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Age Dependent Tag Recovery Analyses of Pacific Halibut Data

by

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Contents

ABSTRACT

We generalize the Brownie 3-age class model for band-recovery data to one allowing for 8-age classes, and apply it to the Pacific halibut tagging data collected by the International Pacific Halibut Commission from 1979-1986 for areas 2B, 2C and 3A. Because of the small sample size, the data collected from three areas were combined together and analyzed as though from a single population. For the halibut data, age information was not recorded at tagging, but an age-length key was available. The age-length was used to form 8 size classes that approximately corresponded to 1-year age classes. The structure of the tag recovery models is generally based on three types of parameters: the annual survival rates, the direct recovery rates (for newly tagged fish) and the indirect recovery rates (for previously tagged fish). We fitted a variety of models based on allowing differing degrees of age and calendar year (at recovery) dependence for all three types of parameters.

We found that the direct recovery rates were low and variable and had to be viewed as nuisance parameters. To simplify the modeling effort and increase precision of estimates we only allowed age dependence of direct recovery rates even though that introduced some lack of fit into our models. We found that indirect recovery rates are strongly dependent on calendar year (at recovery) and age class. These rates were found to increase in an approximately linear manner with age class for the range of ages we considered (6 - >13). We found that survival rates are also strongly age and calendar year (at recovery) dependent. Pacific halibut of age 6 have an annual survival rate of about 56% on average. This rises to almost 78% for age 7 fish and then drops to approximately 70% for fish at age 8, 9, or 10. Fish of ages 11, 12, or >13 have approximately constant survival according to our model selection procedure. Survival estimates are likely to be biased low to some unknown extent due to heterogeneity of capture and survival rates and some possible tag loss. The goodness of fit of our models was good except in the direct (or first year) recovery cells which is not likely to be of practical concern. We did have some difficulty fitting some models iteratively due to the large number of parameters involved. However, the consistency of our estimates across a wide class of models suggest our results are very reliable.

We conjecture that the reporting rate of tags is in the range of 25 - 40% based on assuming that a natural mortality rate of about 0.2 is reasonable for the older age classes examined. We could detect no clear trend in natural mortality rate with age but data limitations suggest caution in interpreting our results here. We suggest the need for special studies to (1) evaluate the bias introduced from tag induced mortality, (2) evaluate the bias introduced by tag loss, (3) estimate reporting rate and (4) explore the need for increasing reward values on tag returns to increase the reporting rate.

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INTRODUCTION

Capture-recapture methods have been widely used in the estimation of demographic parameters of fish and wildlife populations. The basic model which allows estimation of population parameters for an open population is the Jolly-Seber model (Jolly 1965, Seber 1965). The Jolly-Seber model makes the assumption that all animals in the population have the same survival and capture probabilities for each sampling period. This assumption may be true for some species of animals, but is more questionable for fish where the survival rates and recovery rates may depend on size, age, sex, or other factors. Pollock (1981) generalized the Jolly-Seber model to allow for age-dependence of survival and capture probabilities. See also Pollock et al. (1990), Pollock (1991), and Lebreton et al. (1992) for recent general reviews of capture-recapture models.

Brownie et al. (1985) developed a basically equivalent model for tag recovery data where 3 age-classes are identified at tagging and survival and recovery probabilities are allowed to depend on all 3 age classes. In order to examine the relationship between survival and age in more detail, we need models that are more general than those in Brownie et al. (1985). In this paper we generalize the 3-age class model to one allowing for 8-age classes. We also examine a series of reduced-parameter versions of the most general model which make increasingly restrictive assumptions about the effect of calendar year and age on survival and recovery rates. Hypotheses about the effects of year or age on survival and recover rates are tested by comparing different models. These models are applied to some tag-recovery data of Pacific halibut (*Hippoglossus stenolepis*) provided by the International Pacific Halibut Commission (IPHC). We consider separate estimation of fishing and natural mortality rate parameters for a range of hypothetical reporting rates. We also consider indirect methods of estimating the reporting rate. We conclude with a discussion of our estimates and possible future studies.

This work was completed in 1992 but publication has been delayed. If the work were being done now we would use the non-mixing model described in Hoenig et al. (1998a). Also we would possibly use fishing effort as a covariate as described in Hoenig et al. (1998b). However, we do not believe these alternate analyses would change our conclusions substantially.

METHODS

The Tag Recapture Data

Over the past 60 years the IPHC has carried out an extensive tagging program. The tagging has usually been opportunistic during the course of setline or trawl surveys conducted for other purposes. Tag returns have typically been from commercial fishermen although recently there have been some returns from research cruises. Sport caught halibut tag returns are insignificant.

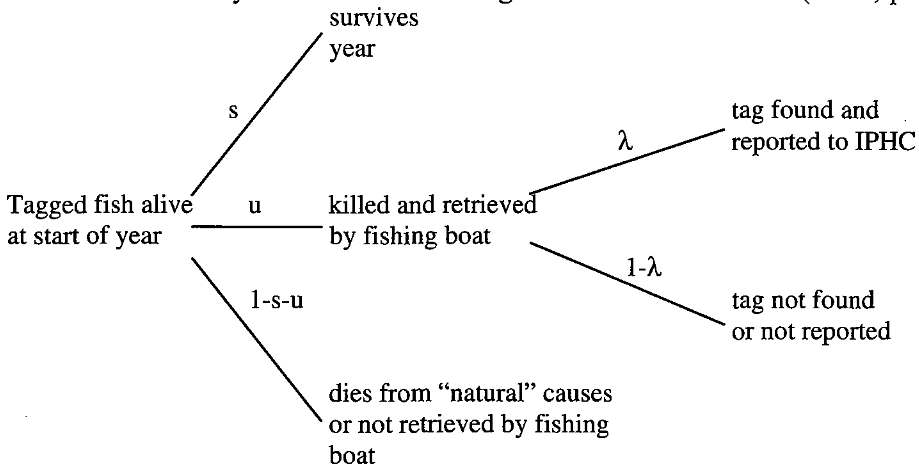
There have been two primary objectives of the tagging studies. The first is to get a clear idea of migration patterns of the halibut while the second is to estimate natural and fishing mortality. R. Deriso carried out some analyses to estimate migration rates but a lot more could be done (Quinn et al. 1985). Myhre (1967) obtained mortality estimates based on a regression model by Gulland (1963).

The halibut tag data were collected by IPHC personnel from 1979 to 1986 in Areas 2B, 2C and 3A. The data collected from those three areas were treated as from one population because of small sample sizes. In order to estimate age-specific survival rates from these data it is necessary to group fish at the time of release into 1- year age classes, except for the final class which contains all older fish. For the halibut data, age information is not available but the length was recorded for each tagged fish at the time of release. In addition to the length information, an age-length key was provided by Pat Sullivan (IPHC) for Pacific halibut (Table 1). The age-length key was used to form 8 size classes that best corresponded to 1-year classes in the following manner.

The age 8, 9, 10, 11 and 12 from the Table 1 on the right are equivalent to size class 3, 4, 5, 6, and 7 respectively shown on the left, and ages greater than 13 were grouped into size class 8. Boundaries for these size classes were the values midway between the mean lengths for age 8 to 13. As the recovery data included a substantial number of fish less than 86 cm in length, two classes were created to represent 6 and 7 year old fish assuming a width of 11 cm for each of the corresponding size classes 1 and 2. Data of fish less than 64 cm in length were omitted from analysis because of the greater uncertainty involved in grouping these into age classes on the basis of size. Each tagged fish greater than 64 cm at release was assigned to one of these 8 age classes, and tag-recovery data were summarized by constructing 8 data arrays, one for each age-class. Each of these 8 data arrays is a recovery matrix (see example on Brownie et al. 1985, p. 118) containing numbers released and recovered for the years 1979 to 1986. For completeness these data arrays are included in Appendix I.

Model Structure and Assumptions

We develop and refine survival and recovery rate estimates based on models developed by Brownie et al. (1985). Let us consider the possible fates of a tagged fish at the start of the year based on the diagrams in Brownie et al. (1985, p.14):



where s = the annual survival rate (finite) or the probability of surviving the year.

u = the exploitation rate (finite) or the probability of being harvested by the fishing fleet

v = 1 - s - u = the natural mortality rate (finite) or the probability of dying from natural causes (if we can assume that all fish killed are retrieved by the fishing fleet).

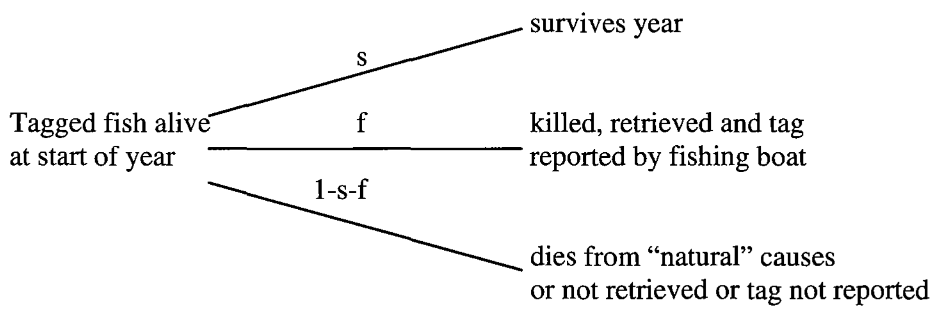
λ = The tag reporting rate, the probability that a tag will be found and reported to the IPHC given that the fish has been harvested.

Table 1. The size class age class classification of Pacific halibut used in tag recovery analysis constructed from an age length key provided by IPHC.

Age class[1]	Length (cm)	Width (cm)	Actual age[2]
1	64-74	11	6
2	75-85	11	7
3	86-95	10	8
4	96-104	9	9
5	105-113	9	10
6	114-121	8	11
7	122-128	7	12
8	≥129		≥13

[1]We used only 8 age classes due to data limitations.
[2]Age-length key provided only started with age 8. We extrapolated back to age 6 to better use the data available.

Note that the type of data we analyze supplies information directly about only those fish which are harvested and their tags reported. Therefore, the product f = λu, the tag recovery rate, is estimable but the component rates λ and u are not estimable without additional information on reporting rate. A modified diagram is as follows:



There are numerous assumptions involved in making inferences from tagging models which are based on Brownie et al. (1985, p. 6)

(1) The sample is representative of the target population.

(2) There is no tag loss.

(3) Survival rates are not influenced by the tagging process itself.

(4) The year of recovery, size at release, location and other important information is correctly tabulated.

(5) The fate of each tagged fish is independent of the fate of all other tagged fish.

(6) All tagged fish within an identifiable class (size, age, sex, ..., etc.) have the same annual survival and recovery rate.

In addition to the assumptions above, we also assume that

(7) The halibut of size class i will increase its length to the size class i + 1 after one year.

Any violation of the assumptions listed above may cause bias in the estimation of survival and recovery rates. Pollock and Raveling (1982) and Nichols et al. (1982) discussed the bias caused by failures (1) to (6). We discuss possible biases due to violation of all assumptions later in this article, including assumptions (7) which has not been discussed elsewhere.

The models used in the analysis of the halibut data are extensions to an 8 age class situation of the models developed by Brownie et al. (1985, chapter 4) for analysis of tag-recovery data for a 3-age class situation. We emphasize that the structure of the tag recovery models is generally based on two types of parameters: the annual survival rate and the annual recovery rate (which are both estimable). In addition, the recovery rates are allowed to differ for newly tagged and previously released fish, because the newly tagged fish may not be so readily available for recapture. These parameters may vary by year or by age class. Here we investigate a series of year or age-specific assumptions for the survival and recovery rates of halibut. Figure 1 outlines the models discussed in the article. The most general model (Model 0) is discussed first, followed by a series of more restrictive models with reduced numbers of parameters.

Model 0 (the so called null model) assumes the survival rate (s_j^i), indirect recovery rate (f_j^i), and direct recovery rate (f_j^{i*}) are both year and age specific where s_j^i denotes the survival rate for age class i in the jth year; f_j^i denotes the indirect recovery rate (i.e. the recovery rate for previously tagged fish) for age class i in the jth year; f_j^{i*} denotes the direct recovery rate (i.e. the recovery rate for newly tagged fish) for age class i in the jth year. Based on these assumptions, the model structure is expressed in terms of the multinomial cell probabilities (see Brownie et al. 1985, p. 119). There are 162 identifiable parameters in Model 0, and the Maximum

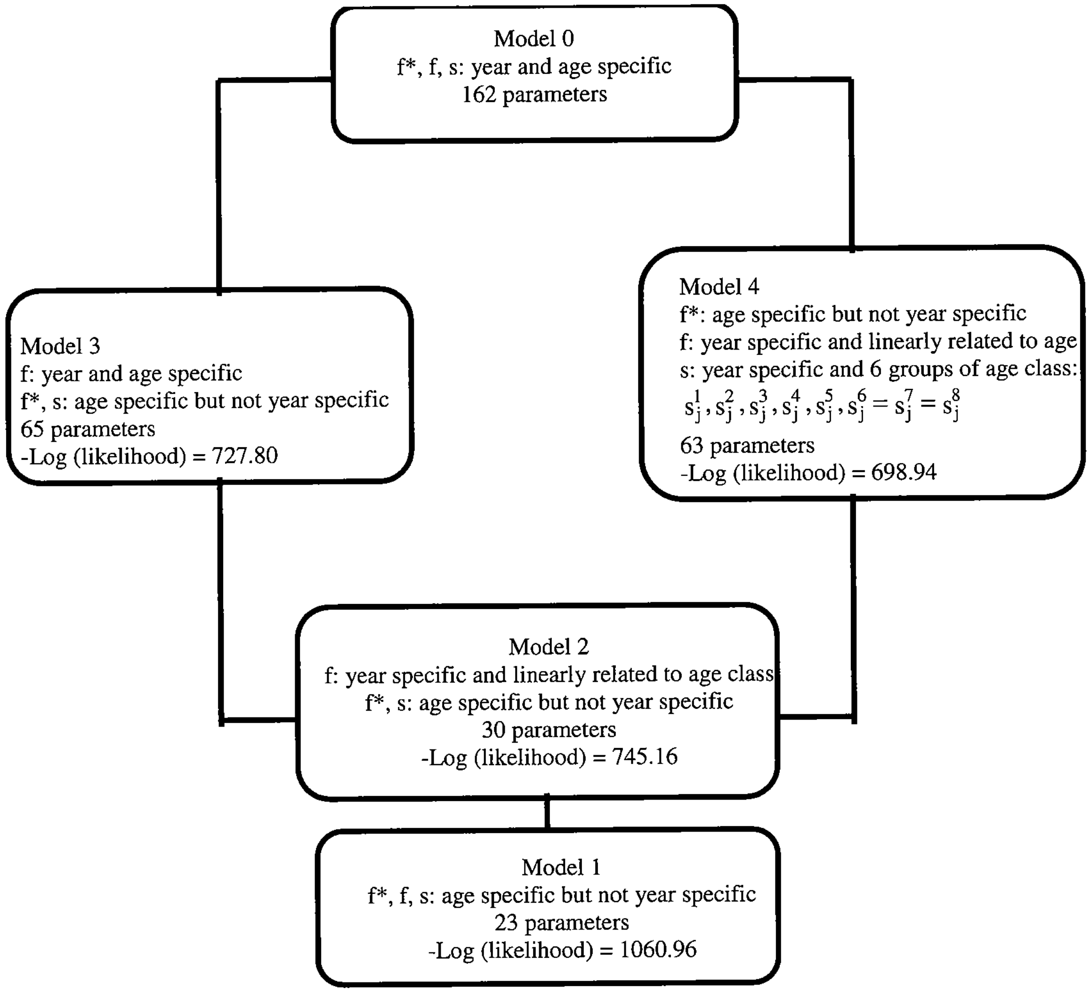


Figure 1. Outline of models discussed.

Likelihood Estimates (MLE's) can be expressed explicitly.

Model 1 is a restriction of Model 0 with age dependence but no year dependence for the survival rates, indirect recovery rates and direct recovery rates. There are 23 parameters, and their MLE's do not have an explicit algebraic form.

Model 2 is a generalization of Model 1 and assumes the relationship between the year-specific indirect recovery rate and age class is linear where $f_j^i = \beta_{0j} + \beta_{1j} xi$. Survival and direct recovery rates are age specific but not calendar year dependent. Under these assumptions there are 30 parameters.

Model 3 is a generalization of Model 2. It allows the indirect recovery rates to be both year and age dependent, but not linearly so. Survival rates and direct recovery rates are age specific only. Under the assumptions there are 65 parameters.

Thus Model 2 is a reduced version of Model 3 and has 30 parameters only (compared to 65 parameters for Model 3).

Models 1, 2, and 3 form a series of increasingly general models which allow different assumptions about the effect of age on recovery rates while assuming survival rates to be age dependent but independent of year. The tests between these models focus on the relationship between recovery rates and age (see Figure 1). A fourth model is used to investigate the relationship between survival rates and the age classes, while allowing calendar year specificity of survival and indirect recovery rates.

Model 4 allows us to model the year dependent effect of survival rates and indirect recovery rates simultaneously. In the model we assume that the survival rates are year dependent and are related to a restructured grouping of ages; the direct recovery rates depend on age but not on year; and indirect recovery rates are a linear function of age class in each year. Six groups of age classes (age class 1, age class 2, age class 3, age class 4, age class 5 and age class 6-8) are depicted in the model. There are 63 identifiable parameters in this model.

Model 4 can thus be viewed as an alternative generalization to Model 2 that is used to explore survival as an year and age dependent process.

The MLE's of the parameters of all the models described above do not have an explicit form, except for those in Model 0. The numerical maximum likelihood estimates for survival rate, indirect recovery rate and direct recovery rate were obtained using SAS PROC NLIN METHOD = DUD (version 5) (SAS 1985) as outlined in Burnham (1989), and also using the program SURVIV (White 1983) on an IBM personal computer. The differences in the models above are due to changes in the assumptions about the survival rates or the indirect recovery rates. Likelihood Ratio Tests and the Akaike Information Criterion (Akaike 1971, 1974) were used for testing between models.

Separation of Fishing and Natural Mortality Rates

Earlier, we emphasized that it is possible to estimate annual survival rate (s) and recovery (f) from a multi-year tagging study. Pollock et al. (1991) developed methodology for separating natural and fishing mortality when an estimate of reporting rate (λ) is available. Here we present their important equations modified slightly because we do not separate solicited and reported tags.

The estimate of exploitation rate (u) is

$$\hat{u} = \hat{f} / \hat{\lambda}$$

and the estimates of natural mortality rate (v) is

$$\hat{v} = 1 - \hat{S} - \hat{u}$$

These are both finite rates. Assuming that Pacific halibut are subject to a type I fishery, (i.e. very short so fishing and natural mortality are not occurring at the same time) we can also estimate instantaneous rates as below. The total instantaneous mortality rate is

$$\hat{Z} = -\log_e(\hat{S})$$

the instantaneous fishing mortality rate is

$$\hat{F} = -\log_e(1-\hat{u})$$

and the instantaneous natural mortality rate is

$$\hat{M} = \hat{Z} - \hat{F}$$

Estimation of Reporting Rate

Ideally reporting rate should be estimated from either a port sampling scheme or a reward tag study (Pollock et al. 1991). For Pacific halibut, however, those special studies have not been done. Therefore we must use an indirect (perhaps circular) argument to estimate reporting rate. P. Sullivan of IPHC (personal communication)[1] indicated that in many of the IPHC modeling activities they use M = 0.2. We looked at our estimates of M over age classes for a range of reporting rates and determined which reporting rate gave M's around 0.2 for all our age classes.

RESULTS

Survival and Recovery Rate Estimates

Model Selection and Goodness of Fit

We considered a variety of models to estimate survival and recovery rates (Figure 1). The most general model (Model 0) allows survival rates and both direct and indirect recovery rates to be both age and year specific. Model 0 has 162 estimable parameters. The most restrictive model (Model 1) only allows survival rates and both direct and indirect recovery rates to be age specific. Model 1 has only 23 parameters that are estimable. In Appendix II all the parameter estimates for all the models are presented.

Before we discuss the survival and recovery rates estimates themselves let us consider the difficult task of model selection. In order to choose a model which has sufficient parameters to provide an adequate description of the data, but not so many as to make estimation inefficient, we examined several sequences of hierarchical models and compared them using likelihood ratio tests, the AIC criteria and consistency of important parameter estimates. Table 2 provides a summary of the likelihood ratio test and AIC results for the model tests.

First let us consider the modeling of the first year (or direct) recovery rates. Because of the timing of the fishery, soon after tagging and perhaps due to behavioral response of the fish to tagging we found that direct recovery rates were low, variable and difficult to interpret. We decided to view these parameters as nuisance parameters because they are difficult to interpret and not very useful biologically. We restricted

[1]Sullivan, P. J. International Pacific Halibut Commission. P.O. Box 95009, Seattle, WA 98145-2009.

Table 2. Comparison of models.

Log-likelihoods and AIC			
Model	**No. of Parameters**	**Log-likelihood of SURVIV**	**AIC[2]**
Model 1	23	-1060.96	2167.92
Model 2	30	-745.16	1550.31
Model 3	65	-727.80[1]	1585.60
Model 4	63	-698.94[1]	1523.88
Model 0	162		

Likelihood ratio tests		
Models	**-2Log-likelihood ratio**	**D.F.**
Model 1 vs. 2	631.61 **	7
Model 2 vs. 3	34.72	35
Model 2 vs. 4	92.44 **	33

[1]The value for this model was estimated from NLIN. All other log-likelihoods are from SURVIV.
[2]AIC: Akaike Information Criterion = 2(No. of parameters - Log-likelihood)

ourselves to models where the direct recovery rates were age dependent but constant between years. This was to reduce the number of parameters to estimate in the hope of increasing precision of the remaining estimates. We note that checking for goodness of fit we found all our models fit quite well except for the first year of tagging. We were encouraged by this because any bias due to lack of fit is likely to mainly influence the direct recovery estimates which are not very important anyway.

Once we had decided on having direct recovery rates age dependent only we had to consider how to model survival and indirect recovery rate parameters. These parameter estimates are very important and we consider a wide variety of models. Examination of Tables 3 and 4 show that both survival and indirect recovery rates under Model 0 (the most general model) are strongly age and year dependent. First we considered how to model the indirect recovery rates. Table 4 shows strong evidence of an increase in recovery rate with age class. This lead to the models 2 and 3 which compared fitting a general age and year dependent model (Model 3) against a restricted model where recovery rate was linearly related to age in each year class (Model 2). The results of the AIC test suggest it is reasonable to model indirect recovery rates as

Table 3. Survival rate estimates under Model 0 classified by age class and calendar year. Estimates are expressed as percentages and rounded to one decimal place.

	Age Class (Age)								
Year	**1 (6)**	**2 (7)**	**3 (8)**	**4 (9)**	**5 (10)**	**6 (11)**	**7 (12)**	**8 (≥ 13)**	**Mean**
1979	55.8	68.2	52.6	34.1	57.0	48.1	47.0	72.9	54.5
1980	51.1	74.8	54.5	100.0	94.4	66.2	56.9	51.8	68.7
1981	38.4	59.4	56.4	66.2	41.1	45.1	47.2	40.6	49.3
1982	84.2	100.0	68.8	72.6	53.5	66.8	56.8	63.2	70.7
1983	56.7	82.4	83.4	77.9	82.2	74.5	72.0	71.8	75.1
1984	67.3	84.6	80.0	72.6	89.1	71.5	75.4	70.8	76.4
Mean	58.9	78.3	66.0	70.6	69.7	62.0	59.2	61.8	65.8

Table 4. Recovery rate estimates for previously tagged fish under Model 0 classified by age class and calendar year. Estimates are expressed as percentages and rounded to two decimal places.

	Age class (Age)*							
Year	**2 (7)**	**3 (8)**	**4 (9)**	**5 (10)**	**6 (11)**	**7 (12)**	**8 (≥ 13)**	**Mean**
1979	0.71	2.84	5.20	3.73	2.70	5.53	3.56	3.90
1980	0.63	2.09	3.43	2.32	4.28	4.31	4.01	3.01
1981	1.33	1.56	1.65	3.67	3.98	5.50	7.59	3.61
1982	4.34	1.09	3.06	3.88	5.75	4.52	5.59	4.03
1983	1.35	2.86	4.11	5.13	5.69	8.22	7.48	4.98
1984	1.48	2.75	4.58	5.02	5.72	7.05	8.68	5.04
Mean	1.64	2.20	3.67	3.96	5.19	5.86	6.15	4.10

*It is not possible to estimate age class 1 or age 6 indirect recovery rates under this model.

linearly related to age in each class, while the likelihood ratio test indicates there would be no significant loss of information in doing so.

Now that we had established the structure of the models for direct and indirect recovery rates (linearly related to age in each year class separately) we began looking in more detail at how to model the survival rate parameters. Examination of Table 3 shows that survival rates are strongly year dependent and strongly age dependent under Model 0. One possible approach is to consider a model that allows age dependence. This gave rise to Model 4. A comparison of estimates indicates that Model 4 appears to be close to the age dependent structure shown in Model 0. If we look at the arithmetic mean survival rates in Model 0 there is a strong suggestion that age classes 6 - 8 have similar values while age class 5 has a much higher value. Considering age classes 6 - 8 constant in survival rate is the structure of Model 4. Therefore, when we consider age dependence later, we will use Model 4 as the basis for our discussions.

Survival Rate Estimates

In Tables 3 and 5 we consider the survival rate estimates for Model 0 and Model 4. The results are very comparable for both models. There is very strong year dependence. For example the average survival rate in 1981 is about 0.49 (or 0.48) compared to a much higher survival rate of 0.75 (or 0.77) in 1983. There is also very strong age dependence in the survival rates. Again the results from the two models

Table 5. Survival rate estimates under Model 4 classified by age class and calendar year. Estimates are expressed as percentages and rounded to one decimal place.

	Age Class								
Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**Mean**
1979	51.7	77.3	59.6	42.6	66.6	51.1	51.1	51.1	56.4
1980	49.9	82.5	69.3	100.0	100.0	66.1	66.1	66.1	75.0
1981	39.5	57.8	48.1	59.9	45.1	45.4	45.4	45.4	48.3
1982	84.5	98.3	75.9	78.8	60.5	53.7	53.7	53.7	69.9
1983	56.0	81.3	91.5	78.7	76.5	78.6	78.6	78.6	77.5
1984	54.0	72.2	80.7	64.6	73.6	66.4	66.4	66.4	68.0
Mean	55.9	78.2	70.8	70.8	70.4	60.2	60.2	60.2	65.8

Table 6. Recovery rate estimates for previously tagged fish under Model 4 classified by age class and calendar year. Estimates are expressed as percentages and rounded to two decimal places.

	Age Class							
Year	2	3	4	5	6	7	8	Mean
1979	1.45	2.40	3.34	4.28	5.23	6.17	7.11	4.28
1980	1.02	1.70	2.38	3.07	3.75	4.43	5.11	3.07
1981	0.81	1.77	2.73	3.69	4.65	5.61	6.57	3.69
1982	0.42	1.48	2.53	3.59	4.64	5.70	6.76	3.59
1983	1.77	2.82	3.87	4.91	5.96	7.01	8.06	4.92
1984	1.98	3.22	4.46	5.70	6.94	8.18	9.42	5.70
Mean	1.24	2.23	3.21	4.21	5.20	6.18	7.17	4.21

are very comparable with the interesting exception of age class 3 where Model 0 given an average of 0.55 compared to 0.71 for Model 4. We believe that the Model 4 result is more reasonable biologically, but do not have an explanation of the difference. We note that there is less data in the younger age classes and that Model 0 has many more parameters so perhaps this estimate is unusual due just to chance.

In Table 7 we decided to consider the age-dependent survival estimates of all the models fitted. Note that all the estimates show very similar patterns. Consider in particular Model 1, Model 4 and Model 0. All three of these models show that the

Table 7. Age-dependent survival rate estimates for a variety of different models.

	Age Class							
Model	1	2	3	4	5	6	7	8
1	56.5	78.0	71.3	74.3	72.5	66.8	62.6	64.8
2	53.5	79.3	74.4	64.5	67.4	60.7	60.9	61.3
3	56.0	77.7	68.8	69.8	67.7	60.8	59.2	61.0
4	55.9	78.2	70.8	70.8	70.4	60.2	60.2	60.2
0	58.9	78.3	66.0	70.6	69.7	62.0	59.2	61.8

Table 8. Age-dependent indirect recovery rate estimates for a variety of different models.

	Age Class						
Model	2	3	4	5	6	7	8
1	1.23	2.90	4.56	5.21	6.48	7.40	8.85
2	1.36	2.49	3.62	4.76	5.89	7.03	8.16
3	1.09	2.63	4.17	4.65	6.17	7.09	7.96
4	1.24	2.23	3.21	4.21	5.20	6.18	7.17
0	1.64	2.20	3.67	3.96	5.19	5.86	6.15

survival rate is low for age class 1, rises markedly for age class 2, declines somewhat for age classes 3, 4 and 5, and then drops markedly for age classes 6, 7, and 8. Model 1 and Model 0 both suggest constant survival for ages classes 6 to 8 which is the structure assumed in Model. 4

Indirect Recovery Rate Estimates

In Tables 4 and 6 we consider the indirect recovery rate estimates for Model 0 and Model 4. The trends are very comparable in both models although the values tend to be higher overall for Model 4. There is a very strong year dependence. There is also very strong age dependence. In fact, as we discussed earlier we have fitted recovery rate as a linear function of age class for each year class separately. This is not surprising because fishing for Pacific halibut is known to be very size (and hence age) selective.

In Table 8 we consider the age-specific indirect recovery rate estimates for all the models fitted. While the trends are very similar there are differences. Model 1 gives the highest recovery rates at the older ages, Model 4 gives medium recovery rates at the older ages, and Model 0 gives the lowest recovery rates at the older ages. We tend to feel most comfortable with estimates under Model 1 and Model 4 because of their higher precision relative to Model 0.

Recovery rate estimates may be viewed as an index to fishing pressure. In the next section we consider how they may be converted to absolute exploitation rates (assuming we have an estimate of reporting rate).

Estimates of Fishing and Natural Mortality Rates

In Tables 9 - 11 we present estimates of fishing and natural mortality for a range of reporting rates based on Models 1, 4, and 0 respectively. In each table finite and instantaneous rates are presented for each age class. We believe the reader should concentrate on the Model 1 estimates because they have the best precision (but they might be a little more biased). Plausible estimates for F and M arise for reporting rates of $\lambda = 0.40$ or 0.33. If we use $\lambda = 0.33$ we obtain estimates of M which are around 0.2 and are approximately constant over the age classes examined. Of course for age class 1 the natural mortality rate is much higher.

In Tables 12 - 14 we present estimates of fishing mortality if we assume Z is calculated from the survival rate and M is equal to the nominal value of 0.2. The estimates do generally increase as one would expect. However, the increase is not as smooth as one might expect. This is because either M is not constant over age or because the lack of precision of the estimates of Z is causing variations which causes the fishing mortality estimates to not increase smoothly.

Reporting Rate Estimates

If we assume Model 1 as a basis and a natural mortality rate M = 0.2 as reasonable for higher age classes the results of Table 9 suggest a λ of 0.40 - 0.33.

If we assume Model 4 as a basis and again a natural mortality M = 0.2 as reasonable for higher age classes the results of Table 10 suggest λ of 0.33 - 0.25.

If we assume Model 0 as a basis and again a natural mortality M = 0.2 as reasonable the results of Table 11 suggest λ of about 0.25.

Table 9. Natural and fishing mortality rates (finite and instantaneous) for a range of possible reporting rates. Model 1 estimates are used as a basis of the calculations.

	Age Class						
Parameter	**2**	**3**	**4**	**5**	**6**	**7**	**8**
S	0.780	0.713	0.743	0.725	0.668	0.626	0.648
1-S	0.220	0.287	0.257	0.275	0.332	0.374	0.352
Z	0.249	0.338	0.297	0.322	0.404	0.468	0.434
			λ=100%				
u	0.012	0.029	0.046	0.052	0.065	0.074	0.089
v	0.208	0.258	0.211	0.223	0.267	0.300	0.263
F	0.012	0.029	0.047	0.053	0.067	0.077	0.093
M	0.237	0.309	0.250	0.269	0.337	0.391	0.341
			λ=50%				
u	0.025	0.058	0.091	0.104	0.130	0.148	0.177
v	0.195	0.229	0.166	0.171	0.202	0.226	0.175
F	0.025	0.060	0.096	0.110	0.139	0.160	0.195
M	0.224	0.278	0.201	0.212	0.265	0.308	0.239
			λ=40%				
u	0.031	0.073	0.114	0.130	0.162	0.185	0.221
v	0.189	0.214	0.143	0.145	0.170	0.189	0.131
F	0.031	0.075	0.121	0.140	0.177	0.205	0.250
M	0.217	0.263	0.176	0.182	0.227	0.264	0.184
			λ=33%				
u	0.037	0.087	0.137	0.156	0.194	0.222	0.266
v	0.183	0.200	0.120	0.119	0.138	0.152	0.087
F	0.038	0.091	0.147	0.170	0.216	0.251	0.309
M	0.211	0.247	0.150	0.152	0.187	0.217	0.125
			λ=25%				
u	0.049	0.116	0.182	0.208	0.259	0.296	0.354
v	0.171	0.171	0.075	0.067	0.037	0.078	0
F	0.051	0.123	0.201	0.234	0.300	0.351	0.434
M	0.198	0.215	0.096	0.088	0.104	0.117	0

While these results are tentative they do suggest a reporting rate in the range of 0.40 - 0.25. Of course an alternative possibility would be that M = 0.2 is not reasonable. The only way we can obtain a more definitive estimate of reporting rate is to do a special study as we discuss later.

DISCUSSION AND CONCLUSIONS

Model Estimates

Based on the results in the previous section we can make the following conclusions about survival and recovery rates of Pacific halibut:

(1) Direct recovery rates are low and non-informative. This may be due to the time tags were applied just previous to the fishing season or to marking influencing the animals behavior.

Table 10. Natural and fishing mortality rates (finite and instantaneous) for a range of possible reporting rates. Model 4 estimates are used as a basis of the calculations.

	Age Class						
Parameter	2	3	4	5	6	7	8
S	0.782	0.708	0.708	0.704	0.602	0.602	0.602
1-S	0.218	0.292	0.292	0.296	0.398	0.398	0.398
Z	0.246	0.345	0.345	0.351	0.508	0.508	0.508
			λ=100%				
u	0.012	0.022	0.032	0.042	0.052	0.062	0.072
v	0.206	0.270	0.260	0.254	0.346	0.336	0.326
F	0.012	0.022	0.033	0.043	0.053	0.064	0.075
M	0.234	0.323	0.312	0.308	0.455	0.444	0.433
			λ=50%				
u	0.025	0.045	0.064	0.084	0.104	0.124	0.143
v	0.193	0.247	0.228	0.212	0.294	0.274	0.255
F	0.025	0.460	0.066	0.088	0.110	0.132	0.154
M	0.221	0.299	0.279	0.263	0.398	0.376	0.354
			λ=40%				
u	0.031	0.058	0.080	0.105	0.130	0.155	0.179
v	0.187	0.234	0.212	0.191	0.268	0.243	0.219
F	0.031	0.060	0.083	0.111	0.139	0.168	0.197
M	0.215	0.285	0.262	0.240	0.369	0.340	0.311
			λ=33%				
u	0.037	0.067	0.096	0.126	0.156	0.185	0.215
v	0.181	0.225	0.196	0.170	0.242	0.213	0.183
F	0.038	0.069	0.101	0.135	0.170	0.205	0.242
M	0.208	0.276	0.244	0.216	0.338	0.302	0.265
			λ=25%				
u	0.050	0.089	0.128	0.168	0.208	0.247	0.287
v	0.158	0.203	0.164	0.128	0.190	0.151	0.111
F	0.051	0.093	0.137	0.184	0.233	0.284	0.338
M	0.195	0.252	0.208	0.167	0.274	0.224	0.170

(2) Indirect recovery rates are strongly age and calendar year (at recovery) dependent. These rates appear to increase in an approximately linear manner as age class increases for the range of ages we examined (Age 6 - Age ≥13).

(3) Survival rates are strongly age and year dependent. Pacific halibut of age 6 have a survival rate of about 56% on average. This rises to about 78% for age 7 fish and then drops to approximately 70% for age 8, 9 and 10 fish. Ages 11, 12 and ≥13 have an approximately constant survival rate of about 60% on average. These results are fairly consistent over the models used to obtain the estimates. Due to violations of

Table 11. Natural and fishing mortality rates (finite and instantaneous) for a range of possible reporting rates. Model 0 estimates are used as a basis of the calculations.

	Age Class						
Parameter	**2**	**3**	**4**	**5**	**6**	**7**	**8**
S	0.783	0.660	0.706	0.697	0.620	0.592	0.618
1-S	0.217	0.340	0.294	0.303	0.380	0.408	0.382
Z	0.245	0.416	0.348	0.361	0.478	0.524	0.481
				λ=100%			
u	0.016	0.022	0.037	0.040	0.052	0.059	0.062
v	0.201	0.318	0.257	0.263	0.328	0.349	0.320
F	0.016	0.022	0.038	0.041	0.053	0.061	0.064
M	0.229	0.394	0.310	0.320	0.425	0.463	0.417
				λ=50%			
u	0.033	0.044	0.073	0.079	0.104	0.117	0.123
v	0.184	0.296	0.221	0.224	0.276	0.291	0.259
F	0.034	0.045	0.076	0.082	0.110	0.124	0.131
M	0.211	0.371	0.272	0.279	0.368	0.400	0.350
				λ=40%			
u	0.041	0.055	0.092	0.099	0.130	0.147	0.154
v	0.176	0.285	0.202	0.204	0.250	0.261	0.228
F	0.042	0.057	0.076	0.082	0.139	0.159	0.167
M	0.203	0.359	0.251	0.257	0.339	0.365	0.314
				λ=33%			
u	0.049	0.066	0.110	0.119	0.156	0.176	0.185
v	0.168	0.274	0.184	0.184	0.224	0.232	0.197
F	0.050	0.068	0.117	0.127	0.170	0.194	0.205
M	0.195	0.348	0.231	0.234	0.308	0.330	0.276
				λ=25%			
u	0.066	0.088	0.147	0.158	0.208	0.234	0.246
v	0.151	0.252	0.147	0.145	0.172	0.174	0.136
F	0.068	0.092	0.159	0.172	0.233	0.267	0.282
M	0.177	0.324	0.189	0.189	0.245	0.257	0.199

Table 12. Natural and fishing mortality rates (instantaneous) calculated from $Z = -\log_e(S)$ with M assumed equal to 0.2. Model 1 estimates are used as a basis of the calculations.

	Age Class						
Parameter	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Z	0.249	0.338	0.297	0.322	0.404	0.468	0.434
M	0.200	0.200	0.200	0.200	0.200	0.200	0.200
F	0.149	0.138	0.097	0.122	0.204	0.268	0.234

Table 13. Natural and fishing mortality rates (instantaneous) calculated from $Z = -\log_e(S)$ with M assumed equal to 0.2. Model 4 estimates are used as a basis of the calculations.

	Age Class						
Parameter	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Z	0.246	0.345	0.345	0.351	0.508	0.508	0.508
M	0.200	0.200	0.200	0.200	0.200	0.200	0.200
F	0.046	0.145	0.145	0.151	0.308	0.308	0.308

Table 14. Natural and fishing mortality rates (instantaneous) calculated from $Z = -\log_e(S)$ with M assumed equal to 0.2. Model 0 estimates are used as a basis of the calculations.

	Age Class						
Parameter	**2**	**3**	**4**	**5**	**6**	**7**	**8**
Z	0.245	0.416	0.348	0.361	0.478	0.524	0.481
M	0.200	0.200	0.200	0.200	0.200	0.200	0.200
F	0.045	0.216	0.148	0.161	0.278	0.324	0.281

model assumptions that we discuss later we suspect these estimates are biased low to some unknown degree.

(4) A reporting rate of $\lambda = 0.4$ - $\lambda = 0.25$ seems plausible under the assumption of a natural mortality rate of $M = 0.2$ for older fish. There does not appear to be any clear trend in natural mortality rate with age but our data limitations suggest caution in conclusions here.

(5) Considering the complexity of the models used here the goodness of fit to our models was very reasonable except for the newly tagged fish recoveries. There was substantial lack of fit in the cells but we suspect this did not have much influence on the important survival and indirect rate estimates we presented.

(6) We did have some difficulty in fitting some of the iterative models here due to the large number of parameters to be estimated. However, the consistency of results between models suggest that our results are reliable.

Model Assumptions

There are numerous assumptions behind the tagging models discussed in this article. We discuss the validity of these assumptions when applied to Pacific halibut tagged data. The discussion is based on Pollock and Raveling (1982) with some extensions.

(1) The Tagged Sample is Representative of the Target Population

This assumption is obvious but very important especially if heterogeneity of survival and recovery rates (Assumption 6) occurs. If, for example, tagging tends to take place in areas with heavy fishing pressure then this could give the appearance of high recovery rates and low survival rates for the whole region under study. This suggest designing tagging studies so that the tagging is dispersed over a wide area of each region under study.

(2) There is No Tag Loss

Nelson et al. (1980) examined this assumption by using simulation and found that its violation causes a negative bias on survival estimates that is worse for species with high survival rates. Unfortunately there is a tag loss for halibut. The recovery rates and hence the exploitation rate estimates will also be negatively biased. There is a need for a new double tagging study to obtain estimates of tag loss so that survival and recovery rates estimates can be adjusted.

(3) Survival Rates are not Influenced by Tagging

This assumption is obviously important because if there is substantial mortality due to the tagging process, the survival estimates would not apply to the untagged fish. Tagging mortality tends to be higher for smaller fish and lower for fish caught on circle hooks (G. St-Pierre, personal communication)[2]. The use of condition codes for stratification should help but St-Pierre also notes that condition codes vary widely among experiments. We do not know if it is practical to consider holding experiments to evaluate short term tagging mortality but we suggest a future study along these lines.

(4) The Year (Fishing Season) of Tag Recovery, Size at Release, Location and Other Important Information is Correctly Tabulated

Sometimes a commercial fisherman may report tags in a later year than when the fish was actually caught. We do not know how likely this is for halibut, but to the extent such incidents occur they operate to produce a positive bias on survival estimates. Other violations could cause positive or negative biases.

[2]St-Pierre, G. International Pacific Halibut Commission. P.O. Box 95009, Seattle, WA 98145-2009

(5) The Fate of Each Tagged Fish is Independent of the Fate of Other Tagged Fish

This assumption is probably violated in almost all practical applications of tag return models. Fish are not independent entities in terms of survival or other characteristics. This will not bias any estimators, but will mean that true sampling variances are larger than those estimated by statistical models. Thus, any collected confidence intervals will be narrower than they should be.

A simple (albeit unrealistic) example for illustration is to consider a population composed of independent pairs of fish that behave as thought they are a single individual. A sample of n individuals from this population is effectively only one half of n and, hence, any sampling variance will be twice those for the models that assume the sample is n independent individuals. The actual situation in real populations is much more complex, with many partially dependent members, but the effective sample size will still be much less than the actual sample size. To get around this problem, Burnham et al. (1987) suggest obtaining empirical estimates of variances by subdividing release cohorts into batches.

(6) All Tagged Fish Within an Identifiable Class Have the Same Annual Survival and Recovery Rates

We believe heterogeneity of survival and recovery rates is likely to occur in practice but we do not know how serious it will be in halibut tagging studies. Pollock and Raveling (1982) and Nichols et al. (1982) examined this assumption using analytical methods and simulation. They found that if only recovery rates are heterogeneous then there is no bias in survival estimates and the recovery rate estimates can be viewed as averages for the population. If survival probabilities are heterogeneous over the population, there is likely to be a strong positive relationship between the survival probabilities of an individual from year to year. There is also likely to be a negative relationship between survival and recovery probabilitites for an individual. In this situation, survival rate estimators will generally have a negative bias. The negative bias will be more serious where the average survival rate is high and for studies of short duration. It is theoretically possible for the survival rate estimator to have a positive bias. This could occur if there were segments of the population with markedly different survival rates but similar recovery rates. This implies that the difference in survival of the segments would have to be mostly due to differences in natural mortality. This might occur if drastically different environmental conditions were encountered by the segments (e.g. disease level, food supply, water temperature, etc.). Some of these factors vary on a local or regional scale.

(7) The Halibut of Size Class i will Increase its Length to the Size Class i + 1 After One Year

If this assumption is not satisfied, it will cause the violation of assumption (6). For example: IPHC released 482 tagged halibut of size class 1 in 1979, and these fish are treated as one cohort (i.e. an identifiable class). Under the assumption (7), we assume the cohort will grow synchronously to size class 2 next year. If some of the fish are still in size class 1 in 1980, their recovery rates may be lower than those fish which increase their length to size class 2 in 1980. Therefore we are saying that non-synchronous growth will cause heterogeneity of recovery rates in a cohort. This could be investigated further using simulation.

Data Limitations

Since the survival rates of Pacific halibut are high, the violation of assumptions (2), (6) and (7) can cause negatively biased survival estimators. With halibut the possible violations of the homogeneity assumption might be caused by fish growth, sexual differences or the violation of assumption (7). Because the sex information is not available for the Pacific halibut data, we cannot test whether heterogeneity exists between male and female fish. The best way to avoid the violation of assumption (7) is to collect the age information at release of the tagged fish if possible. If the age of each tagged halibut is not easy to identify in practice, an age-length key can be used to convert the length to age. An unrealistic age-length key will cause a serious violation of assumption (7).

Another limitation of the data is the small number of tag recoveries for some age classes. This is due to the reporting rate being so low. Later we emphasize how to estimate the reporting rate but here we also emphasize that a method of increasing the reporting rate would be very important to increase the precision of the survival and recovery estimates. Perhaps higher rewards could be given for tag returns. The simple alternative of tagging larger numbers of Pacific halibut is probably not feasible.

Computational Limitations

We have extended a 3 age classes model to an 8 age classes model. Theoretically, Brownie's model can be extended to any number of age classes, if the data are available. However there are limitations to developing extensions in practice, because the MLE's do not have closed form in general, and must be obtained by numerical optimization techniques using a computer. In the research, we have tried both SAS NLIN and program SURVIV to compute the MLE's and we found that SURVIV seems more accurate than NLIN as the number of parameters increases. SURVIV, however, is limited in the maximum number of allowable parameters, and in the ways we can model survival as a function of age. Thus we need better software to handle models with large numbers of parameters, or where survival is modeled as a function of age.

Future Special Studies

It is clear to us that there are several special problems with the halibut data which need to be addressed either by changing procedures or by carrying out special studies to estimate parameters which could be used to adjust and improve survival and exploitation rate estimates.

(1) Tag Loss

Both R. Deriso (personal communication)[3] and St.Pierre (personal communication)[2] reacted to our earlier work by suspecting that our survival rate

[3]Deriso, R. International Pacific Halibut Commission. P.O. Box 95009, Seattle, WA 98145-2009.

estimates were biased low due to tag loss. A double tagging study, although expensive, would be useful in providing an estimate of tag loss which could be used to adjust our estimates.

(2) Tag Induced Mortality

Another potential serious problem with the halibut tagging data is tagging and handling induced mortality. We do not have a good suggestion here. For some species holding experiments are used to estimate short term tagging and handling mortality. If practical this would be very valuable for halibut.

(3) Increased Reward Tags

As we discussed under data limitations an increased reward on tags would increase the reporting rate and hence the number of tag returns. This would increase the precision of survival and recovery rate estimates. We recommend that an increased reward on tags be considered.

(4) Reporting Rate

The parameter we call λ the reporting rate is actually the probability of a tagged halibut having the tag found and reported. This parameter is extremely important in that if it could be estimated then tag recovery rate can be converted to exploitation rate. It also allows natural mortality rate to be estimated by subtraction (Pollock et al. 1991). We explored this approach in a previous section (Estimates of fishing and natural mortality rates) for a range of reporting rates but our conclusions were tentative because we did not have an independent estimate of λ.

The probability of a tag being found is hard to estimate but could possibly be estimated if a special study were set up where total catch of some boats were searched for tags. Given a tag has been found the probability of it being reported could be estimated using a variable reward tagging study. Some tags would need to have known stamped rewards of high amounts so that it would be safe to assume that all of those tags were reported. This would enable us to obtain an estimate of the reporting probability (given the tag found) for regular tags (Pollock et al. 1991).

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APPENDICES

Appendix I. Recovery information for Pacific halibut in Areas 2B, 2C, and 3A.

Appendix II.

Table A2-1. The estimations of identifiable parameters (%) for Model 0.

Tables A2-2 - A2-5. The parameters estimates (%) and standard errors (%) obtained.

APPENDIX 1. Tables A1-1 through A1-8 represent recovery information for Pacific halibut in Areas 2B, 2C, and 3A for different size categories as indicated.

Table A1-1. Size Class 8: ≥ 129 cm

Year	# released	# recovered							
1979	334	6	9	11	3	2	3	0	2
1980	572		13	12	9	7	12	7	2
1981	1817			2	63	26	34	11	16
1982	1000				1	35	31	35	25
1983	1416					21	74	87	61
1984	2066						4	120	138
1985	2116							12	196
1986	1295								1

Table A1-2. Size Class 7: 122-128 cm

Year	# released	# recovered							
1979	108	1	4	1	0	0	1	0	0
1980	188		1	3	6	2	3	0	0
1981	475			0	15	9	8	9	4
1982	258				0	4	10	5	10
1983	379					2	14	26	16
1984	603						1	38	42
1985	539							6	45
1986	365								0

Table A1-3. Size Class 6: 114-121 cm

Year	# released	# recovered							
1979	117	2	4	3	1	1	0	0	0
1980	252		1	7	6	5	3	2	1
1981	516			1	14	10	11	4	1
1982	351				1	8	8	14	15
1983	447					1	22	21	29
1984	881						1	48	43
1985	752							6	52
1986	510								0

Table A1-4. Size Class 5: 105-113 cm

Year	# released	# recovered							
1979	142	1	5	3	2	0	2	0	1
1980	313		3	13	8	4	6	2	5
1981	574			0	6	9	8	4	12
1982	380				2	11	15	10	10
1983	604					4	28	20	35
1984	1166						0	56	67
1985	1035							6	68
1986	702								0

Table A1-5. Size Class 4: 96-104 cm

Year	# released	# recovered							
1979	177	3	3	4	1	1	1	2	0
1980	390		6	10	9	7	8	6	4
1981	515			0	12	10	11	7	12
1982	512				0	10	19	17	17
1983	581					3	20	29	25
1984	1426						3	50	67
1985	1157							7	60
1986	790								0

Table A1-6. Size Class 3: 86-95

Year	# released	# recovered							
1979	280	1	8	5	5	2	1	1	1
1980	583		6	11	9	10	11	3	5
1981	584			2	6	10	14	10	8
1982	676				3	10	27	20	17
1983	674					2	22	24	24
1984	1814						4	70	67
1985	1423							13	67
1986	980								3

Table A1-7. Size Class 2: 75-85 cm

Year	# released	# recovered							
1979	445	5	10	8	5	3	5	1	4
1980	1032		2	18	6	17	13	15	10
1981	823			0	6	13	11	9	18
1982	969				3	14	39	29	37
1983	881					0	20	29	25
1984	2419						1	57	78
1985	2287							11	76
1986	1509								3

Table A1-8. Size Class 1: 64-74 cm

Year	# released	# recovered							
1979	482	1	2	3	3	3	4	4	4
1980	1530		1	5	7	12	12	15	11
1981	978			0	5	2	13	16	14
1982	820				0	3	17	17	24
1983	1228					3	10	17	24
1984	2405						0	24	46
1985	2217							4	18
1986	1459								0

APPENDIX 2.

Table A2-1. The estimations of identifiable parameters (%) for Model 0.

Parameter	Size Class: i; Recovery year: j							
	1	2	3	4	5	6	7	8
f_8^{i*}	0.07	0.20	0.31	0.00	0.00	0.00	0.00	0.08
f_7^{i*}	0.18	0.48	0.91	0.61	0.58	0.80	1.11	0.57
f_6^{i*}	0.00	0.04	0.22	0.21	0.00	0.11	0.17	0.19
f_5^{i*}	0.24	0.00	0.30	0.52	0.66	0.22	0.53	1.48
f_4^{i*}	0.00	0.31	0.44	0.00	0.53	0.29	0.00	0.11
f_3^{i*}	0.00	0.00	0.34	0.00	0.00	0.19	0.00	0.11
f_2^{i*}	0.07	0.19	1.03	1.54	0.96	0.40	0.53	2.27
f_1^{i*}	0.21	1.12	0.36	1.70	0.70	1.71	0.93	1.80
f_7^{i}		1.48	2.75	4.58	5.02	5.72	7.05	8.68
f_6^{i}		1.35	2.86	4.11	5.13	5.69	8.22	7.48
f_5^{i}		4.34	1.09	3.06	3.88	5.75	4.52	5.59
f_4^{i}		1.33	1.56	1.65	3.67	3.98	5.50	7.59
f_3^{i}		0.63	2.09	3.43	2.32	4.28	4.31	4.01
f_2^{i}		0.71	2.84	5.20	3.73	5.70	5.53	3.56
$s_7^i f_8^{i+1}$	6.31	2.84	3.80	4.58	5.99	6.12	7.24	8.70
s_6^{i}	67.30	84.60	80.03	72.61	89.13	71.51	75.42	70.78
s_5^{i}	56.73	82.45	83.36	77.95	82.22	74.50	72.04	71.77
s_4^{i}	84.21	100.0*	68.76	72.57	53.53	66.80	56.80	63.17
s_3^{i}	38.44	59.43	56.45	66.21	41.14	45.15	47.16	40.55
s_2^{i}	51.13	74.83	54.54	100.0*	94.44	66.23	56.91	51.80
s_1^{i}	55.85	68.21	52.59	34.10	56.98	48.07	47.00	72.94

* estimate is above 100%

Table A2-2. **The parameter estimates (%) and standard errors (%) obtained from SURVIV for Model 1.**

Parameter	Size Class: i; Recovery year: j							
	1	2	3	4	5	6	7	8
f_j^{i*} j = 1,..,8	0.09(0.03)	0.24(0.05)	0.48(0.08)	0.40(0.08)	0.33(0.08)	0.34(0.09)	0.38(0.11)	0.57(0.07)
f_j^i j = 2,..,8		1.23(0.17)	2.90(0.24)	4.56(0.36)	5.21(0.41)	6.48(0.54)	7.40(0.68)	8.85(0.45)
s_j^i j = 1,..,7	56.46(4.07)	78.01(5.04)	71.27(4.93)	74.28(5.30)	72.54(5.56)	66.78(5.66)	62.62(4.26)	64.84(1.49)

Table A2-3. **The parameter estimates (%) and standard errors (%) obtained from NLIN for Model 3.**

Parameter	Size Class: i; Recovery year: j							
	1	2	3	4	5	6	7	8
f_j^{i*} j = 1,..,8	0.09(0.03)	0.24(0.05)	0.48(0.08)	0.40(0.08)	0.33(0.08)	0.34(0.09)	0.38(0.11)	0.57(0.07)
f_8^i		1.46(0.35)	4.33(0.47)	6.41(0.64)	8.05(0.79)	10.60(1.03)	12.71(1.32)	16.57(0.97)
f_7^i		1.78(0.38)	3.06(0.41)	5.88(0.66)	6.30(0.69)	7.58(0.88)	9.11(1.10)	11.01(0.71)
f_6^i		1.46(0.48)	3.57(0.62)	5.87(0.74)	5.19(0.96)	6.72(0.88)	8.53(1.23)	8.56(0.65)
f_5^i		0.69(0.35)	1.39(0.33)	2.57(0.47)	3.56(0.61)	4.24(0.81)	4.23(0.88)	4.71(0.51)
f_4^i		0.91(0.43)	1.14(0.32)	1.36(0.37)	3.22(0.69)	3.00(0.71)	4.64(1.05)	5.41(0.57)
f_3^i		0.58(0.28)	2.06(0.48)	2.97(0.74)	3.78(0.94)	5.85(1.43)	4.75(1.51)	4.54(0.83)
f_2^i		0.74(0.54)	2.88(0.98)	4.11(1.53)	2.42(1.54)	5.21(2.37)	5.64(2.91)	4.90(1.34)
s_j^i j = 1,..,7	55.97(4.14)	77.69(5.14)	68.75(4.38)	69.78(5.08)	67.67(5.24)	60.83(5.22)	59.49(4.05)	60.99(1.38)

Table A2-4. The parameter estimates (%) and standard errors (%) obtained from SURVIV for Model 2.

Parameter	Size Class: i; Recovery year: j							
	1	2	3	4	5	6	7	8
f_j^{i*} j = 1,..,8	0.09(0.03)	0.24(0.05)	0.48(0.08)	0.40(0.08)	0.33(0.08)	0.34(0.09)	0.38(0.11)	0.57(0.07)
f_8^i		1.55	3.93	6.31	8.69	11.07	13.45	15.83
f_7^i		1.82	3.33	4.83	6.33	7.84	9.34	10.84
f_6^i		2.32	3.39	4.46	5.53	6.61	7.68	8.75
f_5^i		0.87	1.58	2.28	2.99	3.70	4.41	5.11
f_4^i		0.55	1.29	2.04	2.78	3.53	4.27	5.02
f_3^i		0.90	1.72	2.54	3.37	4.19	5.01	5.84
f_2^i		1.49	2.20	2.91	3.61	4.32	5.03	5.74
s_j^i j = 1,..,7	53.47(3.67)	79.29(3.83)	74.36(3.37)	64.51(3.00)	67.41(3.00)	60.66(2.85)	60.85(2.86)	61.33(1.13)
b0j		0.07(0.96)	-0.75(0.49)	-0.94(0.39)	-0.54(0.46)	0.17(0.64)	-1.18(0.48)	-3.21(0.52)
b1j		0.71(0.24)	0.82(0.13)	0.74(0.09)	0.71(0.10)	1.07(0.13)	1.50(0.11)	2.38(0.14)

where $f_j^i = b0j + b1j \times i$

Table A2-5. The parameter estimates (%) and standard errors (%) obtained from NLIN for Model 4.

Parameter	Size Class: i; Recovery year: j							
	1	2	3	4	5	6	7	8
f_j^{i*} j = 1,..,8	0.09(0.03)	0.24(0.05)	0.49(0.08)	0.40(0.08)	0.33(0.08)	0.34(0.09)	0.37(0.11)	0.56(0.07)
f_7^i		1.98	3.22	4.46	5.70	6.94	8.18	
f_6^i		1.77	2.82	3.87	4.91	5.96	7.01	
f_5^i		0.42	1.48	2.53	3.59	4.64	5.70	
f_4^i		0.81	1.77	2.73	3.69	4.65	5.61	
f_3^i		1.02	1.70	2.38	3.07	3.75	4.43	
f_2^i		1.45	2.40	3.34	4.28	5.23	6.17	
$s_7^k f_8^i$ k = 6,..,8							9.14(0.52)	7.20(0.69)
$s_7^5 f_8^6$						6.69(0.60)		
$s_7^4 f_8^5$					4.82(0.48)			
$s_7^3 f_8^4$				4.62(0.47)				
$s_7^2 f_8^3$			3.40(0.37)					
$s_7^1 f_8^2$		0.81(0.19)						
s_j^i i = 6,..,8	51.09(10.18)	66.06(7.94)	45.44(4.09)	53.70(4.40)	78.55(5.34)	66.44(4.87)		
s_j^5	66.61(19.32)	100.0*(--)	45.11(5.78)	60.49(5.78)	76.51(7.85)	73.62(7.44)		
s_j^4	42.57(12.23)	100.0*(--)	59.86(9.62)	78.79(10.24)	78.70(9.13)	64.58(6.54)		
s_j^3	59.60(12.88)	69.31(11.77)	48.10(7.62)	75.90(10.23)	91.48(11.03)	80.66(8.44)		
s_j^2	77.31(15.67)	82.54(13.08)	57.85(8.99)	98.33(12.64)	81.25(10.71)	72.17(8.57)		
s_j^1	51.67(12.37)	49.91(8.40)	39.48(6.47)	84.50(14.09)	56.03(9.25)	54.03(9.07)		
b0j		-0.44(1.26)	-0.34(0.59)	-1.11(0.62)	-1.69(0.40)	-0.32(0.67)	-0.50(0.67)	
b1j		0.94(0.36)	0.68(0.15)	0.96(0.15)	1.06(0.12)	1.05(0.14)	1.24(0.15)	

where $f_j^i = b0j + b1j \times i$; *estimate is above 100%