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Movements of Juvenile Halibut in IPHC Regulatory Areas 2 and 3

by

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ABSTRACT

In 1980 and 1981, more than 68,000 juvenile halibut were tagged in the Gulf of Alaska and Southeast Alaska in an effort to obtain estimates of movements of juvenile halibut. In this paper we develop a maximum likelihood method for estimating the movement between International Pacific Halibut Commission (IPHC) regulatory Areas 3B, 3A, 2C, 2B and 2A. In addition to the movement rates, we also estimate the size-specific natural mortality, tagging mortality and size selectivity for commercial gear in Areas 3B and 3A. We found that all of these parameters could be estimated with low confounding, and that the predicted recovery pattern of tags conforms closely to the observed recoveries.

The best fitting model estimates that there are substantial southerly movements of juvenile halibut; for example, we estimate that 17% of fish tagged in 3B would recruit as adults to 2B, and that 25% of fish tagged in 3A would recruit as adults to 2B. Further improvements in the analysis could include smaller spatial scale of analysis, and combining tagging analysis with catch-at-age data.

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INTRODUCTION

The Pacific halibut (*Hippoglossus stenolepis*) forms the basis for a major commercial fishery on the west coast of the United States and Canada. The fishery is regulated under an international agreement by the International Pacific Halibut Commission (IPHC), which has conducted scientific investigations on the biology and management of the halibut since the Halibut Convention of 1923. As a result of the continuing biological investigations, it is now believed that there is a general drift of halibut larvae northwest, from Oregon, Washington and B.C. to Alaska. Tagging studies of adult halibut (9 years and older; 80 cm and larger), indicate very little movement, and it is believed that a southerly juvenile migration (from Alaska to B.C. and the lower United States) must exist to balance the documented passive drift of eggs and larvae north (Skud 1977).

Adult halibut are caught predominantly by longline gear, while the juveniles are rarely caught in such gear. Juveniles can be caught, however, in trawl gear and in 1980 and 1981 the IPHC conducted a program of juvenile tagging to investigate the movements of halibut between different portions of its distribution.

MATERIALS AND METHODS

Marking and tag recovery

In 1980, 32,620 halibut were tagged and released from two trawl vessel charters (IPHC 1981), and in 1981, 25,493 fish were tagged from trawl charters. These releases took place in IPHC regulatory Areas 2C, 3A and 3B. Trawls of less than 15 minutes towing time were made, and all halibut recovered were immediately placed in a live-box on deck. Only fish which appeared to be in good condition were then measured for total length, and marked with a spaghetti tag on the dark side of the fish. Figure 1 shows the distribution of tag releases for 1980 and 1981, in Areas 3A and 3B.

We include in the analysis four release groups: group 2, released in statistical Area 3A in 1980; group 3, released in 3B in 1980; group 5, released in 3A in 1981; and group 6, released in 3B in 1981. There were also some releases in Area 2C in 1980 and 1981 (the missing group codes 1 and 4) but the number of releases was very small so we do not consider these data in this analysis.

Fishermen or shore workers who detected a tagged fish were requested to return the tag to the IPHC with information on date and place of capture, as well as the total
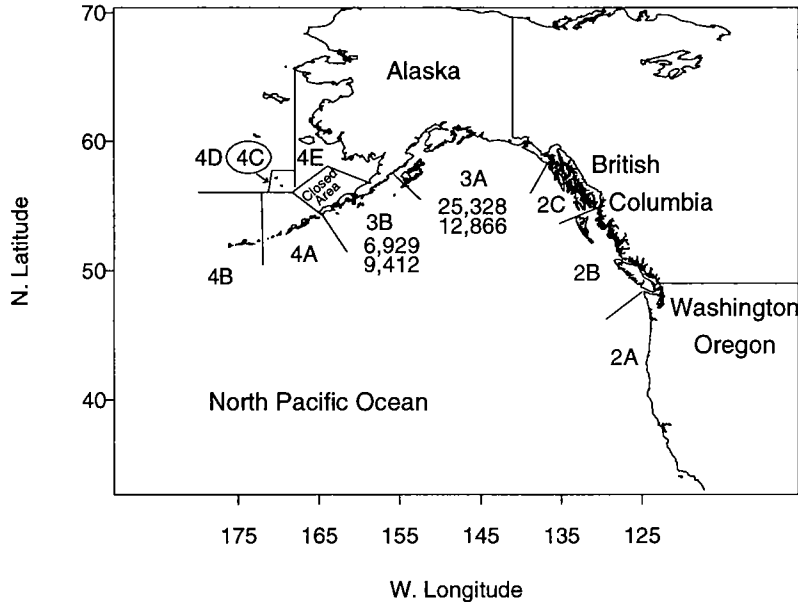
Figure 1. IPHC regulatory areas, number of releases and location in 1980 and 1981.

length of the fish. A reward of an IPHC tag return baseball cap was offered. Most tag returns came from the longline fishery, but there were also returns from trawl, troll, recreational and other fisheries. However, for the purposes of this analysis we only used returns from the longline fishery. Table 1 shows the distribution of recoveries from fish released in regulatory Areas 3A and 3B. These data are aggregated for the two release years of 1980 and 1981.

We see that there is a southerly movement of tags as expected based on the larval biology of halibut. However, most fish released in the Gulf of Alaska, (Areas 3A and 3B) were recovered there and very few tags were recovered as far south as Washington. If the probabilities of recapture and tag return were equal in all areas, then the percentages observed in Table 1 could be used as estimates of movement rates. However, we know that fishing mortality rates, growth rates and size-specific selectivity are different between areas, and fishing mortality and tag reporting rates have changed over time.

Table 1. The distribution of recoveries of fish tagged in Areas 3A and 3B. Given in parentheses is the percentage of all recoveries from an area of release that occur in an area of recovery.

	Area of Release	
Area of Recovery	3A	3B
2A Washington	5 (1.3%)	4 (1.8%)
2B British Columbia	100 (25.4%)	36 (16.0%)
2C Southeast Alaska	35 (8.9%)	22 (9.8%)
3A Eastern Area 3	249 (63.2%)	91 (40.4%)
3B Western Area 3	5 (1.3%)	72 (32.0%)

Length distribution of fish at release.
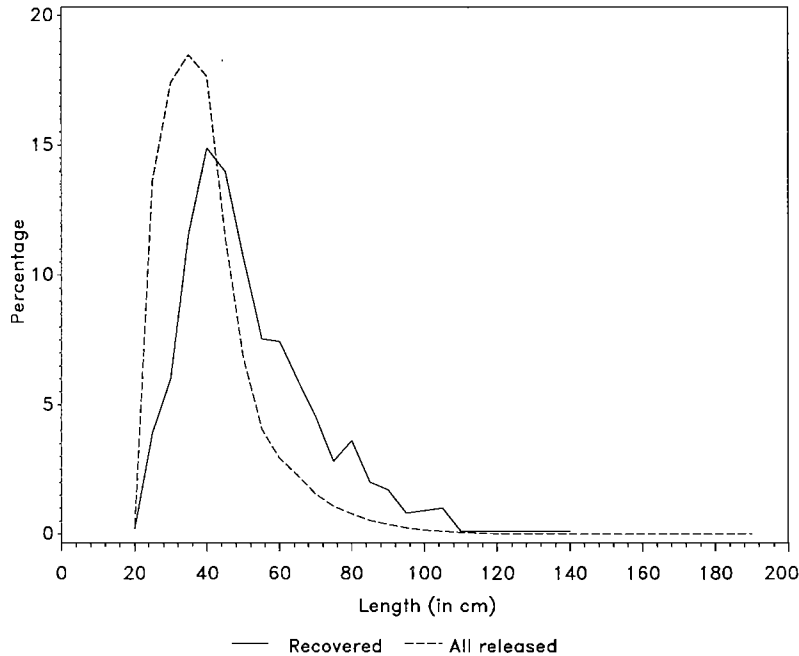
Figure 2. Length distribution of halibut at release (dashed line), and the length distribution at release of individuals that were recovered (solid line).

Therefore, we must construct a model of the expected distribution of recoveries to try to estimate the movement rates given what we know about fishing mortalities, growth, selectivity and tag return rates.

Figure 2 shows the length distributions at release of all fish released and of those that were recovered. Note that most of the fish are tagged at less than 60 cm, although there are fish tagged up to 140 cm. 81 cm is the legal size limit for longline caught halibut. Because we are concerned only with juvenile halibut movement, we initially excluded all individuals > 65 cm at the time of tagging from subsequent analyses. Subsequently we included these larger fish in some analyses. The large fish were also excluded from Table 1.

Although the legal size limit is 81 cm, it is legal to retain tagged halibut of any length. Roughly 25% of the recoveries were of fish less than 80 cm, and 50% were of fish less than 90 cm. Figure 3 shows the proportion of fish recovered as a function of length at release. Clearly, the larger a fish was at the time of tagging the more likely it was to be recovered. This is not at all surprising since the gear is known to select for larger fish, and the fish that were larger at the time of tagging would have fewer years of natural mortality to endure prior to becoming vulnerable to the longline gear. Figure 3 makes it clear that any analysis of movement patterns must explicitly include growth and selectivity.

A critical component of any analysis of mark-recovery data is the proportion of tags that are recovered by fishermen and returned to the scientific staff for analysis. IPHC staff believe that the fishermen make a conscientious effort to return tags, and there are no known reasons why fishermen should believe that returning tags is against

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Percentage of fish recovered by size class.
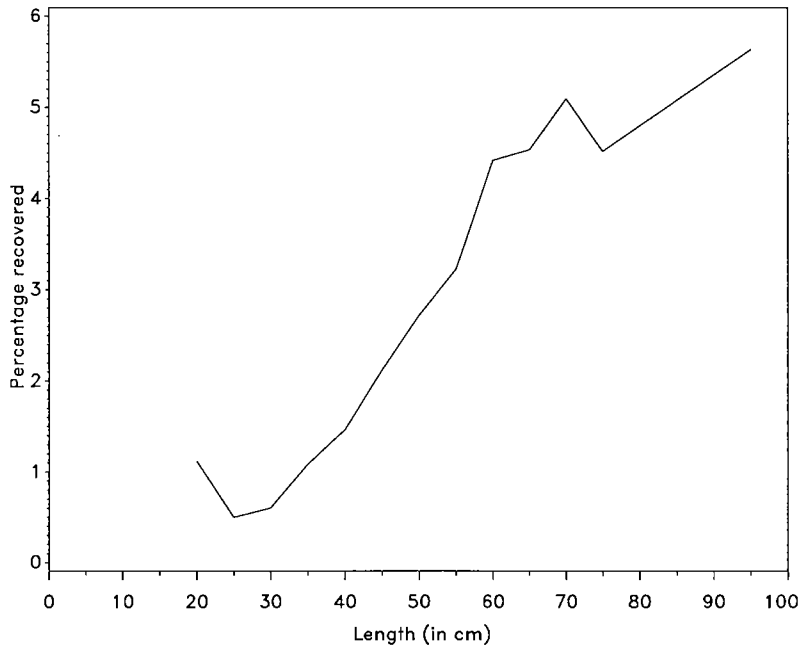
Figure 3. Proportion of tagged fish recovered plotted against length at time of tagging.

their interest. However, non-return of tags is always a problem in any fishery, and as the fishing season for halibut has become progressively shortened, IPHC staff believe that the proportion of tags actually detected by fishermen has decreased, particularly in the Alaskan fisheries where a single boat may land 100,000 pounds of halibut in a 24-hour period. Under these circumstances, individual fish are not carefully examined. Table 2 presents the proportion of the catch landed in ports with IPHC samplers. The IPHC staff believe that these values represent reasonable starting estimates of the reporting rate for a given area and year.

Table 2. Proportion of catch unloaded in ports with IPHC samplers.

Year	3B	3A	2C	2B	2A
1981	0.33	0.79	0.43	0.58	0.84
1982	0.11	0.74	0.63	0.65	0.68
1983	0.38	0.58	0.66	0.60	0.58
1984	0.32	0.53	0.61	0.68	0.65
1985	0.13	0.45	0.55	0.64	0.56
1986	0.49	0.39	0.56	0.74	0.50
1987	0.36	0.57	0.62	0.74	0.48
1988	0.58	0.77	0.58	0.77	0.45
1989	0.33	0.74	0.52	0.75	0.57

Growth curves by regions.
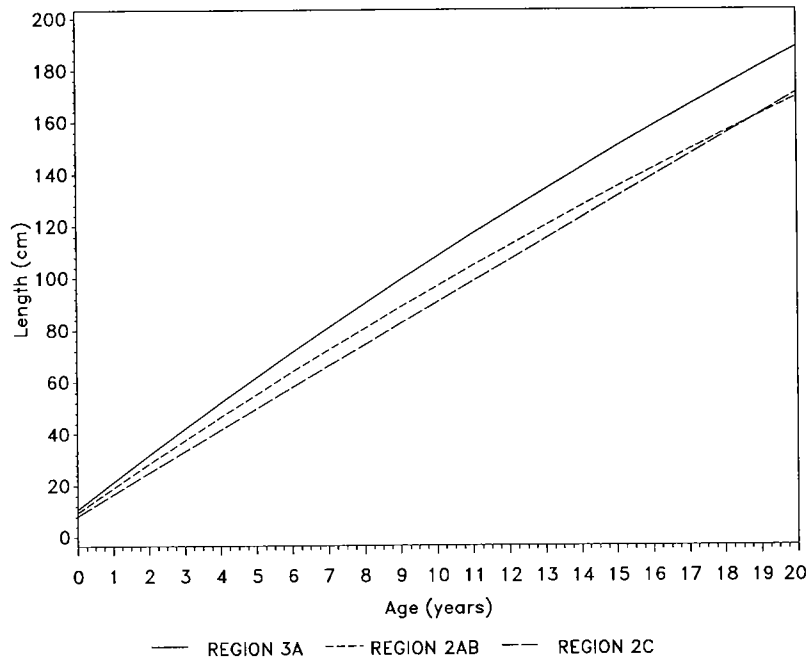
Figure 4. Growth curves for different IPHC statistical areas. Data from IPHC staff.

Growth

In an earlier analysis of these movement data (Skalski et al., 1993), we explored models that included area-specific growth and stochastic growth. We found that models that included area-specific growth and stochastic growth estimated movement rates similar to those obtained from models that ignored area-specific differences in growth. Therefore, in this analysis we have used a single growth relationship for all areas. Shown in Figure 4, is the best estimated average growth relationship for Areas 2A-2B, 2C and 3A. Note although the length at age may differ between areas, the slope of the curve is quite similar so that a fish tagged at 40 cm would be within 5 cm of the same length regardless of which growth curve was used.

Fishing mortality rates

Table 3 shows the year-specific fishing mortalities estimated by IPHC staff from analysis of catch-at-age data. The most obvious trend in the data is the general increase in fishing mortality from 1980 to 1989. The most southern Area, 2A has usually the highest fishing mortality.

The values in Table 3 are estimates of instantaneous fishing mortality on fully recruited individuals and our explicit assumption is that the probability of a tagged fish being captured is the product of an area- and time-specific fishing mortality rate and an area- and size-specific selectivity. The temporal pattern in fishing mortality rates is shown in Figure 5.

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Longline fishing mortalities.
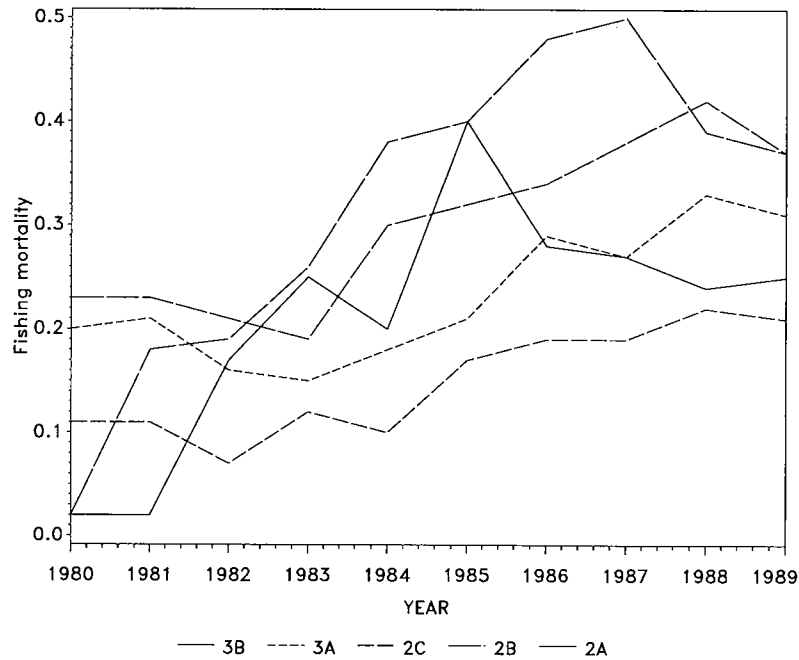
Figure 5. Instantaneous fishing mortality rates by year and area.

Table 3. Area and year-specific longline fishing mortalities for halibut that are fully recruited.

Year	3B	3A	2C	2B	2A
1980	0.02	0.20	0.11	0.23	0.02
1981	0.02	0.21	0.11	0.23	0.18
1982	0.17	0.16	0.07	0.21	0.19
1983	0.25	0.15	0.12	0.19	0.26
1984	0.20	0.18	0.10	0.30	0.38
1985	0.40	0.21	0.17	0.32	0.40
1986	0.28	0.29	0.19	0.34	0.48
1987	0.27	0.27	0.19	0.38	0.50
1988	0.24	0.33	0.22	0.42	0.39
1989	0.25	0.31	0.21	0.37	0.37

Table 4. Area-specific parameters for size-selectivity curves derived from catch-at-age and length data.

Area	b_{1i}	b_{2i}
3A-3B	112.47	0.092
2C	91.75	0.160
2A-2B	83.27	0.216

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Selectivity curve by regions.
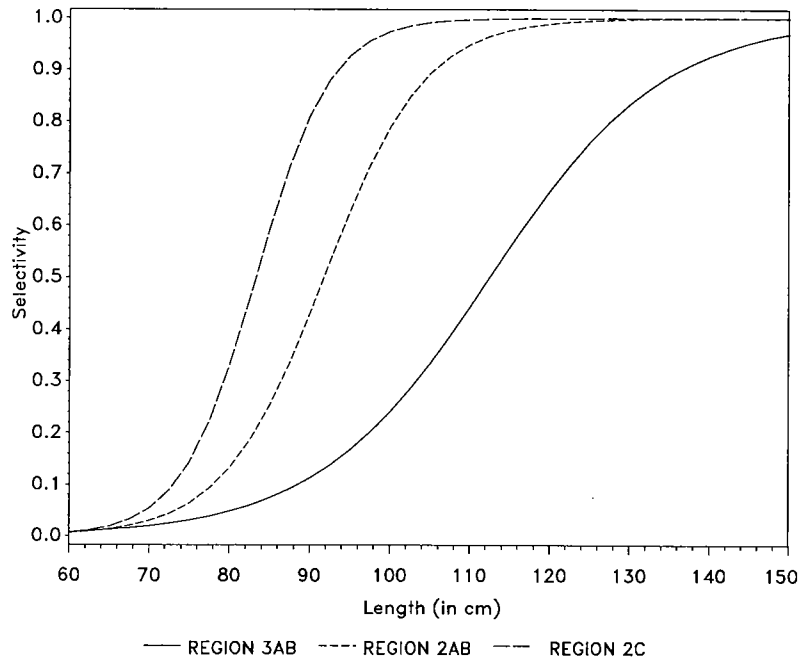
Figure 6. Size-selectivity relationships for Areas 3A-3B, 2C, and 2A-2B provided by IPHC staff.

Size-specific selectivity/vulnerability

The most striking individual difference between areas is on the estimated size-dependent vulnerabilities. These were estimated by the IPHC staff with the model described in Parma and Deriso (1990), using data on size-at-age distributions in the catch and total catch biomass, and fixing the fishing mortalities at the estimates obtained from catch-at-age analysis. Figure 6 shows the relationship, with the parameters of the model given in Table 4. Size-specific selectivities were not estimated separately for Areas 3A and 3B due to the lack of adequate data. The combined selectivity curve estimated for Areas 3A-3B suggests that fish become vulnerable to the fishing gear at a much larger size than in B.C. and Washington (Areas 2A-2B) or in 2C. While it is reasonable to believe that the selectivity curve derived from the analysis of commercial landings, with the associated 81 cm size limit, may be inadequate for tagged fish, we begin our analysis with this relationship. This relationship has been used in earlier analyses of these data.

The model

The following description of the model is based on the fate of a single size-at-release class. The notation for the model is summarized in Table 5. We assume that the annual cycle of events for tagged halibut has three periods (1) movement, (2) fishing, and (3) natural mortality and growth. We also assume that fishing takes place in very short periods of time so that we do not need to consider natural mortality during the fishing period.

A group of tagged fish, g, from a given size-at-release class k is released at year $t(g)$ and in area $i(g)$. To simplify the notation, we drop the subscripts indexing the release group g and the size–at–release k. The expected number of tagged fish alive

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Table 5. Notation used in the model.

g	$=$	index identifying a group of fish tagged and released over a short period of time,
k	$=$	identifies size-at-release class of fish from a given group,
$t(g), i(g)$	$=$	the year and area of release for group g,
l_t	$=$	length of fish at year t,
a, b	$=$	parameters of the von Bertalanffy growth equation,
$N_{i(g)t(g)}$	$=$	Number of fish released in area $i(g)$, year $t(g)$
λ	$=$	probability that a tag is lost due to tag shedding or tag induced mortality,
$\mathbf{n}_t$	$=$	the expected number of tagged fish alive just prior to movement in area i, year t, released in area g at size k
$\mathbf{n}'_t$	$=$	the expected number of tagged fish alive after movement,
$\mathbf{n}''_t$	$=$	the expected number of tagged fish surviving the fishery,
$\mathbf{M}_t$	$=$	transition matrix indicating fractions of fish moving between areas, in year t,
m^0_{ij}	$=$	probability of movement from area j to area i, for a 50cm fish, for fish that were released in group g, at size k,
$z(l_t)$	$=$	size–dependent scalar for the movement parameters,
w	$=$	parameter for the size–dependent movement,
$\mathbf{U}_t$	$=$	exploited fraction of the population of tagged fish in year t,
$\mathbf{C}_t$	$=$	expected catch of tagged fish in year t,
h_{it}	$=$	instantaneous longline fishing mortality rate for fully recruited fish in area i and year t,
$v_i(l_t)$	$=$	selectivity of fish in area i, at length l_t,
b_{1i}, b_{2i}	$=$	parameters of the selectivity function,
$\mathbf{S}^f_t$	$=$	fraction of fish surviving the fishery in year t,
$\mathbf{S}^{tot}_t$	$=$	fraction of fish surviving from recreational fishery and other causes of mortality in year t
$s^{nat}(l_t)$	$=$	survival from natural causes for a fish of length l_t
l_s	$=$	minimum size of fish with constant natural mortality rate,
k_s	$=$	slope parameter of the size-dependent survival function,
$\mathbf{S}^{spt}_t$	$=$	fraction of fish surviving from the recreational fishery in year t,
f^{spt}_{it}	$=$	instantaneous fishing mortality rate from the recreational fishery in area i and year t
$\mathbf{R}_t$	$=$	probability that a fish caught is returned to the IPHC,
$\mathbf{X}_t$	$=$	number of tagged fish recovered in year t, from release group g and released at size k.

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after release is then equal to

$$N_{it} = N_{i(g)t(g)}(1 - \lambda) \tag{1}$$

where λ is the probability that the tag is lost or that the tagged fish died due to tag–induced mortality soon after the release. Using vector notation, if we denote the area–specific expected number of tagged fish available by $\mathbf{n}_t$, then the movement between areas following the release can be represented by

$$\mathbf{n}'_t = \mathbf{M}_t \mathbf{n}_t \tag{2}$$

where $\mathbf{M}_t$ is a transition matrix whose elements m_{ij} represent the proportion of tagged fish that moved to area i from area j in a given time interval. More precisely, the m_{ij} are defined as follows:

$$m_{ij} = \begin{cases} z(l_t)m_{ij}^0, \text{ for } i \neq j \\ 1 - \sum_i z(l_t)m_{ij}^0, \text{ for } i = j \end{cases} \tag{3}$$

Size–dependency in the movement is allowed through $z(l_t)$ which is a scaling factor (relative to a length of 50 cm) calculated as

$$z(l_t) = e^{w\left(\frac{l_t - 50}{50}\right)} \tag{4}$$

so that if $w = 0$ then $z(l_t) = 1$ and the "unadjusted" movement rates are used, but if $w < 0$ then smaller fish are more likely to move than larger fish. According to the above definition of the elements of $\mathbf{M}_t$, the columns of the matrix are constrained to add up to one, therefore preserving the total number of fish. m_{ij}^0 represents the probability of a 50cm fish moving from area j to area i. The expected number of tagged fish surviving the longline fishery is

$$\mathbf{n}''_t = \mathbf{S}_t^f \mathbf{n}'_t \tag{5}$$

where $\mathbf{S}_t^f$ is a diagonal matrix whose non-zero elements represent the probability of survival from the longline fishery. If we define the finite mortality rate in the longline fishery as

$$\mathbf{U}_t = \mathbf{I} - \mathbf{S}_t^f \tag{6}$$

where $\mathbf{I}$ is the identity matrix, the expected catch is then

$$\mathbf{C}_t = \mathbf{U}_t \mathbf{n}'_t \tag{7}$$

$\mathbf{U}_t$ is a diagonal matrix representing the finite longline fishing mortality rate, that is

$$u_{ii} = 1 - e^{-h_{it}v_i(l_t)} \tag{8}$$

where h_{it} is the instantaneous longline fishing mortality rate for fully recruited fish in area i and year t, and $v_i(l_t)$ is the area– and size–specific selectivity to longline gear calculated as

$$v_i(l_t) = \frac{1}{(1 + e^{-b_{2i}(l_t - b_{1i})})} \tag{9}$$

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where l_t is the length at time t of a tagged fish and b_{1i} and b_{2i} are parameters that we assume to be potentially different for each area i.

Growth in length is modelled using a von Bertalanffy model of the form

$$l_{t+1} = a + bl_t \tag{10}$$

After growth, the expected number of tagged fish alive prior to the next movement episode is

$$\mathbf{n}_{t+1} = \mathbf{S}_t^{tot}\mathbf{n}''_t \tag{11}$$

where the total survival, $\mathbf{S}_t^{tot}$, consists of survival from recreational fishing mortality and survival from all other mortalities (predation, incidental catch, disease, etc.)

$$\mathbf{S}_t^{tot} = \mathbf{S}_t^{spt}s^{nat}(l_t) \tag{12}$$

The elements in the diagonal of $\mathbf{S}_t^{spt}$ represent the survival from sport fishing, calculated as

$$s_{ii}^{spt} = e^{-f_{it}^{spt}} \tag{13}$$

where f_{it}^{spt} is the instantaneous fishing mortality rate from the recreational fishery in area i and year t.

The natural survival is allowed to be size-dependent through the following relationship

$$s^{nat}(l_t) = \begin{cases} s^{nat}(l_s)(2 - e^{(\frac{l_t - l_s}{l_s})k_s}), & \text{for } l_t < l_s \\ s^{nat}(l_s), & \text{for } l_t \geq l_s \end{cases} \tag{14}$$

where l_t is the length at time t and l_s is a threshold size (assumed to be 80 cm). In this formulation, the natural mortality depends non-linearly on size through the parameter k_s until a threshold size l_s (e.g: the legal size limit) is reached. From that point on, survival is assumed constant. If we wish to estimate survival as size-independent, we can set $k_s = 0$ and estimate s^{nat} as another parameter.

Given this model, for any parameters, and given the known release data $N_{t(g)i(g)}$, we can use the above equations to predict the expected number of tags from the release group g and size–at–release class k returned to the IPHC in area i, year t, as

$$E(\mathbf{X}_t) = \mathbf{R}_t\mathbf{C}_t \tag{15}$$

where $\mathbf{R}_t$ is a diagonal matrix whose positive elements are the area–specific reporting rates.

Therefore, we can find the likelihood (conditional on the parameters of the model) of the observed recoveries x_{it}, (the elements of the vector $\mathbf{X}_t$) for any group g, released at a size k, using a multinomial likelihood

$$\mathcal{L}_{gk}(x|\text{parameters}) = \frac{N_{t(g)i(g)}!}{(\prod_i \prod_t x_{it}!)v!}(\prod_t \prod_i p_{it}^{x_{it}})q^v \tag{16}$$

where

$$q = 1 - \sum_i \sum_t p_{it}$$
$$v = N_{t(g)i(g)} - \sum_i \sum_t x_{it} \tag{17}$$

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$N_{t(g)i(g)}$ is the number of tagged fish released in this group and size-at-release class, x_{it} is the number of tags returned from the fishery in area i at time t (for this group and size–at–release class). The $p's$ are the probabilities that a tagged fish will be captured and returned from a space-time stratum, q is the probability that a tagged fish will never be returned, and v is the number of tags not returned. The probabilities of recovery, p_{it}, are the positive elements of a matrix $\mathbf{P}_t$, defined as

$$\mathbf{P}_t = \mathbf{R}_t \mathbf{U}_t [\prod_{y=t(g)}^{t-1} (\mathbf{S}_y^{tot} \mathbf{S}_y^f \mathbf{M}_y)](1 - \lambda) \tag{18}$$

The likelihood given above is for a single tag release group and a single size-at-release class. The likelihoods of each release groups and size classes are multiplied to yield a total likelihood for all of the data.

$$\mathcal{L}_{Total}(\mathbf{X}_t | \text{parameters}) = \prod_k \prod_g \mathcal{L}_{gk}(\mathbf{X}_t | \text{parameters}) \tag{19}$$

The parameters in this model may be either estimated or assumed as known from other analyses. These parameters are
(1) the movement rates $\mathbf{M}_t$,
(2) the survival from natural mortality $s^{nat}(l_t)$ (or its related parameter k_s),
(3) the size specific selectivity parameters b_{1i} and b_{2i},
(4) the sport fishing mortality rates f_{it}^{spt},
(5) the longline fishing mortality rates h_{it},
(6) the growth parameters a and b,
(7) the tag-loss/shedding rate λ,
(8) the size-dependent factor affecting movement, w, and finally,
(9) the area- and time-specific probability of a tag being returned $\mathbf{R}_t$.

Table 6 summarizes which parameters are estimated, and the source of the data for those that are assumed known.

The following assumptions are made by this model:
1.- tagged fish are a representative sample of the population,
2.- there is no tag loss except for instantaneous tag loss represented by the parameter λ,
3.- there is no effect of tagging on survival or movement except mortality represented by the parameter λ,
4.- all data on marking and recovery time, area and size are correctly recorded,
5.- tagging does not affect the growth or selectivity of the fish,
6.- the fate of each tagged animal is independent of the fate of other tagged animals.

In an earlier analysis (Skalski et al., 1993) we assumed that movement took place once, instantaneously just after tagging. Since we wish to compare the results of the model considered here with those of a one-time movement model, we can modify the current model to be a one-time movement model simply by setting $m_{ij} = 0$ for all years except the year of tagging.

To compare different variants of the basic model, we use a measure of the discrepancy between the model and the data, known as Akaike's Information Criterion, or AIC. The AIC is defined as (Akaike, 1972):

$$AIC = D + 2p \tag{20}$$

where p is the number of estimated parameters and D is the deviance, defined as (McCullagh and Nelder, 1983)

$$\text{Deviance} = -2(log\,\mathcal{L}(\text{data}|\text{parameters}) - log\,\mathcal{L}(\text{data}|\text{data})) \qquad (21)$$

The second term in the above equation, $log\,\mathcal{L}(\text{data}|\text{data})$, represents the log-likelihood of the "full" model (a model with as many parameters as observations), computed by setting the expected recoveries equal to the observed recoveries. The asymptotic distributional properties of the deviance can be used to build a model selection strategy based on hypothesis testing when the competing models are nested. The models that we present are not nested and, therefore, we based our model comparisons on the AIC statistic, a strategy that does not require the models to belong to the same hierarchy. For a review of the application of the AIC statistic to model selection in mark-recovery experiments, see Lebreton et al. (1992).

RESULTS

We will compare several different versions of the basic model. We begin with all parameters assumed known except the movement rates and natural mortality (Model 1) , and then explore the consequences of trying to estimate parameters for reporting rate/tagging mortality (Model 2), size dependent movement (Model 3), size dependent survival (Model 4), and selectivity in Areas 3A and 3B (Models 5 to 7). Each of these comparisons is a nested version of the same model, allowing for additional free parameters. For Models 5b, 6 and 7 we include the data from fish released at greater than 65 cm, whereas the remainder of the models use only data from fish smaller than 65 cm at the time of release. Finally, we compare the same model with one-time movement to the continuous-movement models tested above. A summary of the results for these models is shown in Tables 6 and 7.

Model 1: Movement and natural mortality

Our first model uses only fish released at 65 cm. or less and estimates movement parameters and a constant natural mortality rate. All other parameters are assumed known from other data. In particular, we assume that the values in Table 2 represent the actual reporting rates. Table 8 summarizes the results of this model. This format is used for all subsequent output so we will examine it carefully the first time through. The first line of the table is the estimated survival rate; in this case 0.615. IPHC staff have used 0.8 as the survival rate for fish greater than 80 cm so this number is reasonable. Next a matrix of estimated movement rates is shown. The columns represent the "from" and the rows represent the "to". Each column is constrained to add to 1.0, so that we are, in theory, estimating 10 parameters. However, the pattern of recoveries does not allow estimation of some movement parameters and we have assumed that the 3B-2B, 3B-2A, 3A-2A and 2C-2A parameters are zero. Essentially we do not allow fish to make these individual moves in one year. Since almost all recoveries occurred after several years, the movement model, with these elements set to zero, still has no trouble in moving fish to where they need to be in time to be recaptured. Therefore, we are estimating 6 movement parameters.

Table 6. Summary of estimated parameters values and discrepancies for Models 1 to 5a. Standard errors for the parameters are given in parentheses. An asterisk indicates fixed values.

	Model 1	Model 2	Model 3	Model 4	Model 5a
Survival, $s^{nat}(l_t)$	0.615(0.019)	0.586(0.049)	0.586(0.049)	0.80*	0.80*
Surv. size factor, k_s	0*	0*	0*	-0.438(0.208)	-0.522(0.176)
Tag loss, $(1-\lambda)$	0*	1.365(0.683)	1.365(0.686)	0.367(0.137)	0.249(0.089)
Movement, m_{ij}					
From 3B to 3A	0.111(0.055)	0.111(0.055)	0.117(0.079)	0.111(0.059)	0.144(0.082)
From 3B to 2C	0.024(0.024)	0.024(0.023)	0.025(0.026)	0.027(0.028)	0.049(0.060)
From 3A to 2C	0.024(0.037)	0.025(0.038)	0.027(0.050)	0.026(0.045)	0.036(0.046)
From 3A to 2B	0.015(0.035)	0.014(0.035)	0.013(0.042)	0.022(0.046)	0.055(0.054)
From 2C to 2B	0.281(0.493)	0.290(0.508)	0.319(0.631)	0.289(0.598)	0.163(0.313)
From 2B to 2A	0.043(0.058)	0.043(0.059)	0.045(0.065)	0.042(0.061)	0.036(0.049)
Mov. size factor, w	0*	0*	-0.147(1.193)	0*	0*
Selectivity,					
b_{13b}	112.47*	112.47*	112.47*	112.47*	77.84(13.98)
b_{23b}	0.092*	0.092*	0.092*	0.092*	0.127(0.095)
b_{13a}	112.47*	112.47*	112.47*	112.47*	87.92(6.93)
b_{23a}	0.092*	0.092*	0.092*	0.092*	0.149(0.056)
Deviance	1005.44	998.19	997.96	1174.69	928.92
AIC	1019.44	1014.19	1015.96	1190.69	952.92

Table 7. Summary of estimated parameters values and discrepancies for Models 5b to 7. Standard errors for the parameters are given in parentheses. An asterisk indicates fixed values.

	Model 5b	Model 6	Model 7
Survival, $s^{nat}(l_t)$	0.80*	0.80*	0.80*
Surv. size factor, k_s	-0.475(0.181)	-0.472(0.182)	-0.475(0.179)
Tag loss, $(1-\lambda)$	0.245(0.683)	0.241(0.075)	0.242(0.089)
Movement, m_{ij}			
From 3B to 3A	0.171(0.091)	0.231(0.087)	0.182(0.072)
From 3B to 2C	0.050(0.060)	0.061(0.056)	0.054(0.050)
From 3A to 2C	0.044(0.062)	0.080(0.101)	0.080(0.101)
From 3A to 2B	0.032(0.060)	0.026(0.094)	0.023(0.094)
From 2C to 2B	0.159(0.340)	0.302(0.487)	0.295(0.461)
From 2B to 2A	0.045(0.073)	0.058(0.068)	0.057(0.049)
Mov. size factor, w	0*	-0.678(1.502)	-0.525(1.586)
Selectivity,			
b_{13b}	80.46(16.37)	77.85(17.89)	88.39(7.91)
b_{23b}	0.120(0.100)	0.118(0.111)	0.125(0.046)
b_{13a}	90.70(8.47)	89.76(8.43)	88.39(7.91)
b_{23a}	0.132(0.055)	0.135(0.057)	0.125(0.046)
Deviance	1478.74	1464.07	1499.94
AIC	1502.74	1490.07	1521.94

Released in Area 3A, 1980   Released in Area 3B, 1980   Released in Area 3A, 1981   Released in Area 3B, 1981
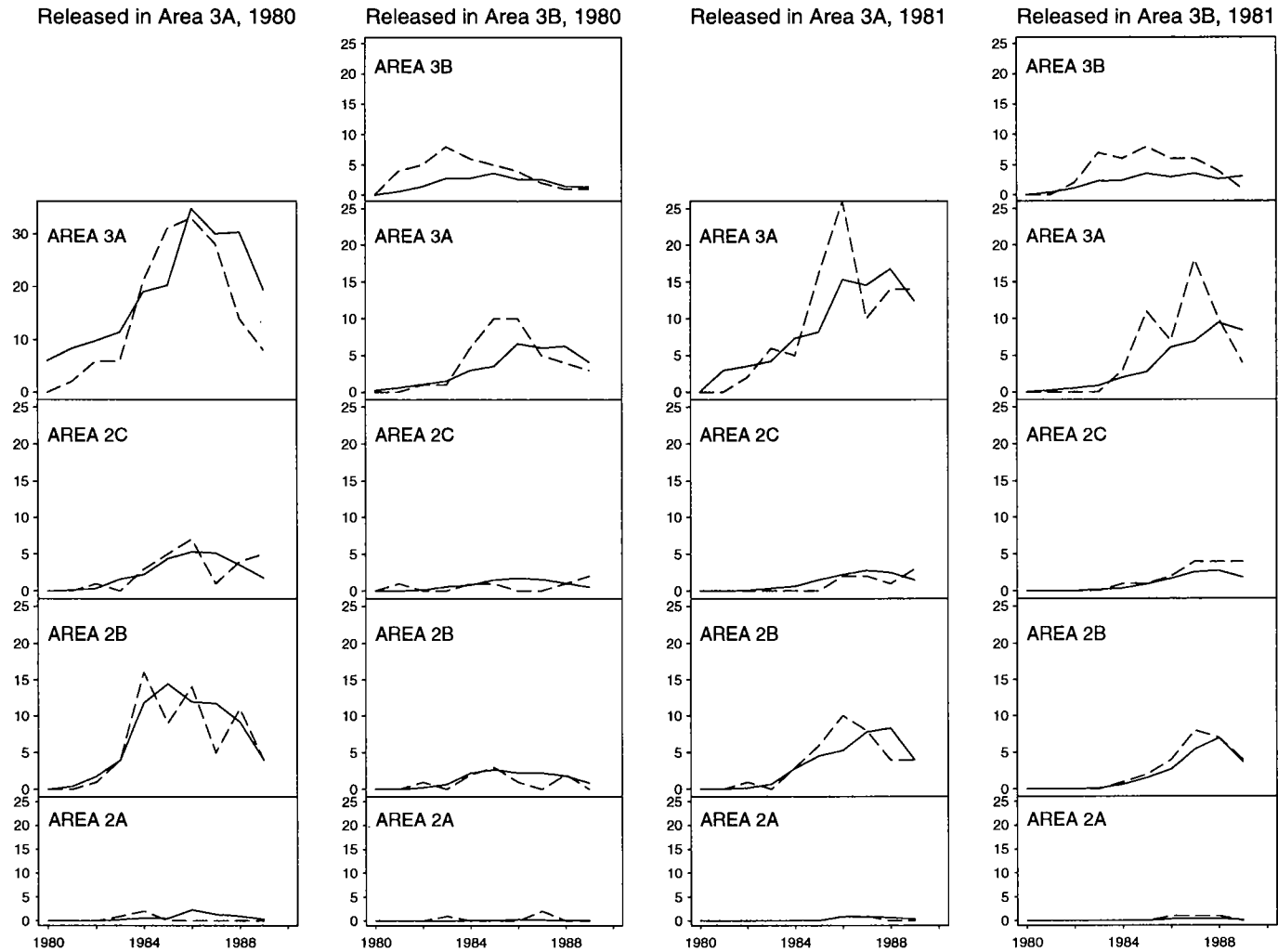

Figure 7. Predicted and observed recovery patterns for Model 1.

Shown below the movement parameters is the parameter correlation matrix computed from the inverse Hessian matrix for all parameters. In general there is very little confounding of parameters with the exception of the correlations between 3A-2C – 3A-2B, 2C-2B – 3A-2C, and 2C-2B – 3A-2B elements in this matrix. These high correlations reflect the fact that one can get approximately the same pattern in recoveries by several "migration routes." Presumably, we could have eliminated at least one of these parameters if we wished to further reduce the number of parameters estimated. At the bottom of the table is the negative log-likelihood, the deviance and the AIC.

Figure 7 shows the observed and predicted recovery patterns for tagged fish for this model. Each panel represents the results for each of the four release groups included in the analysis. The abscissa represents the year, running from 1980 to 1989. Within each panel, there is a separate box for recoveries in each area, with the dotted line representing the observed data, and the solid line the model fit. The height of the graph is the number of observed or expected recoveries and is scaled the same on all graphs. The largest number of observed and expected recoveries were in 3A and 2B for fish released in 3A, and in 3B and 3A for fish released in 3B. The most obvious systematic deviation between observed and expected is recoveries in Areas 3A and 3B from fish released in 3B. The observed recoveries occur well to the left of the expected recoveries. The model is unable to adjust the movement parameters and survival rates in order to recover as many tags as were observed in the early and mid 1980s.

Table 8. Results for Model 1.

Survival $(s^{nat}(l_s))$:   0.615

Movement parameters (m_{ij}):

	3B	3A	2C	2B	2A
3B	0.864				
3A	0.111	0.961			
2C	0.024	0.024	0.719		
2B		0.015	0.281	0.957	
2A				0.043	1.000

Parameter correlation matrix:

	$s^{nat}(l_s)$	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}
$s^{nat}(l_s)$	1.000						
m_{3A3B}	-0.087	1.000					
m_{2C3B}	-0.084	-0.201	1.000				
m_{2C3A}	-0.045	-0.027	-0.128	1.000			
m_{2B3A}	-0.032	0.080	0.033	-0.904	1.000		
m_{2B2C}	0.004	-0.080	-0.081	0.874	-0.907	1.000	
m_{2A2B}	0.013	-0.026	-0.027	0.193	-0.190	0.178	1.000

Negative log-likelihood :   910.03

Deviance :   1005.44
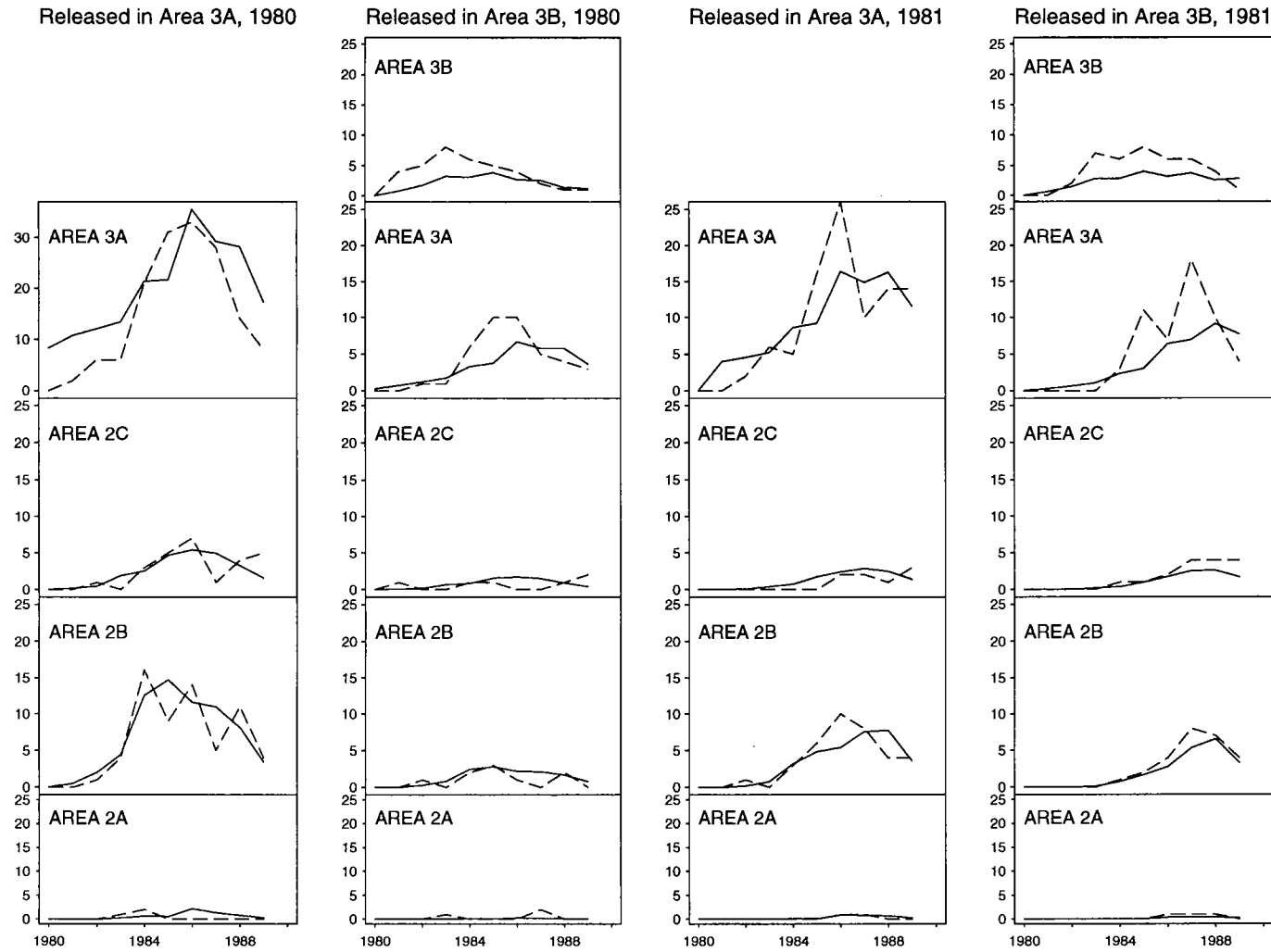
AIC :   1019.44

Figure 8. Predicted and observed recovery patterns for Model 2.

Model 2: Tag loss and rescaling of tag return rates

In Model 1 we assumed that the parameters r_{it}, the tag return rates, are known and equal to the values given in Table 2. In Model 2, we allow for all of these rates to be adjusted by a single scalar. This parameter can be interpreted as measuring the departures of the values in Table 2 from the true reporting rates, and the effect of tag loss or tag induced mortality. We cannot discriminate between these two effects from the data alone, since they operate in the same way in the model, as a one-time event. Therefore, we will interpret as a factor equivalent to $1 - \lambda$ in equation 1. Table 9 shows the results. The model estimates that the return rates in Table 2 should be increased by 36% on average, and that as a consequence the survival estimate was slightly lower. The movement rates have not changed very much, and the overall deviance is reduced by 7.5. There is a strong confounding (indicated by a high correlation) between the reporting rate/tag mortality factor and the survival estimate, which is expected in any model with two mortality terms. More important, the interpretation of this factor should be done with caution, since the product of the reporting rates and this factor actually exceeds unity in some cases.

In spite of this confounding and the difficult interpretation, the addition of the factor increases significantly the likelihood of the model and we will retain this parameter in the following versions of the model.

Figure 8 shows the distribution of observed and expected recoveries. If we compare this Figure with the results for Model 1, we see that the improvement is not causing a noticeable change in the pattern of the residuals.

Table 9. Results for Model 2.

	Survival $(s^{nat}(l_s))$:	0.586
	Reporting rate factor $(1 - \lambda)$:	1.365

Movement parameters(m_{ij}):

	3B	3A	2C	2B	2A
3B	0.865				
3A	0.111	0.962			
2C	0.024	0.025	0.710		
2B		0.014	0.290	0.957	
2A				0.043	1.000

Parameter correlation matrix:

	$s^{nat}(l_s)$	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	Rep.fac
$s^{nat}(l_s)$	1.000							
m_{3A3B}	-0.014	1.000						
m_{2C3B}	-0.010	-0.195	1.000					
m_{2C3A}	-0.043	-0.003	-0.173	1.000				
m_{2B3A}	0.065	0.053	0.090	-0.914	1.000			
m_{2B2C}	-0.029	-0.051	-0.136	0.879	-0.913	1.000		
m_{2A2B}	-0.009	-0.003	-0.038	0.204	-0.202	0.187	1.000	
Rep.fac.	-0.929	-0.019	-0.023	0.027	-0.081	0.032	0.014	1.000

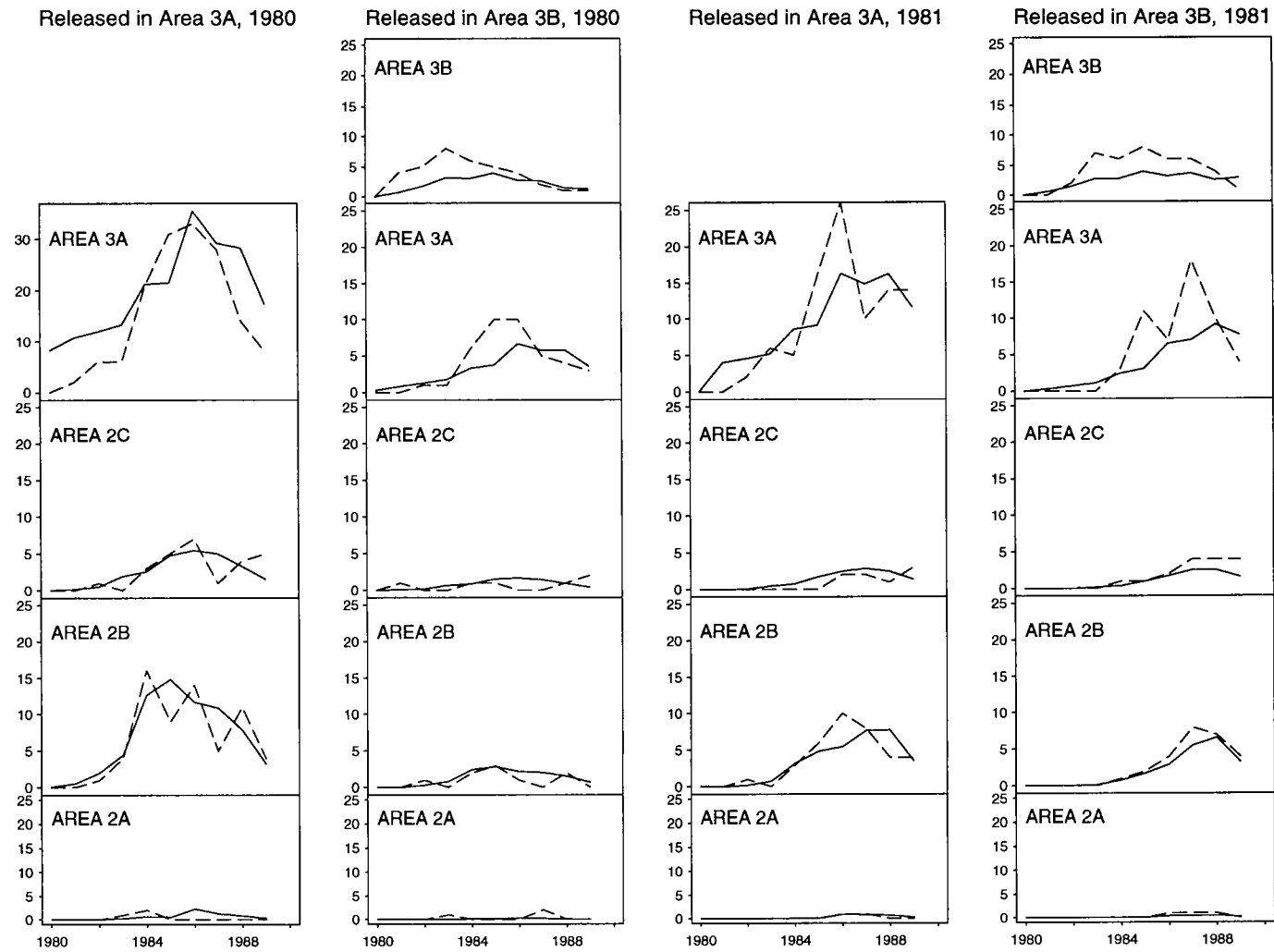|	
Negative log-likelihood :	906.37
Deviance :	998.19
AIC :	1014.19

Figure 9. Predicted and observed recovery patterns for Model 3.

Model 3: Size-specific movement

Given the sedentary nature of adults, it seems reasonable to allow for size-specific movement by estimating the parameter w in equation 3. Table 10 shows the results of this model. The estimated slope of the movement vs size curve is negative, and this suggests that smaller fish are more likely to move, as expected. However, the improvement in the fit of the model is not significant and, therefore, we conclude that adding this type of size-specific movement does not improve the model fit. The correlations between the movement parameters remain similar to those seen in the basic model and the added parameter shows a moderate degree of confounding with the movement parameters, in particular with movement from 3B to 3A. Figure 9 shows the observed and expected results, which again show no difference from Model 1.

Table 10. Results for Model 3.

Survival $(s^{nat}(l_s))$: 0.586
Reporting rate factor $(1 - \lambda)$: 1.365
Movement size factor (w) : -0.147

Movement parameters(m_{ij}):

	3B	3A	2C	2B	2A
3B	0.858				
3A	0.117	0.959			
2C	0.025	0.027	0.681		
2B		0.013	0.319	0.955	
2A				0.045	1.000

Parameter correlation matrix:

	$s^{nat}(l_s)$	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	w	Rep.fac
$s^{nat}(l_s)$	1.000								
m_{3A3B}	0.003	1.000							
m_{2C3B}	-0.000	0.069	1.000						
m_{2C3A}	-0.031	0.309	-0.037	1.000					
m_{2B3A}	0.064	-0.008	0.116	-0.849	1.000				
m_{2B2C}	-0.020	0.240	-0.033	0.910	-0.868	1.000			
m_{2A2B}	-0.004	0.179	0.039	0.311	-0.224	0.285	1.000		
w	-0.021	-0.665	-0.318	-0.446	0.042	-0.387	-0.267	1.000	
Rep.fac.	-0.929	-0.038	-0.036	0.010	-0.077	0.017	0.005	0.037	1.000

Negative log-likelihood : 906.25
Deviance : 997.96
AIC : 1015.96

Model 4: Size-dependent survival

It is widely believed that size-dependent survival is common in fish, and that small fish experience higher natural mortality rates than larger fish. In Model 4, we allow survival to be size dependent, according to equation 14, below the legal size limit of 80 cm. The estimated fishing mortalities used in equation 8 and shown in Table 3 are based on catch-at-age analyses assuming a survival of 0.8 for all fish above 80 cm. Therefore, for consistency, we assumed the same value for the parameter $s^{nat}(l_s)$ in equation 14.
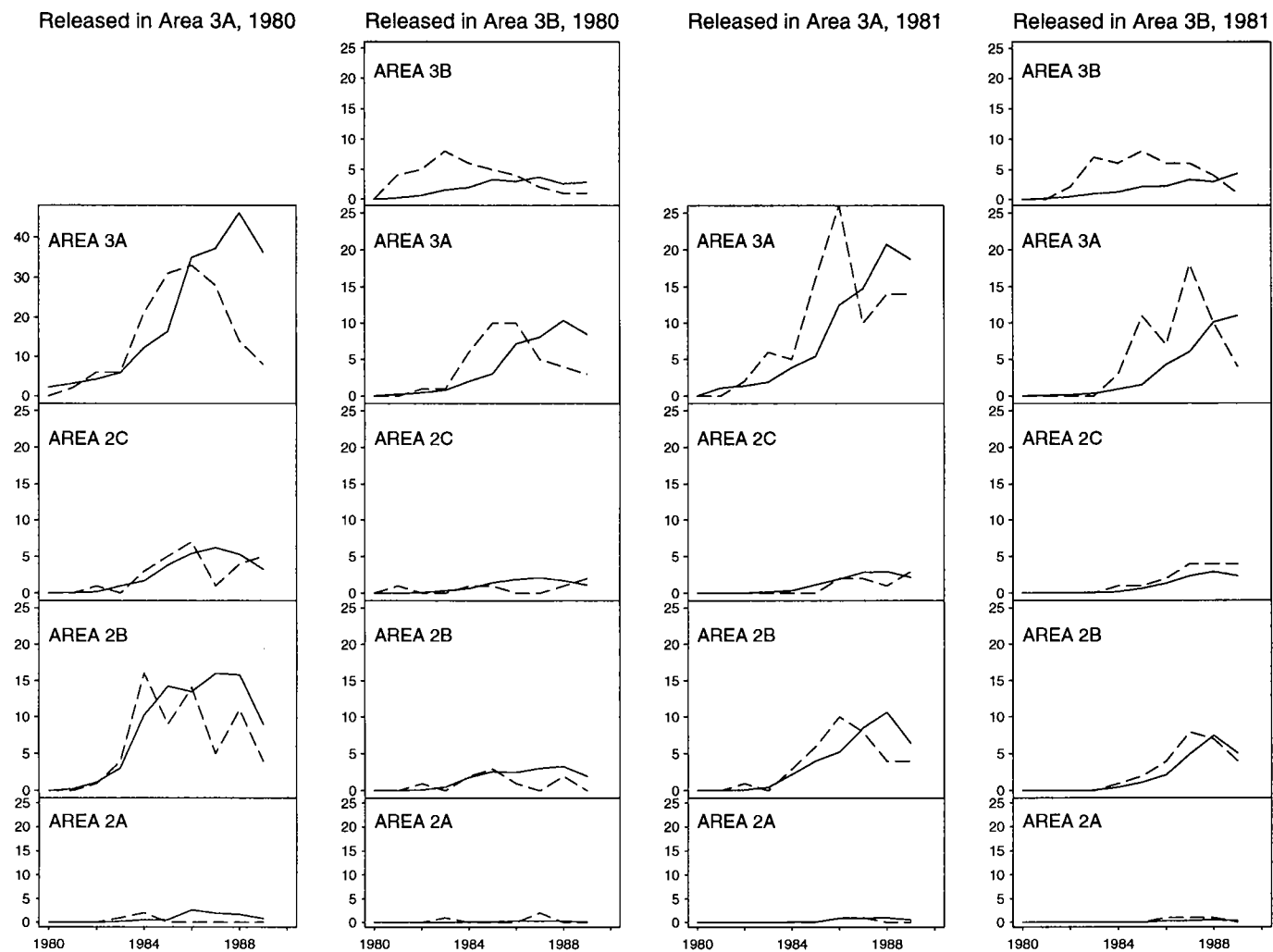
Figure 10. Predicted and observed recovery patterns for Model 4.

Table 11 shows the results of this model. The deviance increased to 1174.69, and an examination of Figure 10 shows that the expected recovery pattern has changed dramatically. The reporting rate factor exhibited a large decline to 0.367. This is not surprising, given the correlation between this parameter and the survival parameter. The new value for the reporting rate factor seems more reasonable than in previous versions of the model. IPHC staff considers that the values in Table 2 probably represent upper limits for the actual reporting rates. If we consider that the factor also measures tag mortality/tag loss a value of 0.37 seems within the range of expected values.

However, the pattern of residuals (Figure 10) and the likelihood are indicating that further changes are necessary in the model to better predict the observed recoveries.

Table 11. Results for Model 4.

Assumed survival $(s^{nat}(l_s))$: 0.800

Reporting rate factor $(1 - \lambda)$: 0.367

Survival size factor (k_s) : -0.438

Movement parameters(m_{ij}):

	3B	3A	2C	2B	2A
3B	0.863				
3A	0.111	0.952			
2C	0.027	0.026	0.681		
2B		0.022	0.289	0.955	
2A				0.042	1.000

Parameter correlation matrix:

	k_s	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	Rep.fac
k_s	1.000							
m_{3A3B}	-0.012	1.000						
m_{2C3B}	-0.056	-0.230	1.000					
m_{2C3A}	-0.048	-0.094	0.014	1.000				
m_{2B3A}	0.003	0.151	-0.116	-0.907	1.000			
m_{2B2C}	-0.031	-0.150	0.077	0.897	-0.913	1.000		
m_{2A2B}	-0.003	-0.020	0.001	0.186	-0.181	0.174	1.000	
Rep.fac.	-0.858	-0.038	0.012	0.032	-0.025	0.037	0.007	1.000

Negative log-likelihood : 994.62

Deviance : 1174.69

AIC : 1190.69

Models 5, 6 and 7: Estimating size–selectivity

Thus far we have been assuming that their size-selectivity relationships for tagged halibut are those estimated by the IPHC staff from the commercial catch data. However, these relationships might not be adequate for tagged halibut, since tagged fish may be retained by the fishermen regardless of the size. In fact, a significant proportion of the longline recoveries of tags in Areas 3A and 3B were from individuals under the legal size of 80 cm, as shown in Figure 11. This figure also suggests that a difference in selectivity might be possible between Areas 3A and 3B. Therefore, we decided to estimate the parameters of size-selectivity functions for these two areas. This involves adding four
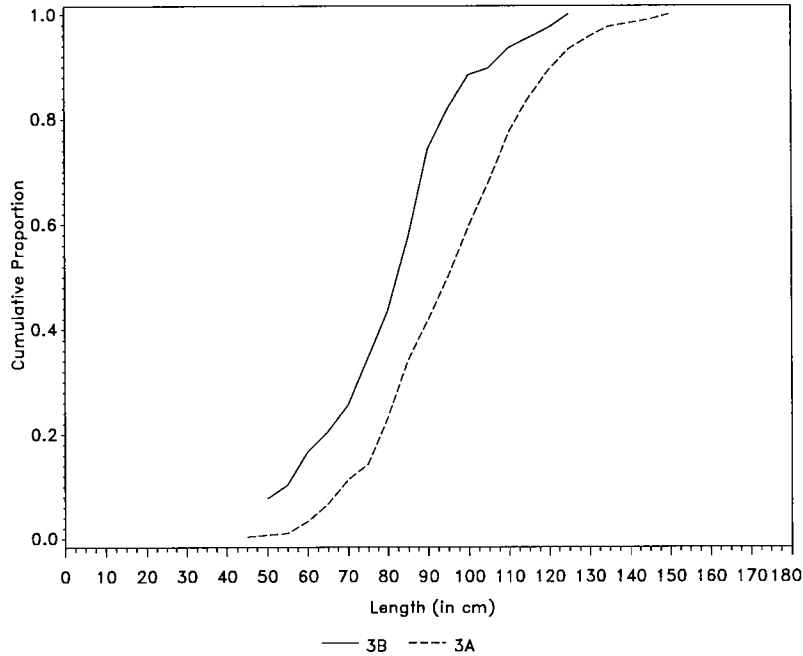
Length distribution at recovery.

Figure 11. Cummulative length distribution of fish at recovery.

additional parameters (see equation 9). In principle, we could have attempted to also estimate selectivities for the remaining regulatory Areas (2C, 2B and 2A). However, the number of recoveries in these areas is too small to obtain good estimates of additional parameters. We retain the assumption that fish greater than 80 cm have a survival of 0.8 that decreases for fish below 80 cm, and we also estimated the multiplier for the reporting rates.

Table 12 shows the results of Model 5. Adding the four additional selectivity parameters reduces the deviance by over 240. This is the first major change in deviance from all the alternative models examined. Figure 12 shows the observed and expected values and the fit is clearly better. The problem we observed earlier with recoveries in 3A and 3B from fish released in 3B has diminished. The only systematic problem we can see in these graphs is that the recoveries in 2B seem to precede the predicted values for fish released in 1981, but not for fish released in 1980. Movement rates are greater, indicating that more fish move to the southern areas. The movement rate from Area 2C to 2B is much lower than before. This is probably a consequence of more fish leaving the northern areas earlier than in previous models.

However, there is a problem with the basic tagging data used so far. Since the primary purpose of this analysis was to estimate movement rates for juvenile halibut, only those fish that were tagged at sizes less than 65 cm were used in the analyses. As fish grow, the size range of the tagged fish still alive also moves until they gradually become more vulnerable to the gear. Therefore, the estimated selectivities can accommodate time trends in other effects, not explicitly included in the model. In other words, the experimental design lacks orthogonality. In order to reduce this problem, we decided to incorporate the data from fish tagged at sizes greater than 65 cm.

A new complication arises with the additional data; the extended size range includes older fish that cannot be considered juveniles and therefore are less likely to move, according to what is assumed about the biology of the halibut. The data offer some

Table 12. Results for Model 5a.

Assumed survival $(s^{nat}(l_s))$: 0.800
Reporting rate factor $(1 - \lambda)$: 0.249
Survival size factor (k_s) : -0.522
Selectivity parameter (b_{13B}) : 77.841
Selectivity parameter (b_{23B}) : 0.127
Selectivity parameter (b_{13A}) : 87.917
Selectivity parameter (b_{23A}) : 0.149

Movement parameters(m_{ij}):

	3B	3A	2C	2B	2A
3B	0.807				
3A	0.144	0.909			
2C	0.049	0.036	0.837		
2B		0.055	0.163	0.964	
2A				0.036	1.000

Parameter correlation matrix:

	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	k_s	b_{13B}	b_{23B}	b_{13A}	b_{23A}	Rep.fac
m_{3A3B}	1.000											
m_{2C3B}	-0.464	1.000										
m_{2C3A}	-0.269	0.274	1.000									
m_{2B3A}	0.342	-0.422	-0.799	1.000								
m_{2B2C}	-0.386	0.423	0.814	-0.839	1.000							
m_{2A2B}	-0.056	0.060	0.145	-0.149	0.150	1.000						
k_s	0.016	-0.009	-0.027	0.005	-0.028	0.003	1.000					
b_{13B}	-0.344	-0.096	0.059	-0.037	0.071	0.015	-0.000	1.000				
b_{23B}	0.207	0.055	-0.037	0.023	-0.044	-0.008	-0.020	-0.745	1.000			
b_{13A}	0.157	-0.064	-0.096	-0.098	-0.004	0.020	0.101	0.009	0.014	1.000		
b_{23A}	-0.085	0.032	0.060	0.089	-0.013	-0.015	-0.124	-0.009	-0.005	-0.779	1.000	
Rep.fac.	-0.008	0.000	-0.025	-0.003	-0.024	-0.010	0.823	-0.097	0.016	-0.131	0.017	1.000

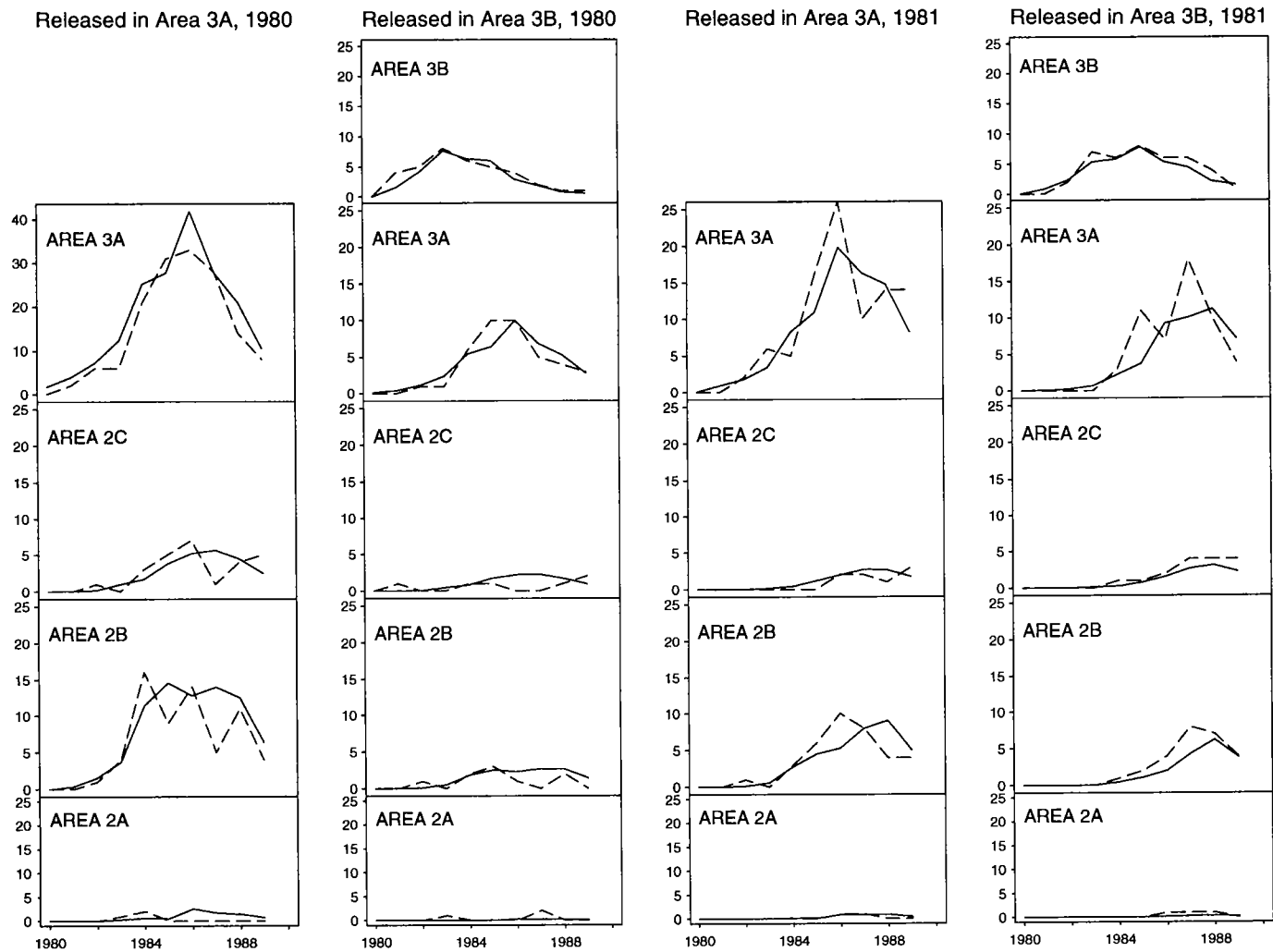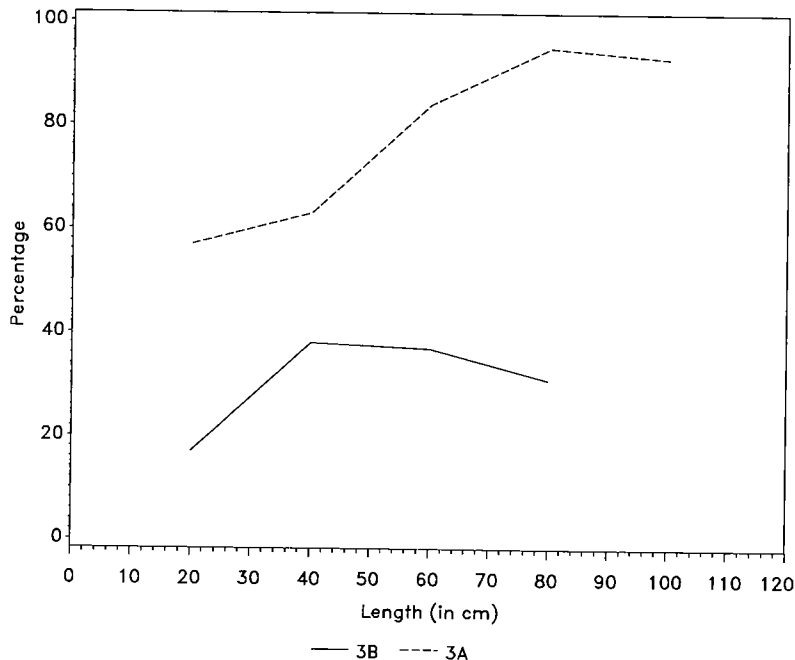Negative log-likelihood : 871.49
Deviance : 928.92
AIC : 952.92

Figure 12. Predicted and observed recovery patterns for Model 5.

Percentage of tagged fish recovered in area of release.

Figure 13. Percentage of tagged fish that were recovered in the area of release versus length-at-release.

support for this latter assumption since large fish released in 3A tended to be recovered in the area of release more often than small fish (Figure 13). This pattern could have been explained, to some extent, by the size dependency in the probability of capture; large fish tend to be captured sooner and therefore are more likely to be recovered in the area of release before they leave. However, in that case, we would have expected to see the same pattern in both Areas 3A and 3B and Figure 13 shows that the proportion of fish recovered by size-at-release is relatively constant for Area 3B. This interpretation should be done with caution, since similarly different patterns can also arise form area-specific differences in probabilities of capture; for example, large fish might tend to stay in Area 3B, but the ones that leave might have a much greater probability of being captured in other areas.

Therefore, there is some evidence of size-dependency in the movement rates when we extend the range of sizes considered in the analysis. To deal with this problem, and to keep the movement rates relative to juvenile fish, we incorporated in the model the constraint that fish larger than a given size do not move. This constraint was not necessary in the previous models; the size dependency in movement rates did not seem to be an important effect, as we concluded from Model 3. As an alternative to fixing the maximum size at which a fish could move, we could have incorporated the size restriction as an additional parameter to be estimated. However, when we tried this approach, the minimization algorithm failed to find a global minimum, since the value of the objective function was relatively insensitive to small changes in this parameter. Therefore, we fitted the model assuming different values for the maximum size at which a fish is allowed to move (from 100 cm to 120 cm at 5 cm intervals) , and chose the value that gave the smallest objective function (Figure 14). As a result, we will assume in the next version of the model that fish above 115 cm do not move.

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Negative log-likelihood as function of cutoffpoint.
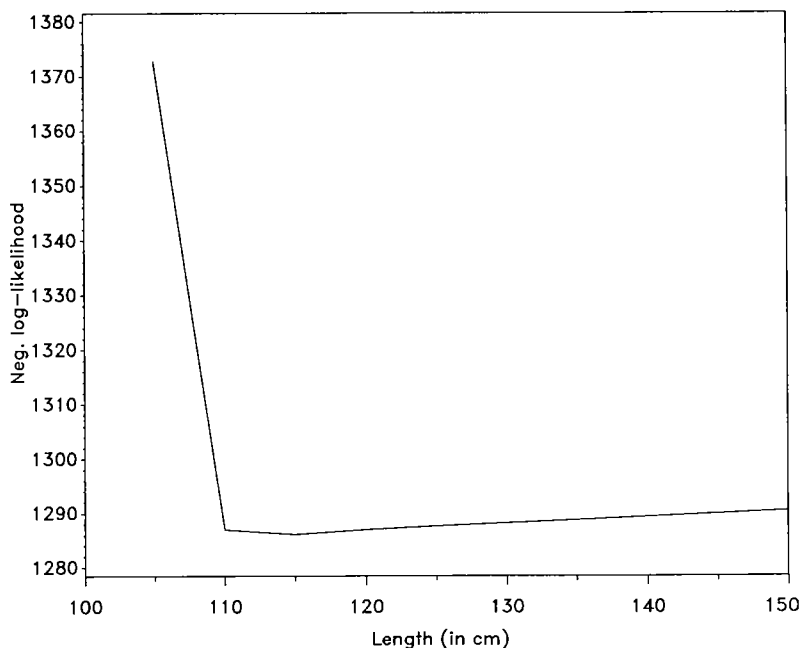
Figure 14. Value of the negative log-likelihood function versus maximum size of fish moving.

Table 13 and Figure 15 show the results of these modifications of Model 5. The comparison with previous models is complicated by the fact that we are adding more observations, and the negative log-likelihood and deviances naturally increased. However, the pattern in the residuals suggests that the fit has not been improved by the changes introduced in the data and the model. The movement rates now suggest that fish leave Area 3B more frequently than in previous model versions. The estimated selectivity parameters show slightly larger correlations with other parameters than before and they predict now that fish become vulnerable at larger sizes (see Tables 12 and 13).

One problem with the structure of Model 5 is that is not fully capturing the level of size-dependency in the movement of larger fish suggested by Figure 13. Therefore, we decided to incorporate again the size-dependency in the movement, as described in equation 4, in Model 6. Table 14 and Figure 16 show the results of this version. The relative improvement in the deviance is small but significant. A comparison of Figures 15 and 16 does not show differences in the pattern of the residuals. This similarity can probably be due to the fact that, for the figures, residuals are summed across size classes. If the addition of the size-dependent movement parameter improved the distribution of recoveries among the size classes, this improvement would not be noticeable in the residuals as shown in the figures. The new parameter seems to be moderately confounded with the movement rate from 3B to 3A and the estimated selectivity curve parameters for Area 3B, probably a consequence of the trade-offs between the apparently different patterns in size-dependent movement between Areas 3B and 3A. Estimated movement rates are larger, in particular, for fish leaving Area 2C. This a consequence of the size-dependency incorporated in the model and the fact that the movement parameters are now relative to a 50-cm fish. In the model, the movement rates decrease exponentially with size, so to be able to move fish from Area 2C at a significant rate, the movement rate (of a 50-cm fish) has to increase considerably. As a consequence, the movement rate from 3A to 2C has also increased while the movement from 3A to 2B has decreased.

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Table 13. Results for Model 5b. Based on data comprising all sizes at release, fish greater than 115 cm do not move.

Assumed survival $(s^{nat}(l_s))$:	0.800
Reporting rate factor $(1 - \lambda)$:	0.245
Survival size factor (k_s) :	-0.475
Selectivity parameter (b_{13B}) :	80.456
Selectivity parameter (b_{23B}) :	0.120
Selectivity parameter (b_{13A}) :	90.701
Selectivity parameter (b_{23A}) :	0.132

Movement parameters (m_{ij}):

	3B	3A	2C	2B	2A
3B	0.778				
3A	0.171	0.924			
2C	0.050	0.044	0.841		
2B		0.032	0.159	0.955	
2A				0.045	1.000

Parameter correlation matrix:

	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	k_s	b_{13B}	b_{23B}	b_{13A}	b_{23A}	Rep.fac
m_{3A3B}	1.000											
m_{2C3B}	-0.375	1.000										
m_{2C3A}	-0.039	-0.089	1.000									
m_{2B3A}	0.108	-0.045	-0.852	1.000								
m_{2B2C}	-0.121	0.000	0.819	-0.883	1.000							
m_{2A2B}	-0.022	-0.010	0.235	-0.241	0.239	1.000						
k_s	0.037	-0.013	-0.082	0.070	-0.102	-0.011	1.000					
b_{13B}	-0.356	-0.112	0.057	-0.053	0.065	0.022	0.000	1.000				
b_{23B}	0.204	0.061	-0.035	0.030	-0.041	-0.011	0.016	-0.739	1.000			
b_{13A}	0.165	-0.063	-0.122	-0.059	-0.017	0.011	0.144	0.026	0.009	1.000		
b_{23A}	-0.092	0.036	0.092	0.046	0.007	-0.005	-0.117	-0.023	-0.002	-0.768	1.000	
Rep.fac.	-0.001	-0.002	-0.070	0.084	-0.062	-0.030	0.689	-0.116	0.050	-0.228	0.113	1.000

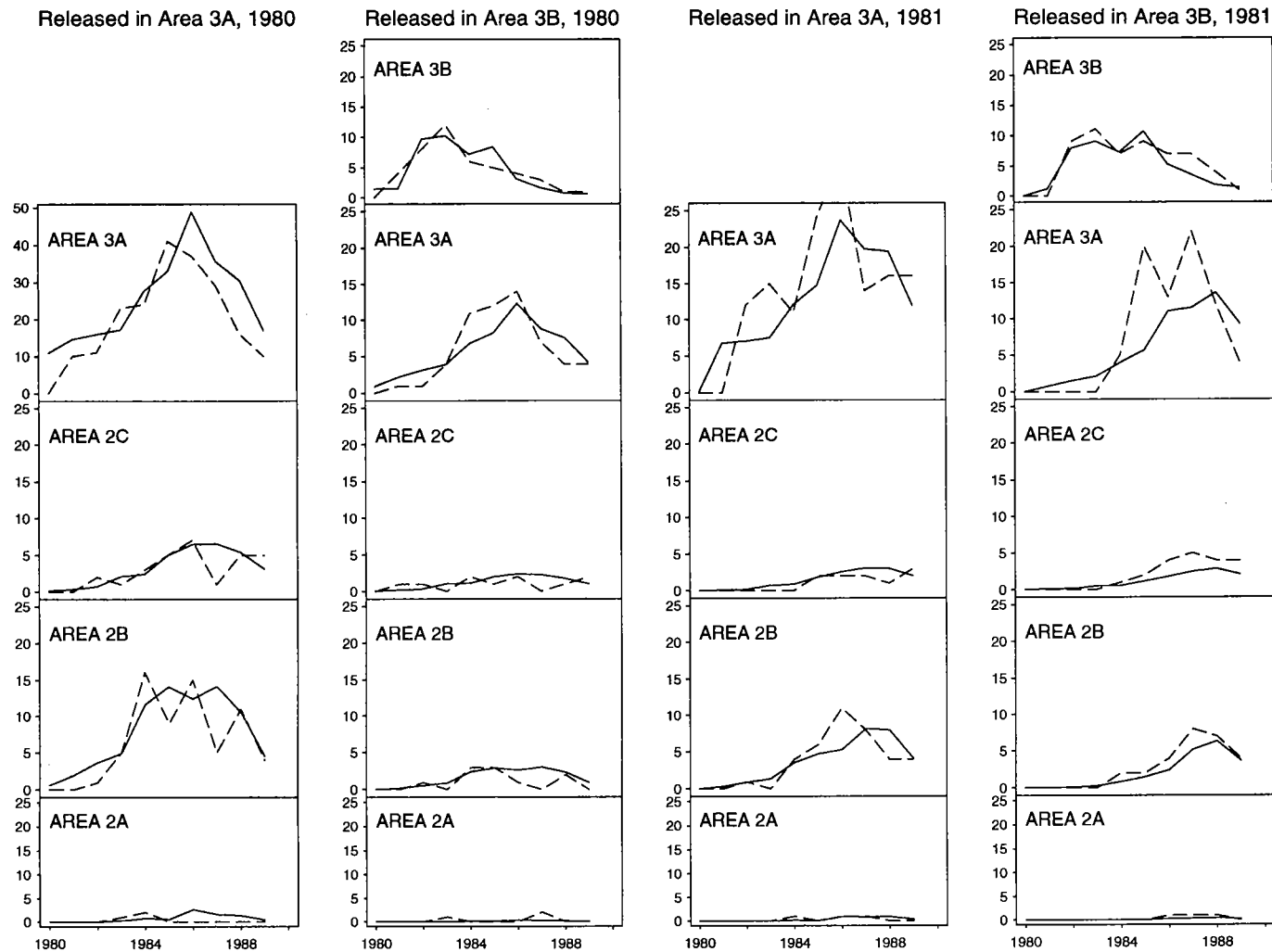|	
Negative log-likelihood :	1286.12
Deviance :	1478.74
AIC:	1502.74

Figure 15. Predicted and observed recovery patterns for Model 5, extended data set.

Table 14. Results for Model 6. Based on data comprising all sizes at release, assuming that fish greater than 115 cm do not move.

Assumed survival $(s^{nat}(l_s))$:	0.800
Reporting rate factor $(1-\lambda)$:	0.241
Survival size factor (k_s) :	-0.472
Movement size factor (w) :	-0.678
Selectivity parameter (b_{13B}) :	77.848
Selectivity parameter (b_{23B}) :	0.118
Selectivity parameter (b_{13A}) :	89.760
Selectivity parameter (b_{23A}) :	0.135

Movement parameters(m_{ij}):

	3B	3A	2C	2B	2A
3B	0.708				
3A	0.231	0.894			
2C	0.061	0.080	0.698		
2B		0.026	0.302	0.942	
2A				0.058	1.000

Parameter correlation matrix:

	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	k_s	b_{13B}	b_{23B}	b_{13A}	b_{23A}	Rep.fac	w
m_{3A3B}	1.000												
m_{2C3B}	-0.272	1.000											
m_{2C3A}	0.293	-0.274	1.000										
m_{2B3A}	-0.134	0.272	-0.923	1.000									
m_{2B2C}	0.241	-0.269	0.922	-0.933	1.000								
m_{2A2B}	0.145	-0.117	0.444	-0.428	0.430	1.000							
k_s	0.034	0.038	-0.115	0.130	-0.136	-0.038	1.000						
b_{13B}	-0.376	-0.126	-0.006	-0.039	0.009	0.003	-0.038	1.000					
b_{23B}	0.109	0.038	-0.047	0.032	-0.046	-0.024	0.026	-0.692	1.000				
b_{13A}	0.039	-0.079	-0.133	-0.000	-0.046	0.022	0.109	0.048	0.008	1.000			
b_{23A}	-0.025	0.039	0.092	-0.005	0.030	-0.015	-0.097	-0.031	-0.002	-0.760	1.000		
Rep.fac.	-0.034	0.046	-0.080	0.115	-0.083	-0.040	0.703	-0.149	0.060	-0.233	0.114	1.000	
w	-0.547	-0.148	-0.331	0.078	-0.272	-0.177	-0.031	0.168	0.061	0.147	-0.071	-0.081	1.000

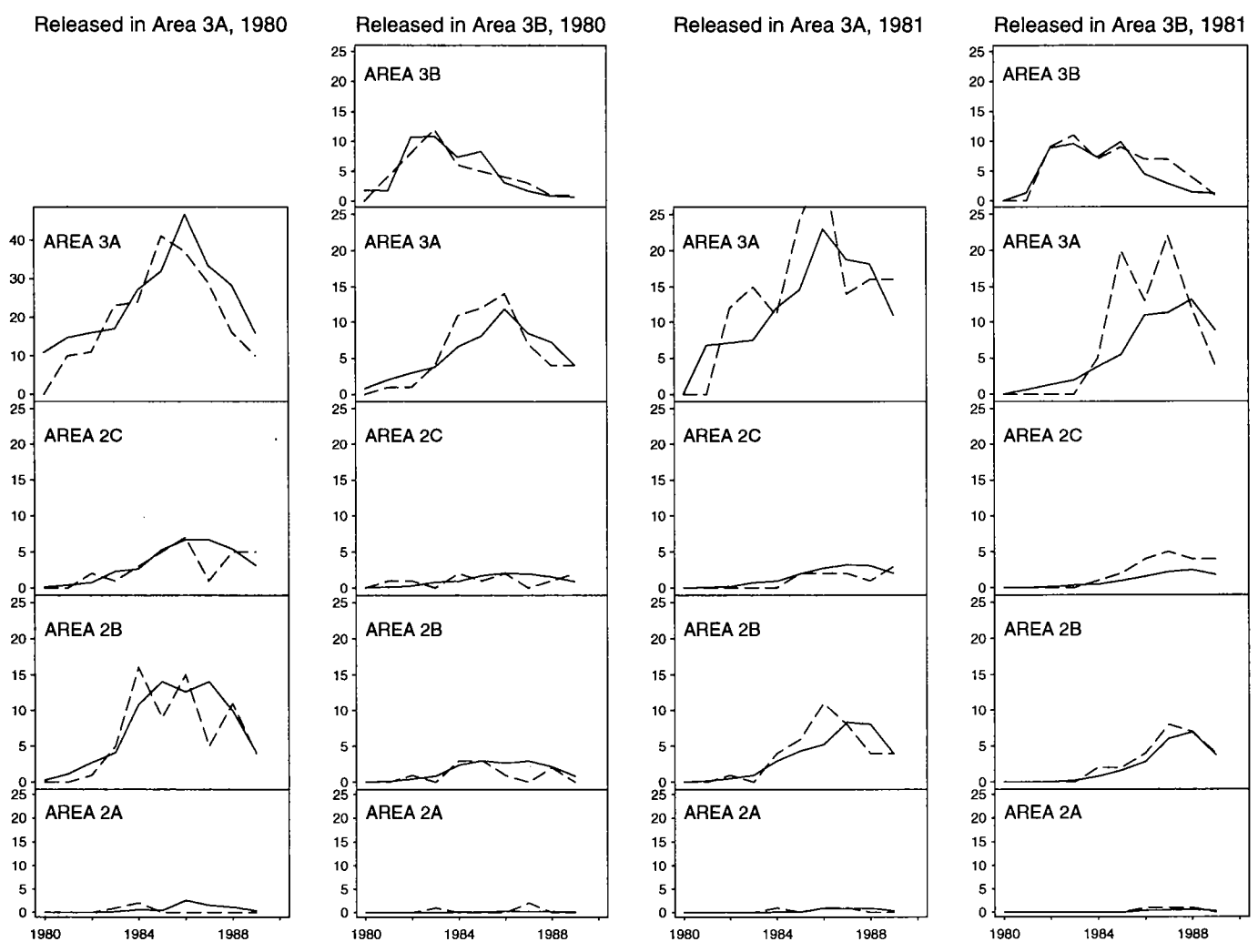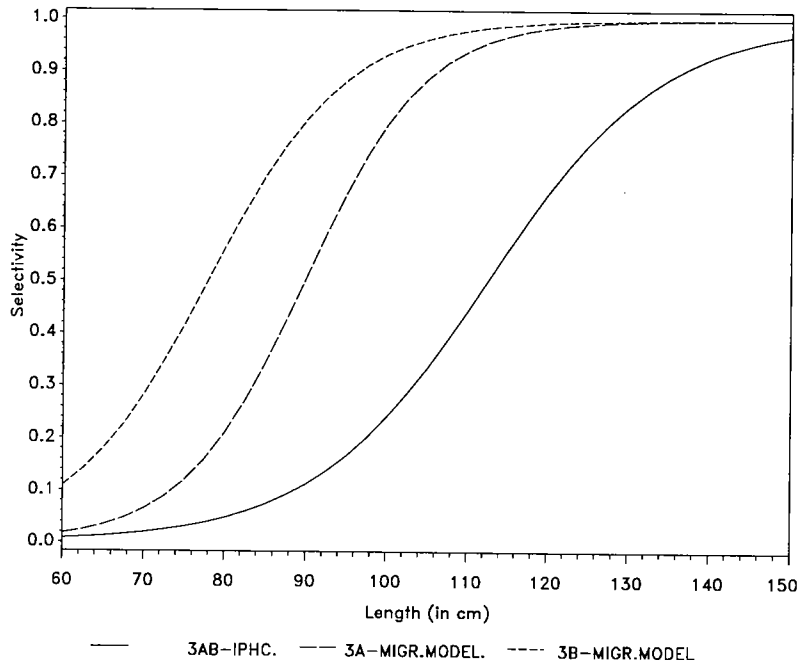|	
Negative log-likelihood :	1279.16
Deviance :	1464.07
AIC :	1490.07

Figure 16. Predicted and observed recovery patterns for Model 6.

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Comparison of selectivity curves.

Figure 17. Size-selectivity relationships from catch-at-age analysis converted to length and as estimated from Model 6 for Areas 3A and 3B.

Figure 17 shows the selectivity relationships for 3A and 3B as estimated from the tagging data, and as derived from the commercial catch data. The model estimates that fish become vulnerable to the gear much earlier than the parameters derived from catch-at-age data indicate, and by implication the reason the previous models could not get recoveries in 3A and 3B early enough, was that the selectivity curves derived from catch data were not adequate for the tagged fish.

Table 14 shows a significant difference in the movement rates for this model compared to those of Table 10. We see much higher movement rates; the proportion of fish staying in 3A drops from 96% to 89%, a doubling in the proportion of fish that leave 3A each year. In earlier runs with the assumed selectivities the best fits were obtained by holding fish in 3A and 3B so that there would be enough still there to provide recoveries given the very delayed selectivity relationship. By allowing fish to become vulnerable earlier in 3A and 3B, the model can move more fish south and still have enough fish in 3A and 3B to show up as recoveries.

The parameter correlation matrix in Table 14 shows low correlation between most of the parameter estimates. There is no serious correlation between the selectivity parameters and the movement rates. The only large correlation are the ones already indicated between the movement rates in the southern areas, between the tag loss/reporting rate parameter and the size mortality parameter, and between the two parameters of each of the selectivity curves. There is a moderate correlation between the size-dependent movement factor and the movement rate from 3B to 3A.

Model 7 is a variation on Model 6 in which we estimate a single selectivity relationship for Areas 3A and 3B combined. Because of the large contribution of the 3A data to the total likelihood, the combined selectivity is closer to the one previously estimated

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Table 15. Results for Model 7.

Assumed survival $(s^{nat}(l_s))$: 0.800
Reporting rate factor $(1 - \lambda)$: 0.242
Survival size factor (k_s) : -0.475
Movement size factor (w) : -0.525
Selectivity parameter (b_{13Ab}) : 88.389
Selectivity parameter (b_{23Ab}) : 0.125

Movement parameters (m_{ij}):

	3B	3A	2C	2B	2A
3B	0.764				
3A	0.182	0.897			
2C	0.054	0.080	0.705		
2B		0.023	0.295	0.943	
2A				0.057	1.000

Parameter correlation matrix:

	m_{3A3B}	m_{2C3B}	m_{2C3A}	m_{2B3A}	m_{2B2C}	m_{2A2B}	k_s	b_{13Ab}	b_{23Ab}	Rep.fac	w
m_{3A3B}	1.000										
m_{2C3B}	-0.190	1.000									
m_{2C3A}	0.355	-0.166	1.000								
m_{2B3A}	-0.143	0.189	-0.908	1.000							
m_{2B2C}	0.280	-0.169	0.912	-0.918	1.000						
m_{2A2B}	0.163	-0.066	0.438	-0.416	0.421	1.000					
k_s	-0.018	0.013	-0.097	0.113	-0.120	-0.032	1.000				
b_{13Ab}	-0.130	-0.140	-0.127	-0.013	-0.040	-0.021	0.081	1.000			
b_{23Ab}	0.044	0.070	0.065	0.013	0.006	0.004	-0.080	-0.753	1.000		
Rep.fac.	0.040	0.046	-0.074	0.110	-0.076	-0.039	0.701	-0.272	0.125	1.000	
w	-0.608	-0.184	-0.436	0.143	-0.365	-0.217	-0.003	0.181	-0.050	-0.058	1.000

Negative log-likelihood: 1297.10
Deviance: 1499.94
AIC : 1521.94

Released in Area 3A, 1980   Released in Area 3B, 1980   Released in Area 3A, 1981   Released in Area 3B, 1981
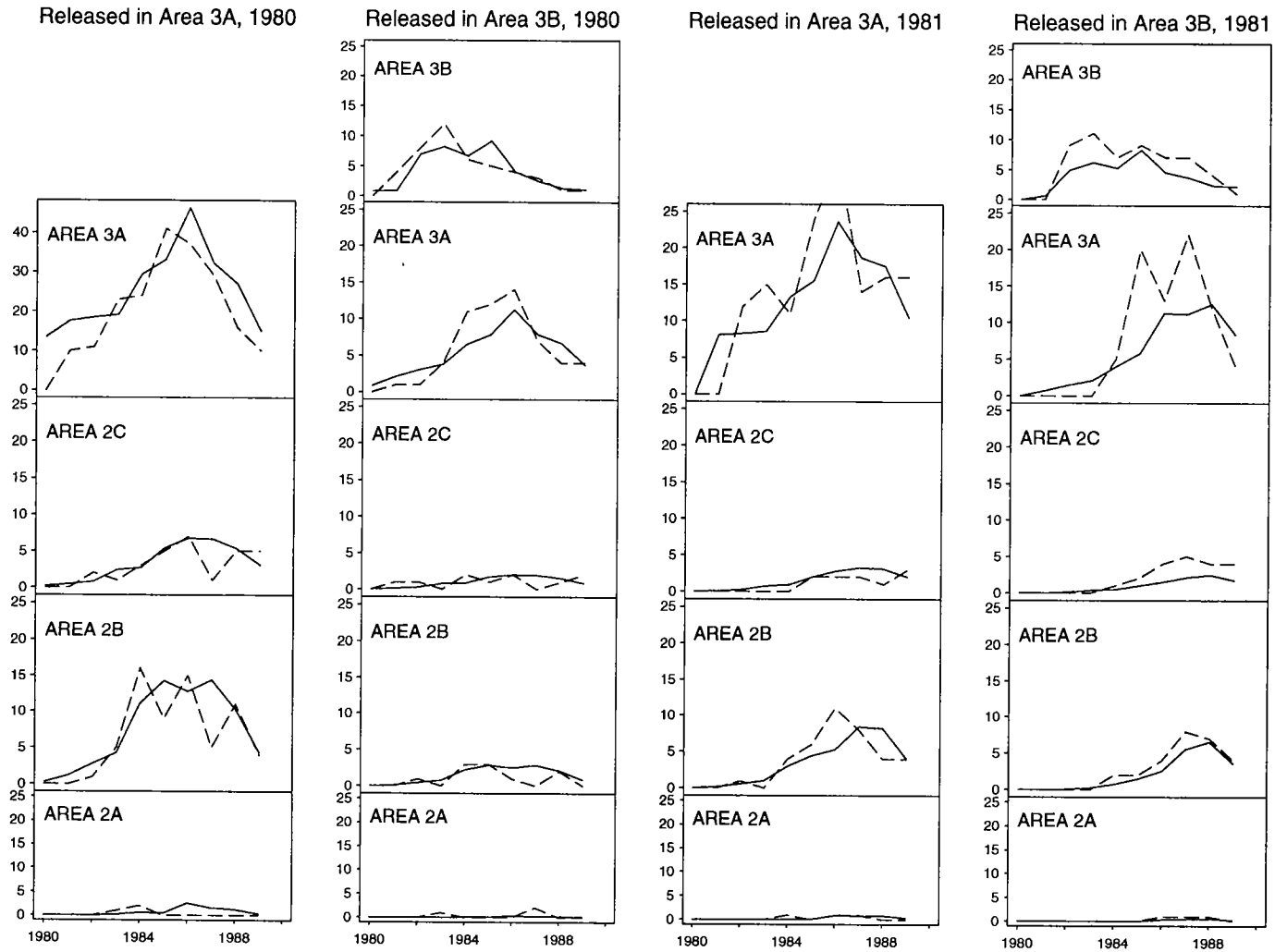

Figure 18. Predicted and observed recovery patterns for Model 7.

for 3A, and we can see that the predicted recoveries for Area 3B show again systematic departures from the observed values. The results in Table 15 show that the deviance is significantly higher than in Model 6, and therefore the latter is preferred. Figure 18 shows the residuals from Model 7.

The annual movement rates presented in each of our output tables are difficult to interpret, in particular if we want to compare them to the raw recovery data of Table 1. To facilitate the comparison we show the results of applying the estimated annual movement rates to an initial distribution of fish.

Most juveniles were 3-5 years old when tagged and most commercial catch is age 8-10. This implies that most tags were at large 4-6 years. We therefore simulated the final distribution of 100 fish of 40 cm placed in Area 3A and 3B and allowed to move for 5 years using the movement rates estimated from Models 1, 5b and 6. The final distribution of fish as a proportion is independent of the mortality rate assumed as long as mortality rates are equal in all areas. The simulation was run by setting the fishing mortality to zero and to 0.3 in all areas, using the area-specific selectivities corresponding to each of the models.

Table 16 shows the results of this experiment for the case of zero fishing mortality. Allowing for differences in selectivity among areas had an almost negligible effect on the resulting proportions. The movement rates from Model 1 suggest that 80% of juveniles in 3A and 3B would remain in 3A or 3B 5 years later. Few fish would have moved to Area 2C, 2B or 2A. Since there are many halibut caught in British Columbia (2B), and few juveniles have been found there the question would be – where do the adults in 2B come from? However, when we consider Model 6, there is a greatly different pattern after 5 years. Many more fish have moved to southern areas. Perhaps most interestingly, the results from Model 6 are very similar to the raw data from Table 1.

Table 16. Distribution of individuals from Areas 3A and 3B after 5 years of movement. All numbers are percentages of fish still alive after 5 years, assuming an initial size of 40 cm for all fish and zero fishing mortality. Parameter values for Models 5b and 6 are from data comprising all sizes of fish at release.

| | Model 1 (Table 8) | | Model 5b (Table13) | | Model 6 (Table 14) | | Raw Data (Table 1) | |
To Area	3B	3A	3B	3A	3B	3A	3B	3A
3B	42		22		17		32	
3A	43	79	47	62	48	55	40	63
2C	7	6	16	14	16	16	10	9
2B	8	13	13	21	17	25	16	25
2A	1	1	1	2	1	3	2	1

One-time versus annual movement

Models 1 to 7 presented here represent movement as a annual rather than a one-time event. We have carried out a one-time movement analysis of our current model, essentially analogous to Model 1. Table 17 shows the parameters estimated and Figure 19 shows the residuals. The results are very similar to the estimated movement rates

Table 17. Results for one-time movement model.

Survival $(s^{nat}(l_s))$:   0.557
Reporting rate factor $(1 - \lambda)$:   1.624

Movement parameters(m_{ij}):

	3B	3A
3B	0.418	
3A	0.376	0.707
2C	0.088	0.097
2B	0.098	0.179
2A	0.021	0.012

Parameter correlation matrix:

	$s^{nat}(l_s)$	m_{3A3B}	m_{2C3B}	m_{2B3B}	m_{2A3B}	m_{2C3A}	m_{2B3A}	m_{2A3A}	Rep.fac.
$s^{nat}(l_s)$	1.000								
m_{3A3B}	-0.001	1.000							
m_{2C3B}	-0.025	-0.205	1.000						
m_{2B3B}	-0.004	-0.175	-0.071	1.000					
m_{2A3B}	0.000	-0.089	-0.036	-0.030	1.000				
m_{2C3A}	-0.040	-0.001	0.001	-0.001	-0.000	1.000			
m_{2B3A}	0.040	0.007	0.003	0.014	0.004	-0.124	1.000		
m_{2A3A}	0.007	0.001	0.000	0.001	0.000	-0.035	-0.036	1.000	
Rep.fac	-0.935	-0.017	0.015	-0.030	-0.009	0.041	-0.090	-0.011	1.000

Negative log-likelihood :   932.51
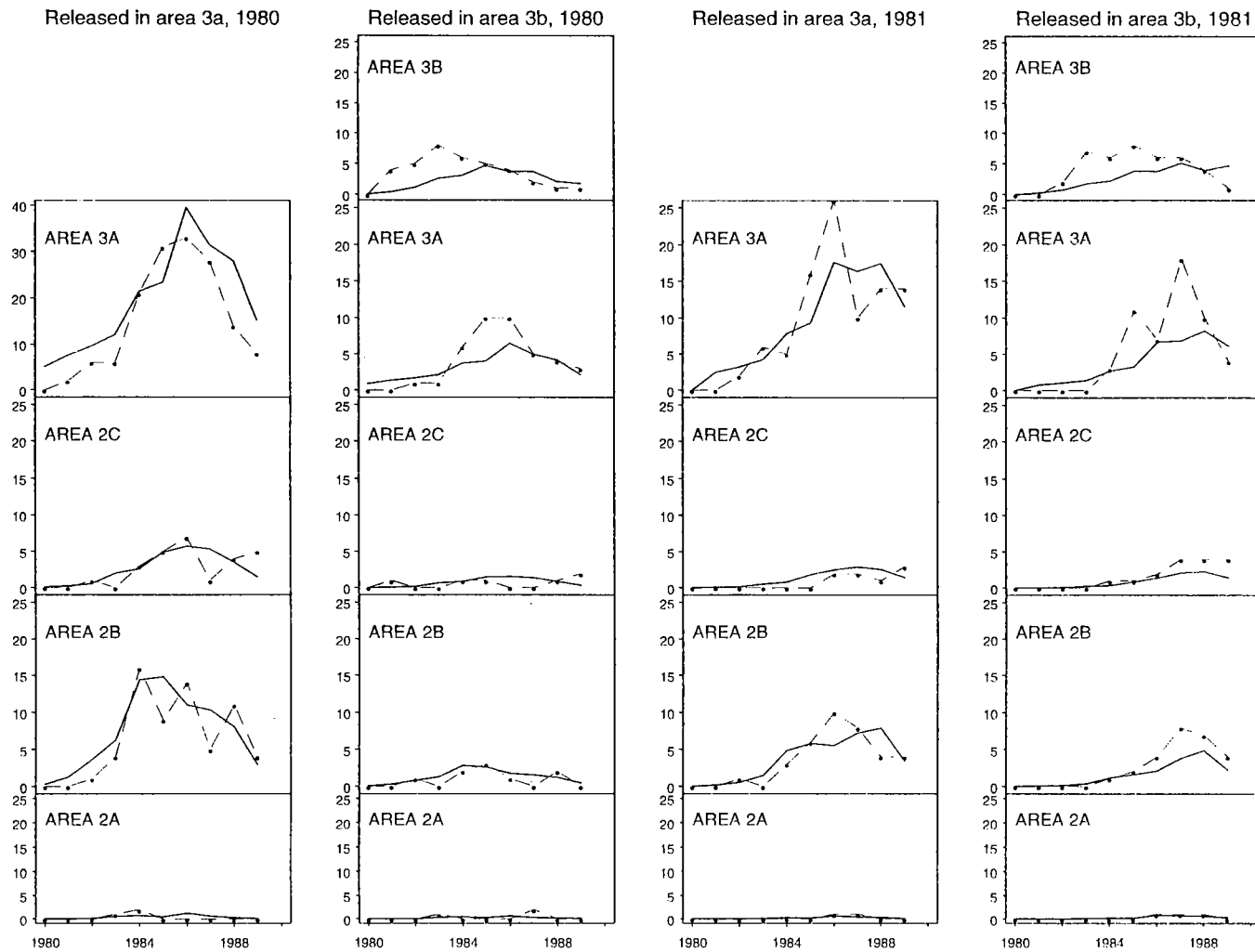Deviance :   1050.40
AIC :   1068.40

Figure 19. Predicted and observed recovery patterns for one-time movement model.

from Model 1. In particular compare the one-time movement parameters (Table 17) to the net movement after five years from Model 1 (Table 16). We therefore conclude that there is little difference in a one-time or continuous movement model.

Estimating fishing mortality rates

In principle, it is possible to estimate the fully recruited fishing mortalities provided that we assume as known the selectivity curves. We attempted to carry this out but, in the process, we encounter a number of difficulties that forced us to abandon the project. First, we can only estimate fishing mortalities for those years and areas were there were some recoveries. Second, there is a high degree of confounding between the estimable mortalities that caused severe convergence problems. Besides these problems in implementation, it is also uncertain the interpretation of fishing mortality estimates obtained in this way. These estimates would apply to tagged fish only since, as we have seen, they are not subject to the legal size limit.

DISCUSSION

Reporting rate/Tag Loss factor and Survival

A major source of uncertainty in most tagging studies when the recoveries are obtained from commercial operations are the reporting rates and this study is not the exception. The conclusions of the analysis, in particular the estimated movement rates, will be dependent on the spatial differences between reporting rates being accurately reflected by the differences in the values of Table 2.

One of the largest confounding between parameters that we obtain is between the survival and the reporting rate/tag loss parameter. This confounding can be explained if we consider that these two parameters determine the number of tags available from a given release group at a given time, if we exclude the fishing mortality. In that sense, the survival and the reporting rate/tag loss factor are analogous to a slope and intercept parameter of a regression.

The estimates of the reporting rate/tag loss factor seem to be too high in the earlier versions of the model, until we impose the additional condition that the survival should reach 0.8 at the legal size limit. However, this yields an unsatisfactory set of predictions about the pattern of recoveries. It is not until we include the estimation of the selectivities that we can obtain a reasonable set of estimates that explain well the residuals.

Selectivities

Perhaps the most important technical advance in this analysis over our earlier work is the estimation of selectivity parameters in Areas 3B and 3A from the tagging data rather than using estimates derived from the analysis of commercial catch-at-age/length data. This has made a major change in the interpretation of movement as shown in Table 16. As we mentioned earlier, we have not attempted to estimate selectivities in 2C, 2B and 2A from the tagging data. Since most of the recoveries come from Areas 3A and 3B, estimating more selectivities is unlikely to improve significantly the likelihood values (particularly if we consider that two more parameters are added for each selectivity curve estimated).

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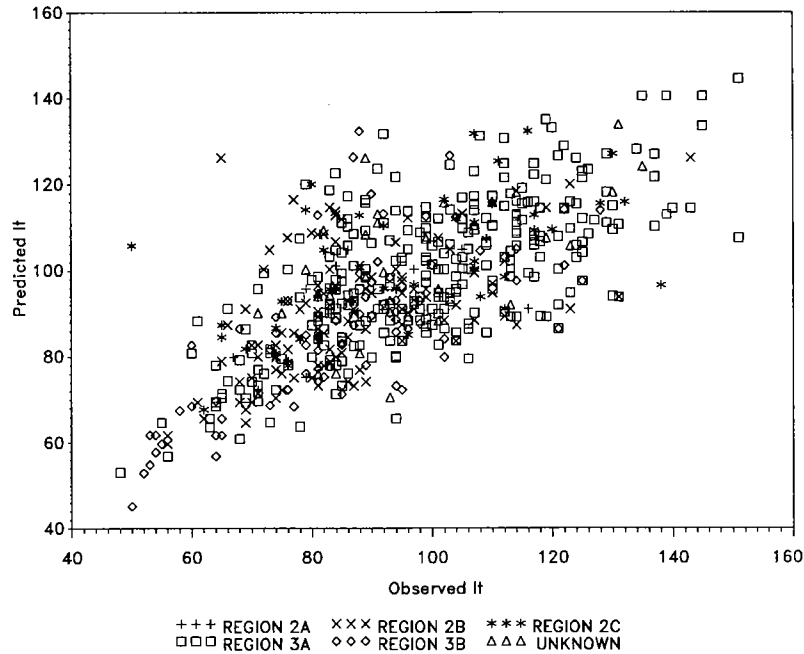Predicted vs observed lengths at recovery.

Figure 20. Observed and predicted size at recovery by regulatory area.

The parameter correlation matrix in Table 14 suggests that the selectivity parameters for Areas 3B and 3A are well defined and that such a tagging analysis is a powerful way to determine the selectivity curves. One of the main advantages of estimating the selectivity parameters from tagging data is that we know the initial size distribution of the fish. Unfortunately, there are few recoveries from any release group in its year of release (and prior to any movement of the fish), so some confounding between the selectivity parameters and other parameters in the model can be expected. In principle, the low correlations between the parameters seem to indicate that this is not a major problem. However, the correlation matrix measures the linear relationship between the parameters and, if the parameters are non-linearly related (as is often the case with constrained parameters) these correlations might be underestimating the degree of confounding. A more adequate way to assess the confounding between the parameters (but expensive in terms of computing time) would be to apply a bootstrap procedure and do pairwise plots of the bootstrap parameter estimates, or carry out a profiling of the parameters. Considering that the selectivity of the tagged fish is not affected by a legal size limit, we speculate that selectivity curves estimated through our model might be more appropriate for tagged fish, than the ones derived from catch-at-age methods. In this case, the need for estimating selectivities from the tagging data must be taken into account in the design of future experiments.

Another possible way of explaining the differences (at least partly) in the selectivities estimated from our model with those estimated from the catch-at-age data is that they are due to differences in growth. If, for example, fish grow faster in Areas 3A and 3B than the average growth curve that we assumed in our model, they will become vulnerable earlier. In other words, we can obtain the same prediction as a difference in selectivities or a difference in growth. However, the distribution of size-at-recovery indicates that tagged fish are more likely to be retained by the fishery at smaller sizes than the untagged fish. Furthermore, when we compare the observed sizes at recovery

with the sizes predicted by the growth model (Figure 20), no large biases are apparent.

Juvenile and Adult Movement Rates

The movement rates of Table 14 are (we believe) the best estimates of juvenile movement to use. It appears that there is substantial southerly migration of juveniles, and this conforms with the existing biological understanding that juveniles recruit in Areas 3 and 4 and then migrate southward. It is not clear if these rates are sufficient to explain the observed abundances of adults in Areas 2A, 2B, and 2C. This question will be discussed further below.

Quinn et al. (1985) used movement rates of age 8 and above halibut for migratory catch-at-age analysis. These movement rates had been estimated from tagging data. Table 18 shows a comparison of the annual movement rates from Table 14, with the annual movement rates of age 8 halibut used by Quinn et al. (1985). In all cases our estimates of movement of the juveniles are considerably higher than the estimates for older halibut.

The patterns shown in Figure 13 and, in particular, the differences between Areas 3A and 3B might deserve further study. In particular, due to the small number of recoveries, the data used in the figure had to be pooled over years and this might have introduced some growth-related bias. Assuming that this bias is small, one possible explanation for the difference is that fish tend to leave Area 3B irrespective of their size at release, but smaller fish are more likely to leave Area 3A than larger fish. As we mentioned before, an alternative explanation might be based on differential probabilities of capture. If area-specific differences in size-dependency in movement rates seem plausible, future versions of the model might incorporate this feature.

Table 18. **Comparison between annual movement rates as listed in Quinn et al. (1985) and those estimated by Model 6.**

Movement Parameters m_{ij}	Quinn et al. (1985)	Model 6
From 3B to 3A	0.074	0.231
From 3B to 2C	0.021	0.061
From 3A to 2C	0.011	0.080
From 3A to 2B*	0.009	0.026
From 2C to 2B*	0.020	0.302
From 2B to 2A	-*	0.058

* Quinn et al. (1985) pooled areas 2A and 2B into a single area.

Potential extensions and modifications of the method

There are a number of obvious extensions to this analysis. First we have run our analysis on a very coarse spatial and temporal scale. The movement rates estimated from 3B to 3A and 3A to 2C may be very sensitive to how close the major tag release sites are to the boundary between the regulatory areas. It would be possible to use a much smaller spatial scale; IPHC maintains catch records by statistical sub-area which are 60 miles north to south. There is no computational problem in performing such

an analysis; the current analysis takes a few minutes on a 386 personal computer and it would likely be only a few times longer with a finer scale. Assuming the data were analyzed with 20 or more spatial strata, the number of movement parameters would still have to be kept small, presumably by assuming that the probability of moving to the next stratum south was the same within each regulatory area.

While the earlier analysis (Skalski et al., 1993) included stochastic growth and area specific growth, we see no evidence in this analysis that it is useful or necessary to consider these two factors. The results from Model 6 are so much more consistent with the data that we believe that considering the area specific selectivity is perhaps more important than considering area specific growth and stochastic growth.

An obvious extension of the current work is to take the movement rates estimated for juveniles in this paper, and the adult movement rates used in Quinn et al. (1985) and see if the known distribution of juveniles is sufficient to explain the observed distribution of adults.

We believe the most interesting and challenging extension of the movement model we have used is to combine it with tagging data for adults, juvenile survey data, catch-at-age data, and adult survey and CPUE data in a unified analysis. This would be a large and complex analysis but may prove to be very powerful.

ACKNOWLEDGMENTS

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