size group and substock. Tagging studies can be thought of as comprising two types: designed studies and post-hoc analyses. In the former, the investigator plans the study to estimate certain parameters. In the latter, the investigator attempts to make inferences from an existing tag data base.

Best results are obtained when the investigator has control over the design of the tagging programs. In this case, the investigator may wish to release fish in multiple years to make use of Brownie models (Brownie et al. 1985) to estimate total mortality. If a catch sampling program, or a variable reward tagging study, is implemented it is possible to estimate tag reporting rate, which, in turn, makes it possible to estimate exploitation rates (Pollock et al. 1991). It may also be necessary to estimate tag shedding rates by a double tagging study (see Barrowman and Myers 1996) and to estimate tag-induced mortality with cage or pen holding studies.

We have found that much useful information can be gained from the post-hoc analysis of existing tag data bases. In the present case, we were able to estimate selectivity of various gear types. This is particularly important because it sheds light on a controversy that arose in the tuning of the virtual population analyses for these stocks: whether the partial recruitment (or selectivity) vector should be flat topped or dome shaped. The change in trawl selectivity over time noted in our analysis implies that it is inappropriate to use models that require the assumption that selectivity is constant over time. In addition, we have shown that total mortality rates could be estimated for subcomponents of these populations (Myers et al. 1995, 1997*b*). A comprehensive analysis of the movement patterns and stock structure remains to be done.

We conclude that use of tagging data deserves far greater consideration than it is given at present. All assessment methods, including virtual population analysis (Myers and Cadigan 1995*a*), are subject to a variety of biases. Analysis of tagging data can be used to provide independent estimates of mortality and population size, and to provide necessary auxiliary information such as on gear selectivity.

There are clear implications of our analysis for the management of the cod fishery. Myers et al. (1997*a*) recently argued that the principal reason for the collapse of cod in Eastern Canada was high fishing mortality on juvenile cod, which includes both the directed fishery and discarding. If their hypothesis is correct, then elimination of fishing gear that selects mainly small cod, e.g., cod traps as traditionally deployed and otter trawls with liners, should be a priority. The implications of fishing with different mixtures of fishing gear can now be explored using yield per recruit and egg per recruit analyses. This should be a fundamental part of most stock assessments and should be carried out for Canadian cod fisheries in particular.

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Appendix

Estimation in SAS

This appendix demonstrates how to fit the proposed model to data with a single gear type. In the SAS data step, a data set is created with four variables per observation: the length-class (denoted length), an experiment identity (denoted exp), the number of fish released (denoted released), and the number returned (denoted return), respectively.

The SAS code for fitting the model is

```
Proc genmod;
    class exp length;
    model return/released = exp length / dist
                                  = binomial link = log;
```

If a continuous model were fit, then length would not be a class variable. For a normal selectivity model, one would want to fit length and length squared. See Millar and Holst (1996) for directions on fitting continuous models.