MODEL-BASED ANALYSES OF TRENDS OVER TIME IN THE AGE CORRESPONDING TO THE TRANSITION PHASE FOR ANTARCTIC MINKE WHALES IN THE JARPA RESEARCH AREA

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ABSTRACT

This study applies a model-based approach similar to that of Thomson *et al*. (1999) to the transition phase data obtained from JARPA surveys to examine trends in the age at maturity for the I and P stocks of Antarctic minke whales. The results, which takes into account various potential biases related to examining trend in transition phase data (i.e. truncation and fringe effects, differences between readers, and readers learning over time) suggest that the age at maturity of Antarctic minke whales declined from about 11 years in the late 1940s to 7 years in the late 1960s for both stocks, and these declining trends are statistically significant at the 5% level. The analyses also suggest that the age at maturity increased slightly from the late 1960s to the late 1970s and has stabilized thereafter. These trends are consistent with the results obtained from VPA (Mori *et al*. 2006), which suggest that for both the I and P stocks, abundance increased from the 1940s to the late 1960s and thereafter has been stable or declined somewhat. This consistency enhances the confidence to be placed in estimates of parameters (such as natural mortality and MSYR) from such VPA analyses that may be of value for management purposes. It also serves to demonstrate the utility of age-at-maturity as an index to monitor stock status, and suggests that continued monitoring of this parameter is desirable both for this purpose and for contributing to the understanding of the dynamics of the Antarctic ecosystem.

KEYWORD ANTARCTIC MINKE WHALES, AGE AT TRANSITION, TRANSITION PHASE, AGE AT MATURITY

INTRODUCTION

It is widely accepted that the position where growth layer spacing changes (the transition phase) in the earplugs of whales is related to the age at physical and sexual maturity of the animal (Lockyer 1972, Masaki 1979, Kato 1983). Lockyer (1972) explains that the ear plug layer formation during the juvenile growth phase is very irregular and the layers are unevenly spaced; however, after maturity, the new layers become more compact and evenly spaced. Based on the analysis of the transition phase in the earplug of Antarctic minke whales collected from the commercial whaling samples, several authors report a decline in age at transition (and hence at sexual maturity) of this species from the 1940s cohorts to the late 1960s cohorts (Masaki 1979, Best 1982, Kato 1983, 1985). Zenitani and Kato (2005, 2006) also report this decline based on the analysis of samples collected from the JARPA surveys.

Whether or not this decline in age at transition of Antarctic minke whales is a real phenomenon has long been under debate. Details of the discussions are well summarised in Zenitani and Kato (2006), and will thus not be repeated here. However, in brief, these queries arose essentially because the nominal trend in the mean age at transition may be subject to some potential biases as a measure of any real trend, such as arise from the truncation and fringe effects, differences between readers and readers "learning" over time. The truncation bias arises from the under-representation of older animals in the most recent cohorts sampled, the fringe effect relates to the low proportion of animals recorded as having an age-at-transition phase close to their age at capture (presumably as lack of contrast between widely and narrowly spaced rings in such circumstances makes the phase difficult to identify), and "learning" effect is that as readers gain experience, they tend to detect transition layers in a greater proportion of the sample (Thomson *et al*. (1999)). The analyses of Thomson *et al*. (1999) took all of these effects into account and led to the conclusion that for those animals that were caught in the IWC Management Area IV, a decline in the average age at transition from roughly 11 for the cohorts of the 1950s to roughly 7 for those of the 1970s had occurred.

At the meeting to review the Japanese Whale Research Program under Special Permit in the Antarctic (JARPA) called by the Government of Japan in 2005, it was recommended that a model-based transition phase analysis of the kind of Thomson *et al*. (1999) (as explained above) be updated utilizing further JARPA survey data that have become available since that time. In response to this recommendation, and further to update results presented to the IWC's mid-term JARPA review meeting (IWC 1998), the analyses of Thomson *et al*. (1999) are updated here. The main difference between this work and that of Thomson *et al*. (1999) is that this study conducts the analyses for what seems to be the most plausible stock-hypothesis at this stage: an I-stock (distributed from Area IIIE to Area VW) and P-stock (distributed from Area VE to Area VIW) (Pastene *et al*. (2005)). Furthermore, given that questions were raised at the mid-term JARPA review meeting (IWC 1998) about possible differences between ageing of the commercial and JARPA catches, the analyses here utilize only the data obtained from the JARPA surveys, so that conclusions are independent of such considerations.

An important aspect of these analyses is that they provide a basis to check trends in abundance estimates for this species calculated from VPA, which suggest increases in recruitment and abundance from the 1940s to the late 1960s (Mori *et al*. 2006), by examining whether there are co-incident changes in biological parameters in the directions that might be expected in such circumstances.

DATA

The data analyzed pertain to Antarctic minke whales sampled by the JARPA surveys that took place in Antarctic Management Areas IIIE to VIW from 1987 to 2004[1]. Not all the samples could be aged and only those that were aged were used in the analyses. The analyses are conducted for the two possible stocks identified by Pastene *et al*. (2005), which are the I-stock (distributed from Area IIIE to Area VW) and P-stock (distributed from Area VE to Area VIW).

For the I-stock, 3897 Antarctic minke whales were aged from samples taken between 1987 and 2004, and among those, transition phases were identified for 1831 animals. For the P-stock, the corresponding figures are 1891 whales aged from samples between 1988 and 2004, with transition phases identified for 968. The earplugs taken from 1987-1989 and 1992 were read by H. Kato, and others were read by R. Zenitani. The proportion of earplugs that were aged and were assigned a transition phase for each year by each reader are shown in Figure 1. Pre-1941 cohorts were excluded from these analyses for the I-stock, as the associated sample sizes are small. For the P-stock, the corresponding cut-off date was 1944.

METHODOLOGY

The methodology used here is almost the same as that used in Thomson *et al*. (1999), which basically fits the data to two models based on different hypotheses: one model assumes that the transition phase is an artefact, and the other assumes that the transition phase is a real phenomenon. Details of the models are described below.

Model 1: The transition phase is an artifact

As in Thomson *et al*. (1999), we first assume that the transition phase is not a real phenomenon. This means that the reader assigns a transition phase in some random fashion in relation to the number of growth layers. To reflect such mechanism, we assume that the readers assign the transition phase according to a normal distribution which is centered at a fixed proportion of the length and hence age of the earplug (μ_{plug}), with standard deviation σ_{plug} .

The proportion of earplugs in each age group that are assigned a transition phase is described by a vector of points P_l^R where l =5, 7, 9, 11 or 13[2] and refers to the age of the animal at capture, and R=Kato or Zenitani, indicating the person who read the earplug. The probability of assigning a transition phase in earplugs of other ages is calculated by linear interpolation between successive points, and is assumed to remain constant after the age of 13. The probability of recording an age at transition equal to the age at capture is assumed to be zero.

The values of l given above were selected by examination of model fits, in which a much larger number of values were used. The subset of values needed to adequately describe the resultant function was then chosen, primarily on the basis of the Akaike Information Criterion (AIC).

Since a "learning" effect amongst the readers was identified in Thomson *et al*. (1999), we also allow for this possibility, so that the probability of reader R assigning a transition phase in age group l is assumed to be:

$$P_{l,y_s}^R = P_{l,y_{\min}}^R \cdot \left[1+\beta_l^R \cdot (y_s - y_{\min})\right] \tag{1}$$

where P_{l,y_s}^R is the probability of reader R assigning a transition phase to an earplug aged l, sampled in year y_s ,

$P_{l,y_{\min}}^R$ is the probability of reader R assigning a transition phase to an earplug aged l in his/hers first year

[1] Whaling takes place during the austral summer, so that each whaling season spans two years. For convenience of expression the austral summer of 1987-1988, for example, is referred to as the year 1987.

[2] This was taken up to age 15 for the P-stock when Kato was the reader, since this gave better fit to the data in terms of AIC.

$y_{\min}$ of reading, and

β_l^R is the slope of the straight line that accounts for "learning".

$y_{\min}$ is taken to be 1987 for Kato and 1990 for Zenitani. P_{l,y_s}^R is assumed to be less than 1.

Given the assumption that the readers assign the transition phase according to a normal distribution which is centered at a fixed proportion of the age of the earplug (μ_{plug}), with standard deviation σ_{plug} , the probability that this transition phase, observed in an earplug of age *a*, would be assigned to an age at transition *tm* can be calculated from:

$$\varphi_{a,tm} = \begin{cases} \int_{tm-1}^{tm} N^*\left(\mu_{plug}, \sigma_{plug}^2\right) & \text{for } 1 \le tm \le a \\ 0 & \text{otherwise} \end{cases} \quad (2)$$

where N^* is a normal distribution which has been truncated at the ends of the earplug (i.e. *tm*=0 and *tm*=*a*). The area under the truncated distribution is scaled upwards so that it is equal to one.

Model 2: The transition phase is a real phenomenon

As in Thomson *et al*. (1999), in this model it is assumed that the transition phase does reflect a real signal (probably related to the age at maturity), and that individual whales belonging to a particular cohort (y_c) mature according to a normal distribution with mean tm_{y_c} and standard deviation σ_{y_c} .

The variance of this distribution may be higher for cohorts for which the mean age at transition is greater. This is taken into account through the following equation as in Thomson *et al*. (1999):

$$\sigma_{y_c} = \sigma_{1965} + \gamma \cdot \left(tm_{y_c} - tm_{1965}\right) \quad (3).$$

The mean age at transition for each cohort (tm_{y_c}) is assumed to change from T_1 to T_2 between cohorts Y_1 and Y_2 and T_2 to T_3 between cohorts Y_2 and Y_3 according to:

$$tm_{y_c} = \begin{cases} T_1 & y_c \le Y_1 \\ T_1 - (T_1 - T_2)\left(\frac{y_c - Y_1}{Y_2 - Y_1}\right)^{1-\alpha} & Y_1 \le y_c \le Y_2 \\ T_2 + (T_3 - T_2)\left(\frac{y_c - Y_2}{Y_3 - Y_2}\right) & Y_2 \le y_c \le Y_3 \\ T_3 & y_c \ge Y_3 \end{cases} \quad (4)$$

where T_1 is the mean age at transition in year Y_1 ,

T_2 is the mean age at transition in year Y_2 ,

T_3 is the mean age at transition in year Y_3 , and

α is a shape parameter such that α =0 corresponds to a straight line.

The probability of recognizing transition phase when one is present, given the number of layers that have accumulated after the transition phase (a_{tm}) is given by a vector of points P_{λ,y_s}^R . Choices of λ were made in the same way as described for the *l* values of Model 1. In this case, λ values of 1 and 3 were selected for reader Kato, and 1, 3 and 6 for reader Zenitani. Linear interpolation is used between successive points. Further the probability that reader Kato detects a transition phase is taken to remain constant once at least three layers have accumulated after the transition phase. For reader Zenitani, such constancy occurs only after six layers. "Learning" may be taken into account in the same way as described for Model 1.

Parameter estimation

The parameter estimation methodology is again that of Thomson *et al*. (1999). The parameter values for both models were estimated by maximizing a log-likelihood based itself on the assumption of multinomial distributions:

$$\ln L = \sum_{y_c}\sum_{a}\left[\sum_{tm=1}^{a} N_{y_c,a,tm}\cdot\ln\left(\rho_{y_c,a,tm}\right) + N_{y_c,a}^{imm}\cdot\ln\left(1-\sum_{tm=1}^{a}\rho_{y_c,a,tm}\right)\right] \quad (5)$$

where $N_{y_c,a,tm}$ is the number of earplugs sampled and read from cohort y_c which have age *a* and age at transition *tm*,

$N_{y_c,a}^{imm}$ is the number of earplugs sampled and read from cohort y_c which have age *a* that were considered not to have a transition phase, and

$\rho_{y_c,a,tm}$ is the model-estimated probability of assigning a transition phase at age *tm* in an earplug of age *a* from cohort y_c . For Model 1, $\rho_{y_c,a,tm} = P_{a,y_s}^{R}\cdot\varphi_{a,tm}$ and a similar equation follows for Model 2.

The number of samples of age *a* in cohort y_c in the model ($\hat{N}_{y_c,a}$) is taken to be exactly equal to the observed number of samples $N_{y_c,a}$. The model then determines how $\hat{N}_{y_c,a}$ is distributed across the transition phase ages. The model-estimated number of earplugs ($\hat{N}_{y_c,a,tm}$) for cohort y_c , age *a* and age at transition *tm*, is calculated as:

$$\hat{N}_{y_c,a,tm} = \hat{N}_{y_c,a}\cdot\rho_{y_c,a,tm} \quad (6).$$

The estimated number of earplugs from cohort y_c of age *a* for which no transition phase was assigned ($\hat{N}_{y_c,a}^{imm}$), is thus given by:

$$\hat{N}_{y_c,a}^{imm} = \hat{N}_{y_c,a}\cdot\left(1-\sum_{tm=1}^{a}\rho_{y_c,a,tm}\right) \quad (7).$$

For convenience of expression, these animals are termed “immatures”. Under the assumptions of Model 1, these are earplugs that were considered not to have a transition phase. However under Model 2, this group includes not only earplugs that do not have a transition phase but also earplugs whose transition phase was not detected by the earplug reader.

Estimates of precision for the parameters of both Model 1 and Model 2 were obtained based upon the Hessian approximation calculated using AD Model Builder.

RESULTS

Results for the I-stock (distributed from Area IIIE to Area VW)

Model 1: The transition phase is an artefact

Table 1 shows the estimated parameter values and the associated log-likelihoods ($\ln L$) for different forms of the model in which the transition phase assumed to be an artefact (Model 1) for the I-stock. Based on the AIC, the model with *l*=5, 7, 9, 11, 13 for defining P_{l,y_s}^{R} and which assumes no “learning” (for either Zenitani or Kato) was chosen. In terms of this model, both Zenitani and Kato position the transition phase at about 40% of the total age on average (Figure 2a). Zenitani appears to have been a little more conservative than Kato, recording a lower proportion of transition phases for younger earplugs (for ages 5 to about 10) (Figure 3a). Both readers recognized a transition phase in roughly 75% of all older earplugs.

The ability of Model 1 to reflect the data can be judged from plots of the observed and model-predicted distribution of age after transition (a_{tm}). This model does not achieve a good fit to the distribution of those values in cases where a transition phase was assigned, and there are clear indications of systematic deviations in the residuals (Figure 4a, lower plot).

Model 2: The transition phase is a real phenomenon

Table 2 shows the estimated parameter values and associated log-likelihoods ($\ln L$) for different forms of the model in which the transition phase is a real phenomenon (Model 2) for the I-stock. Based on the AIC, the model with λ =1 and 3 for P^K_{λ,y_s} and with λ =1, 3 and 6 for P^Z_{λ,y_s}, and which assumes no "learning" (for either Zenitani or Kato) was chosen. Zenitani again appeared to have been a little more conservative than Kato, recording a lower proportion of transition phases with fewer layers after the transition phase (Figure 5a). Both readers assigned a transition phase in some 70% of the earplugs when there were more than six layers after the transition phase.

Compared to Model 1 (see Figure 4a), Model 2 appears to fit the observed distribution of age after transition very well (Figure 6a). Both Model 1 and Model 2 fit the number of "immatures" very well. Model 2 indicates that a real decline in the mean age at transition with cohort occurred for the Antarctic minke whales classified as belonging to the "I-stock" (Figure 7a): roughly from about 11 years for the 1948 cohort to 7 years for the 1967 cohort. This decline is statistically significant at the 5% level (estimated mean of T_2-T_1 = -4.50, standard error = 0.20, t = 22.1, P<0.05).

The slight increase estimated in the mean age at transition from the 1968 cohort to the 1981 cohort is again statistically significant at the 5% level (estimated mean of T_3-T_2 = 0.59, standard error = 0.09, t = 6.8, P<0.05). The drop in the observed average age at transition from around 1997 is a reflection of the truncation effect impacting results for recent cohort (Figure 7a).

Results for the P-stock (distributed from Area VE to Area VIW)

Model 1: The transition phase is an artefact

Table 3 shows the estimated parameter values and the associated log-likelihoods ($\ln L$) for different forms of Model 1 for the P-stock. Based on the AIC, the model with l=5, 7, 9, 11, 13 for reader Zenitani, and l=5, 7, 9, 11, 13, 15 for reader Kato for defining P^R_{l,y_s}, and which assumes no "learning" for either reader was chosen. As for the I-stock, both Zenitani and Kato positioned the transition phase at about 40% of the total age on average (Figure 2b). For this stock, Kato appeared to have been a little more conservative than Zenitani, recording a lower proportion of transition phases for younger earplugs (for age 5 to about 10) (Figure 3b); however, there are only two years for which Kato read the earplugs for this stock, and the standard error estimates in Table 3 indicate that the difference between the two readers is not significant at the 5% level.

As was the case for I-stock, this model does not achieve a good fit to the distribution of age after maturity for instances where a transition phase was assigned, and there are clear indications of systematic deviations in the residuals (Figure 8a, lower plot).

Model 2: The transition phase is a real phenomenon

Table 4 shows the estimated parameter values and associated log-likelihoods ($\ln L$) for different forms of Model 2 for the P-stock. Based on the AIC, the model with λ =1 and 3 for P^K_{λ,y_s} and with λ =1, 3 and 6 for P^Z_{λ,y_s}, and which assumes no "learning" was chosen. The probability of detecting a transition phase after some layers have accumulated are lower for reader Kato compared to Zenitani, but again this could be a result of low sample sizes for Kato (Figure 5b), for whom this result differs from that for the I-stock. In contrast, results for Zenitani are very similar to hers for the I-stock.

As was the case for the "I-stock", when compared to Model 1 (see Figure 8a), Model 2 appears to fit the distribution for age after transition very well (Figure 9a). Both Model 1 and Model 2 fit the number of "immatures" very well. Model 2 indicates that a real decline in the mean age at transition with cohort occurred for the Antarctic minke whales classified as belonging to the "P-stock" (Figure 7) from roughly about 11 years for the 1946 cohort to 7 years for the 1966 cohort. This trend is very similar to that of the I-stock, and this decline is again statistically significant at the 5% level (estimated mean of T_2-T_1 = -3.79, standard error = 0.22, t = 16.9, P<0.05). The slight increase in the mean age at transition from the 1969 cohort to the 1977 cohort is again statistically significant at the 5% level (estimated mean of T_3-T_2 = 0.56, standard error = 0.111, t = 5.0, P<0.05). As was observed for the I-stock, the impact of the truncation effects on recent cohorts is evident after about 1997 (Figure 7b). The final steady mean age at transition T_3 is estimated to be reached a few years earlier than for the I-stock, but the difference is not statistically significant at the 5% level.

DISCUSSION

These analyses, which take into account various potential biases that arise in the interpretation of trends in transition phase data, indicate that the age at transition (and hence likely maturity) of Antarctic minke whales declined from about 11 years at the end of the 1940s to 7 years in the late 1960s for both the I- and P-stocks, and that these declining trends are statistically significant at the 5% level. This result is similar to that suggested by various authors previously from examinations of these data (Masaki 1979, Best 1982, Kato 1983, 1985, Thomson *et al*. 1999, Zenitani and Kato 2005, 2006). These analyses also suggest that the age at maturity of this species increased slightly from the late 1960s to late 1970s, and has stabilized thereafter. Again this result is similar to that of Zenitani and Kato (2006).

These trends are also consistent with the results obtained from VPA, which suggest that for both I and P stocks, abundance increased from the 1940s to the late 1960s, and thereafter has been stable or declined somewhat (Mori *et al*. 2006). This consistency enhances the confidence to be placed in estimates of parameters (such as natural mortality and MSYR) from such VPA analyses that may be of value for management purposes.

The reason for the decline in age-at-maturity of minke whales from the 1940s to the 1960s could be a result of the krill surplus, which likely became available due to the extensive whaling of the large baleen whales (Laws 1977, Kato 1983, 1987). We surmise that during this period, the feeding conditions for minke whales improved due to the krill-surplus and resulted in their attaining sexual maturity at an earlier age. We also surmise that the constant (perhaps even slightly increasing) trend in age at maturity since the 1970s suggest that the period of "krill-surplus" came to an end around this time, so that more recently the species may be more restricted in its feeding. Various recent studies suggest the recovery of the large baleen whales (e.g. humpback whales, blue whales, fin whales) that were once heavily exploited (e.g. Matsuoka *et al*. 2006). These whales share the same prey (krill) with Antarctic minke whales and so may be playing a role in such enhanced feeding restrictions (see also Mori and Butterworth (2006)).

A trend in age-at-maturity can provide a good indication of the trend in stock abundance, and hence provide a useful index for stock monitoring. Continued monitoring of the age-at-maturity of the stock, both to monitor stock status and for contributing to the understanding of the dynamics of the Antarctic ecosystem is desirable.

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Table 1. Parameter estimates and log-likelihoods ($\ln L$) for different forms of the model in which the transition phase is assumed to be an artefact (Model 1) for the **I-stock**. The figures shown in parenthesis are standard deviations provided by the Hessian approximation. Results are shown for various choices for the *l* values of equation (1) and for cases where the probability that an earplug reader will assign a transition phase to an earplug either does not (no "learning"), or does (with "learning") increase over time. For the results with "learning", the values quoted for P_l refer to the reader's first year of sampling ($y_{\min}$) – 1987 for Kato and 1990 for Zenitani. The "best" model form is selected on the basis of AIC.

					BEST MODEL							
	l=5,7,9···35 No "learning"		*l*=5,7,9···15 No "learning"		*l*=5,7,9···13 No "learning"		*l*=5,7,9···11 No "learning"		*l*=5,7,···9 No "learning"		*l*=5,7,9···13 With "learning"	
	Kato	Zenitani	Kato	Zenitani	Kato	Zenitani	Kato	Zenitani	Kato	Zenitani	Kato	Zenitani
μ_{plug}	0.397	0.363	0.397	0.363	0.397 (0.008)	0.363 (0.004)	0.397	0.363	0.397	0.363	0.397	0.363
σ_{plug}	0.151	0.159	0.151	0.159	0.151 (0.006)	0.159 (0.003)	0.151	0.159	0.151	0.159	0.151	0.159
P_5	0.000	0.000	0.000	0.000	0.000 (0.000)	0.000 (0.000)	0.000	0.000	0.000	0.000	0.000	0.000
P_7	0.219	0.025	0.219	0.025	0.219 (0.053)	0.025 (0.010)	0.221	0.025	0.197	0.021	0.219	0.022
P_9	0.400	0.224	0.400	0.224	0.398 (0.083)	0.225 (0.032)	0.380	0.205	0.662	0.682	0.398	0.178
P_{11}	0.558	0.551	0.559	0.551	0.568 (0.094)	0.544 (0.042)	0.688	0.729			0.568	0.545
P_{13}	0.759	0.707	0.750	0.709	0.698 (0.023)	0.746 (0.011)					0.698	0.695
P_{15}	0.660	0.763	0.694	0.750								
P_{17}	0.685	0.668										
P_{19}	0.745	0.733										
P_{21}	0.703	0.651										
P_{23}	0.540	0.760										
P_{25}	0.647	0.803										
P_{27}	0.603	0.743										
P_{29}	0.823	0.707										
P_{31}	0.698	0.831										
P_{33}	0.804	0.779										
P_{35}	0.792	0.787										
β_5											0.006	0.000
β_7											0.000	0.021
β_9											0.000	0.037
β_{11}											0.000	0.000
β_{13}											0.000	0.010
$\ln L$	−6415.75		−6428.18		−6428.88		−6441.50		−6539.23		−6424.46	
AIC	6487.75		6460.18		6456.88		6465.50		6559.23		6472.46	

Table 2. Parameter estimates and log-likelihoods (*ln*L) for different forms of the model in which the transition phase is a real phenomenon (Model 2) for the **I-stock**. The figures shown in parenthesis are standard deviations provided by the Hessian approximation. Results are shown for various choices for the λ values, and both with and without a "learning" effect. For the results with "learning", the values quoted for P_λ refer to the reader's first year of sampling ($y_{\min}$).

a)

	Lamda=1-6	Lamda=1-7	Lamda=1-10	Lamda=1,3,6	Lamda=1,3,6	Lamda=1-6	Lamda=1-3	Lamda=1,3	Lamda=1,3,6
	Readers pooled	Readers pooled	Readers pooled	Readers pooled	Kato only	Kato only	Kato only	Kato only	Zenitani only
Y_1	1948.4	1948.4	1948.4	1948.4	1946.0	1947.7	1948.1	1948.4	1948.5
Y_2	1968.6	1968.6	1968.6	1968.6	1967.0	1965.5	1965.5	1965.4	1969.3
Y_3	1978.0	1978.0	1978.0	1978.0	1985.1	1981.0	1981.0	1981.0	1977.9
T_1	11.1	11.1	11.1	11.1	11.3	11.0	11.0	10.9	11.1
T_2	6.6	6.6	6.6	6.6	7.0	7.2	7.2	7.2	6.5
T_3	7.2	7.2	7.2	7.2	6.3	6.4	6.4	6.4	7.2
α	0.010	0.010	0.010	0.010	0.058	0.010	0.010	0.010	0.010
σ_{1965}	1.055	1.055	1.055	1.055	1.320	1.311	1.311	1.311	0.960
γ	6.35E-03	6.36E-03	6.08E-03	6.33E-03	0.050	0.054	0.054	0.054	1.16E-05
P_1	0.152	0.152	0.152	0.162	0.274	0.284	0.284	0.273	0.125
P_2	0.426	0.427	0.427			0.448	0.447		
P_3	0.551	0.551	0.550	0.590	0.685	0.723	0.689	0.688	0.559
P_4	0.621	0.613	0.613			0.543			
P_5	0.719	0.691	0.695			0.868			
P_6	0.733	0.833	0.850	0.734	0.689	0.685			0.744
P_7		0.729	0.663						
P_8			0.795						
P_9			0.616						
P_{10}			0.736						
ln$L$	−4376.19	−4375.03	−4372.87	−4376.99	−896.886	−895.981	−896.928	−896.969	−3417.68
AIC	4406.19	4407.03	4410.87	4400.99	920.886	925.981	920.928	918.969	3439.68

b)

BEST MODEL

	No "learning"		With "learning"	
	Kato	Zenitani	Kato	Zenitani
Y_1	1948.4 (1.029)		1948.4	
Y_2	1968.3 (0.435)		1968.6	
Y_3	1981.2 (2.208)		1978	
T_1	11.1 (0.191)		11.1	
T_2	6.7 (0.072)		6.6	
T_3	7.2 (0.050)		7.2	
α	0.010 (0.002)		0.010	
σ_{1965}	1.057 (0.019)		1.055	
γ	0.005 (0.019)		0.006	
P_1	0.356 (0.099)	0.122 (0.032)	0.352	0.111
P_3	0.698 (0.022)	0.558 (0.042)	0.699	0.481
P_6		0.743 (0.011)		0.696
β_1			0.000	0.014
β_3			0.000	0.021
β_6				0.009
ln$L$	−4370.64		−4365.01	
AIC	4398.64		4403.01	

Table 3. Parameter estimates and log-likelihoods ($\ln L$) for different forms of the model in which the transition phase is assumed to be an artefact (Model 1) for the **P-stock**. The figures shown in parenthesis are standard deviations provided by the Hessian approximation. Results are shown for various choices for the *l* values of equation (1) and for cases where the probability that an earplug reader will assign a transition phase to an earplug either does not (no "learning"), or does (with "learning") increase over time. Because there were only two years for which Kato read earplugs for this stock, and because he had already acquired considerable experience by that time, no allowance was made for possible "learning" in his case here. For the results with "learning" the values quoted for P_l refer to the reader's (Zenitani's) first year of sampling ($y_{\min}$).

					BEST MODEL			
	l=5,7,9⋯35 No "learning"		l=5,7,9⋯15 No "learning"		l=5,7,9⋯13 (15) No "learning"		l=5,7,9⋯13 With "learning"	
	Kato	Zenitani	Kato	Zenitani	Kato	Zenitani	Kato	Zenitani
μ_{plug}	0.380	0.360	0.380	0.360	0.380 (0.012)	0.360 (0.005)	0.380	0.360
σ_{plug}	0.128	0.148	0.128	0.148	0.128 (0.009)	0.148 (0.004)	0.128	0.148
P_5	0.000	0.000	0.000	0.000	0.000 (0.000)	0.000 (0.000)	0.000	0.000
P_7	0.000	0.033	0.000	0.033	0.000 (0.001)	0.033 (0.022)	0.000	0.033
P_9	0.088	0.203	0.088	0.203	0.088 (0.060)	0.203 (0.049)	0.088	0.147
P_{11}	0.372	0.587	0.372	0.587	0.372 (0.116)	0.591 (0.064)	0.372	0.506
P_{13}	0.386	0.768	0.384	0.769	0.384 (0.110)	0.754 (0.014)	0.384	0.681
P_{15}	0.631	0.758	0.645	0.753	0.645 (0.039)		0.645	
P_{17}	0.554	0.712						
P_{19}	0.787	0.708						
P_{21}	0.446	0.756						
P_{23}	0.545	0.771						
P_{25}	0.768	0.807						
P_{27}	0.531	0.698						
P_{29}	0.739	0.694						
P_{31}	0.800	0.902						
P_{33}	0.986	0.773						
P_{35}	0.596	0.750						
β_5							−	0.001
β_7							−	0.000
β_9							−	0.045
β_{11}							−	0.019
β_{13}							−	0.012
$\ln L$	−3282.95		−3292.18		−3292.23		−3287.97	
AIC	3354.95		3324.18		3322.23		3327.97	

Table 4. Parameter estimates and log-likelihoods (*ln*L) for different forms of the model in which the transition phase is a real phenomenon (model 2) for the **P-stock**. The figures shown in parenthesis are standard deviations provided by the Hessian approximation. Results are shown for various choices for the λ values, and both with and without a "learning" effect. For the results with "learning", the values quoted for P_λ refer to the reader's first year of sampling ($y_{\min}$).

a)

	Lamda=1-6	Lamda=1-7	Lamda=1-10	Lamda=1,3,6	Lamda=1,3,6	Lamda=1-6	Lamda=1-3	Lamda=1,3	Lamda=1,3,6
	Readers pooled	Readers pooled	Readers pooled	Readers pooled	Kato only	Kato only	Kato only	Kato only	Zenitani only
Y_1	1946.0	1946.0	1946.0	1946.0	1946.0	1946.0	1946.0	1946.0	1948.0
Y_2	1969.3	1969.2	1969.2	1969.2	1971.2	1971.5	1972.6	1971.7	1969.1
Y_3	1975.1	1975.1	1975.1	1975.1	1979.0	1977.0	1986.9	1985.4	1975.0
T_1	11.5	11.4	11.4	11.4	12.4	12.4	12.5	12.5	11.2
T_2	6.6	6.6	6.6	6.6	6.8	6.8	6.7	6.8	6.5
T_3	7.2	7.2	7.2	7.2	7.3	7.2	8.0	7.7	7.2
α	0.028	0.013	0.011	0.013	0.473	0.474	0.496	0.482	0.010
σ_{1965}	0.978	0.978	0.978	0.978	0.976	0.977	0.982	0.981	0.974
γ	1.10E-02	9.56E-03	9.62E-03	9.67E-03	0.000	0.000	0.000	0.000	0.021
P_1	0.053	0.053	0.053	0.060	0.138	0.000	0.000	0.000	0.064
P_2	0.352	0.353	0.353			0.443	0.397		
P_3	0.444	0.445	0.444	0.526	0.175	0.000	0.580	0.584	0.615
P_4	0.673	0.670	0.668			0.381			
P_5	0.608	0.600	0.601			0.413			
P_6	0.734	0.765	0.780	0.733	0.632	0.635			0.751
P_7		0.733	0.728						
P_8			0.634						
P_9			0.801						
P_{10}			0.734						
ln$L$	-2226.9	-2226.83	-2226.03	-2228.09	-318.211	-312.555	-322.513	-322.77	-1894.42
AIC	2256.9	2258.83	2264.03	2252.09	342.211	342.555	346.513	344.77	1918.42

b)

BEST MODEL

	No "learning"		With "learning"	
	Kato	Zenitani	Kato	Zenitani
Y_1	1946.0 (0.004)		1946.0	
Y_2	1969.0 (0.005)		1969.0	
Y_3	1976.5 (1.639)		1976.5	
T_1	11.4 (0.308)		11.4	
T_2	6.6 (0.090)		6.6	
T_3	7.2 (0.050)		7.2	
α	0.014 (0.109)		0.017	
σ_{1965}	0.979 (0.024)		0.979	
γ	0.012 (0.034)		1.20E-02	
P_1	0.000 (0.001)	0.064 (0.036)	0.000	0.065
P_3	0.581 (0.035)	0.617 (0.061)	0.581	0.371
P_6		0.751 (0.014)		0.690
β_1			–	0.000
β_3			–	0.077
β_6				0.010
ln$L$	-2221.56		-2216.65	
AIC	2249.56		2254.65	

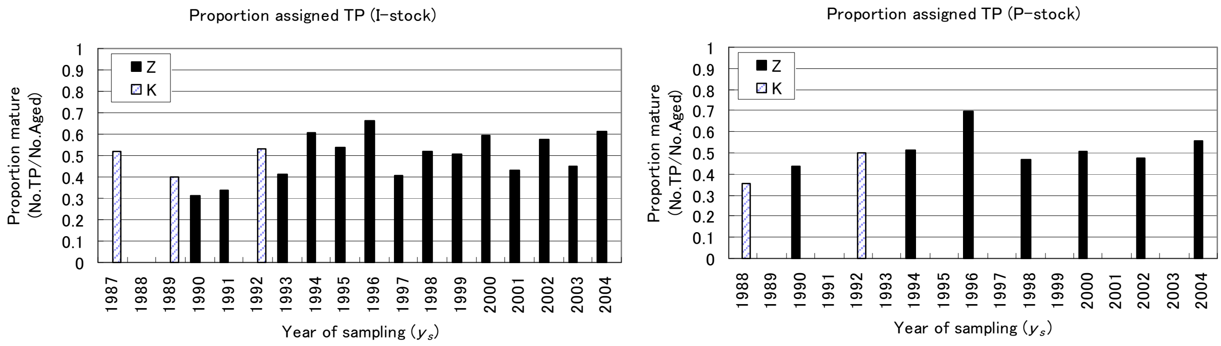


Figure 1. Proportion of earplugs sampled and read in year y_s, for which a transition phase was detected. “Z” refers to reader Zenitani, and “K” refers to reader Kato.

a) b)

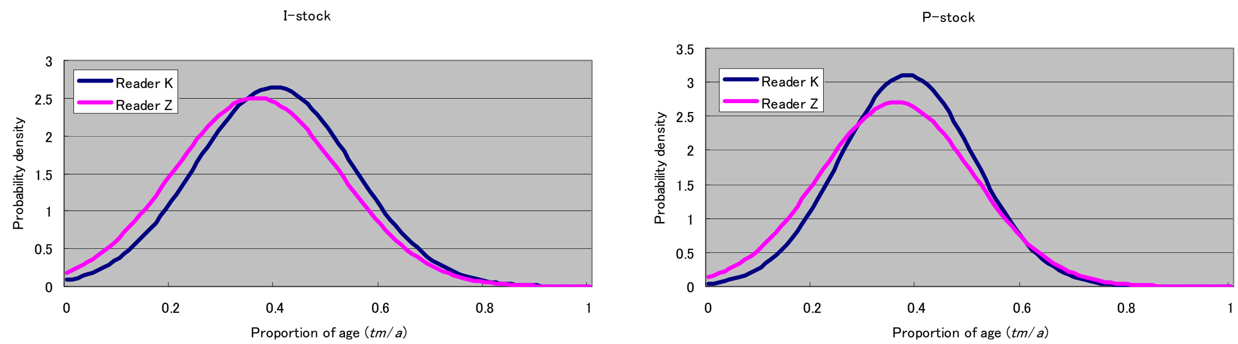


Figure 2. Probability density functions that Zenitani (or that Kato) identified a transition phase at certain proportion of the total extent of an earplug (expressed as *tm*/*a* where *tm* is age at transition and *a* is age at capture) for Model 1 without “learning”. The left hand side plot shows results for the I-stock, and the right hand side plot for the P-stock.

a) b)

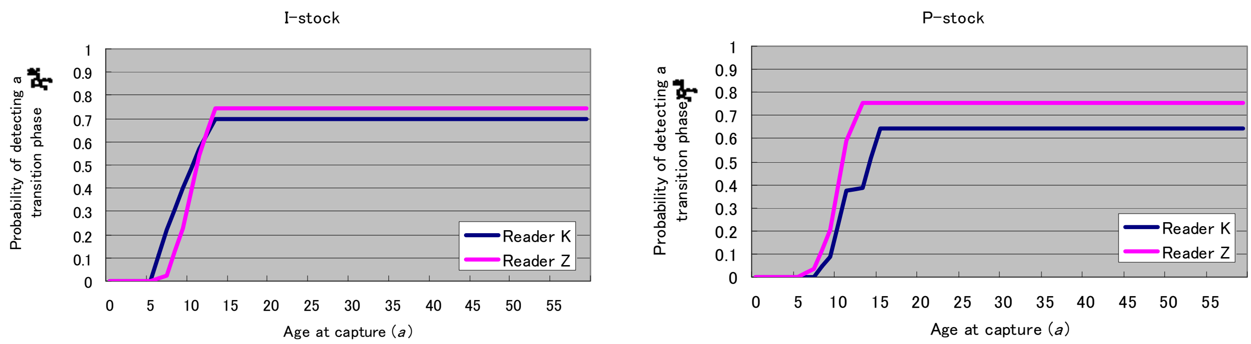


Figure 3. Probability that Zenitani (or that Kato) identified transition phase in earplug as function of age at capture (*a*) reading for that earplug for Model 1 without “learning”. The left hand side plot shows results for the I-stock and the right hand side plot for the P-stock.

I-stock (Model 1 – the transition phase is an artefact)

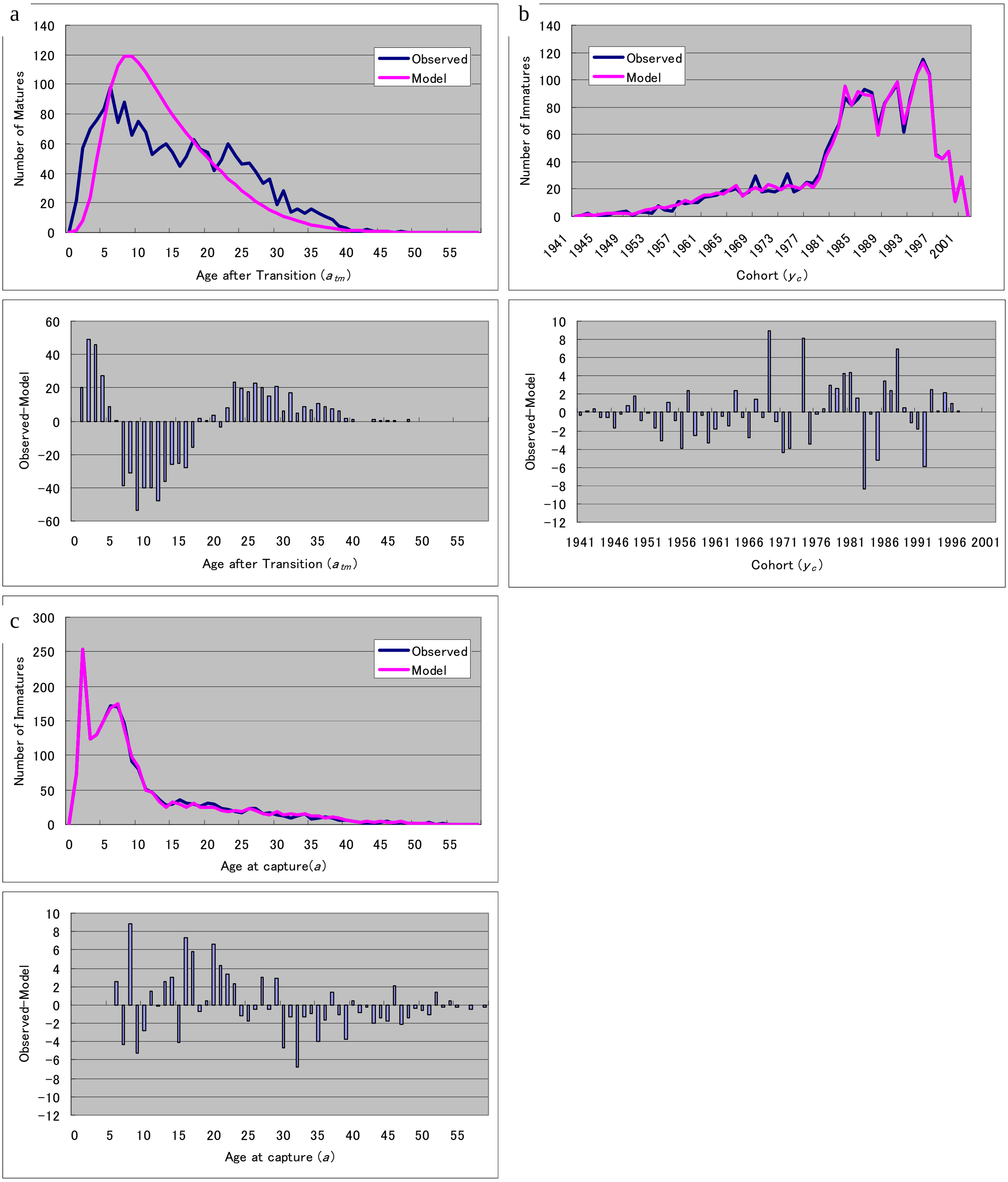


Figure 4. Observed and model-predicted distributions of age after transition (a_{tm}) for the complete dataset (upper plot), and residuals for this fit (lower plot) for **Model 1** without "learning" are shown in (a). Similar representations for the number of "immatures" against cohort and against age are shown in (b) and in (c), respectively [results for the **I-stock**].

a) b)

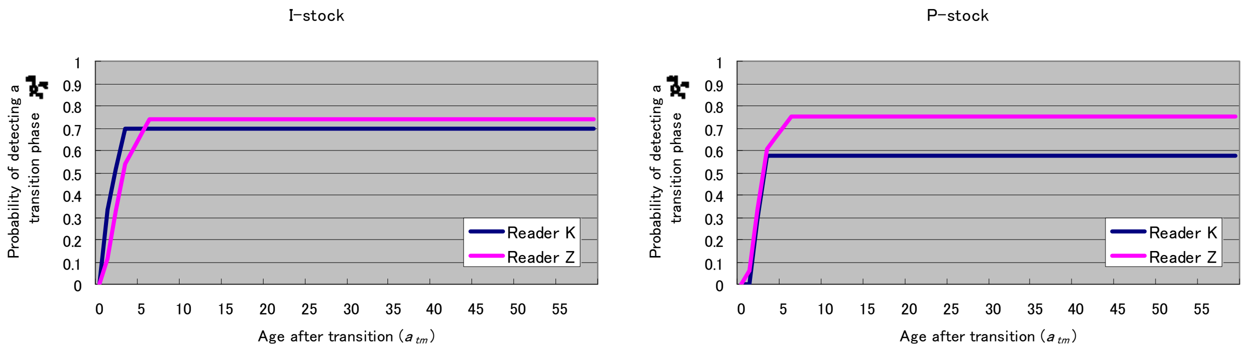


Figure 5. Probability that Zenitani (and that Kato) detected a transition phase in an earplug in which a_{tm} layers have accumulated since onset of transition for **Model 2** without “learning”. The left hand side plot shows results for the I-stock and the right hand side plot shows those for the P-stock.

I-stock (Model 2 – the transition phase is a real phenomenon)

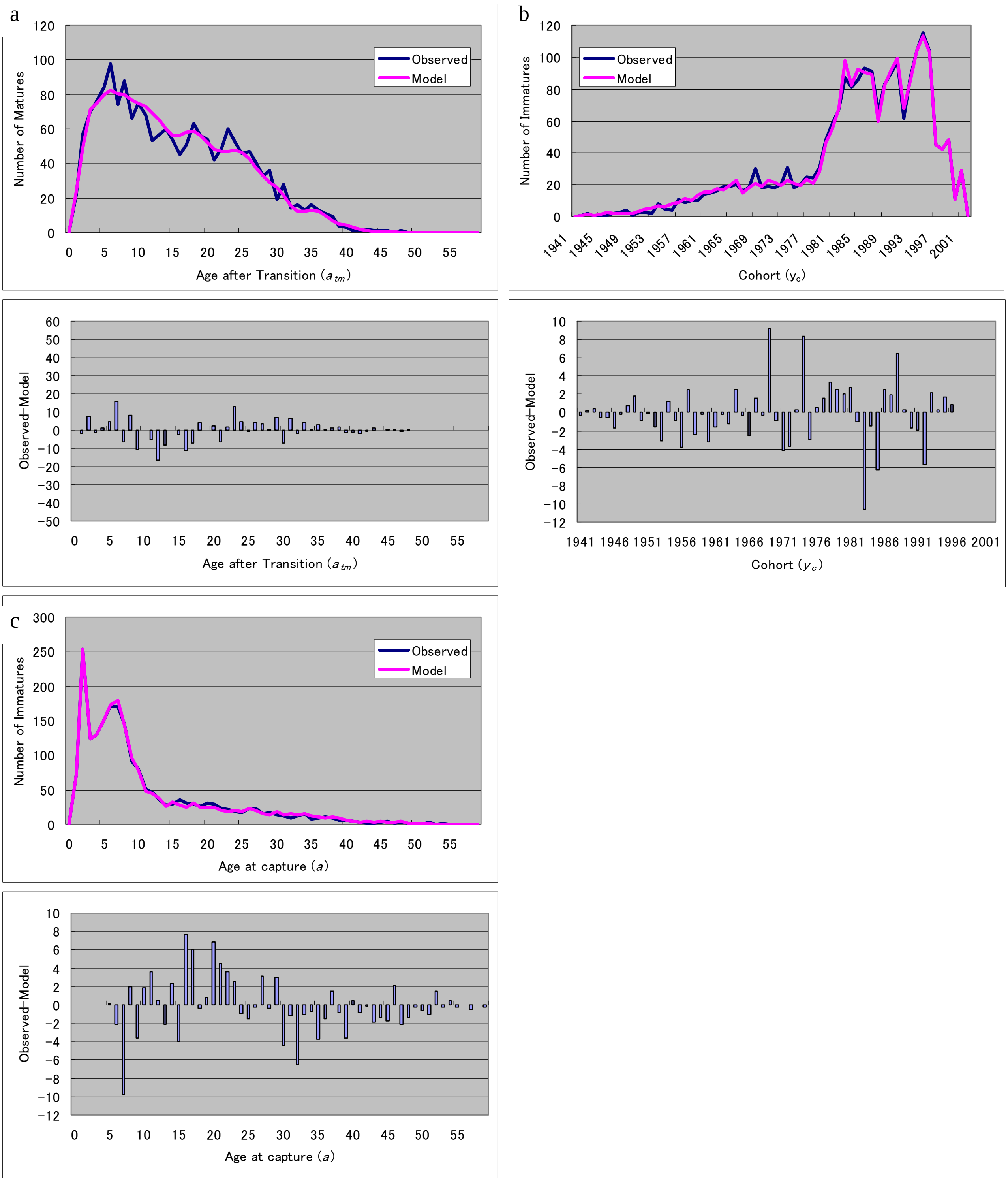
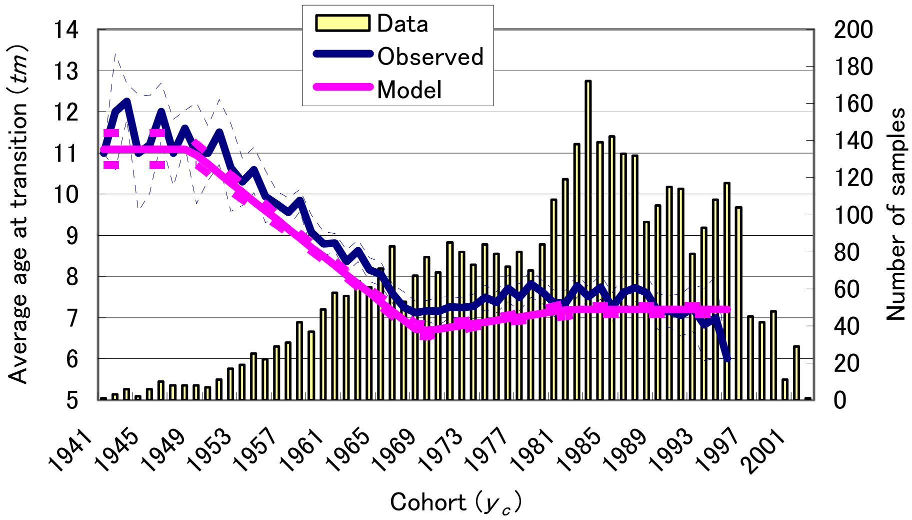


Figure 6. Observed and model-predicted distributions of age after transition (a_{tm}) for the complete dataset (upper plot), and residuals for this fit (lower plot) for **Model 2** without "learning" are shown in (a). Similar representations for the number of "immatures" against cohort and against age are shown in (b) and in (c), respectively [results for the **I-stock**].

a) I-stock



b) P-stock

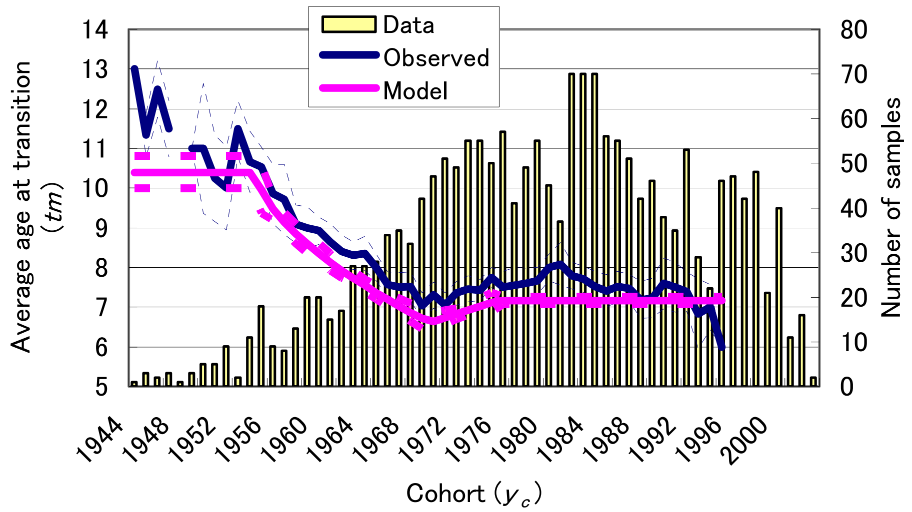


Figure 7. Observed mean age at transition *tm* against cohort compared to "true trend" as predicted by **Model 2** without "learning". A histogram of number of whales sampled (and aged) in each cohort is also plotted. Probability intervals (mean ±2SE) are also shown for the observed and model estimated average age at transition. The upper plot (a) is for the I-stock, and the lower plot (b) for the P-stock. Note that the fringe effect causes observations to be above true values for most cohorts, but for the most recent cohorts this effect is more than compensated by the truncation effect working in the opposite direction.

P-stock (Model 1 – the transition phase is an artefact)

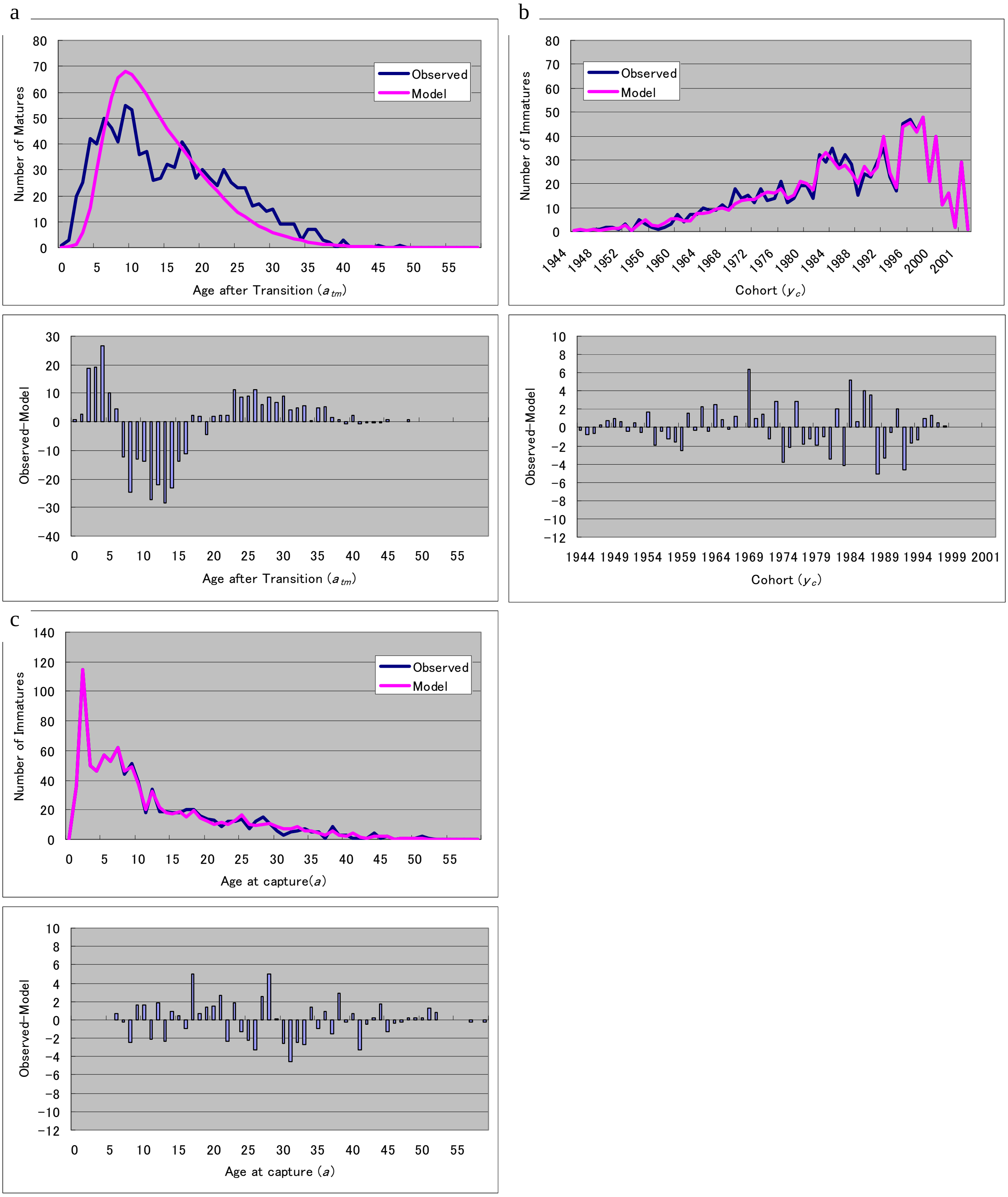


Figure 8. Observed and model-predicted distributions of age after transition (a_{tm}) for the complete dataset (upper plot), and residuals for this fit (lower plot) for **Model 1** without "learning" are shown in (a). Similar representations for the number of "immatures" against cohort and against age are shown in (b) and in (c), respectively [results are for the **P-stock**].

P-stock (Model 2 – the transition phase is a real phenomenon)

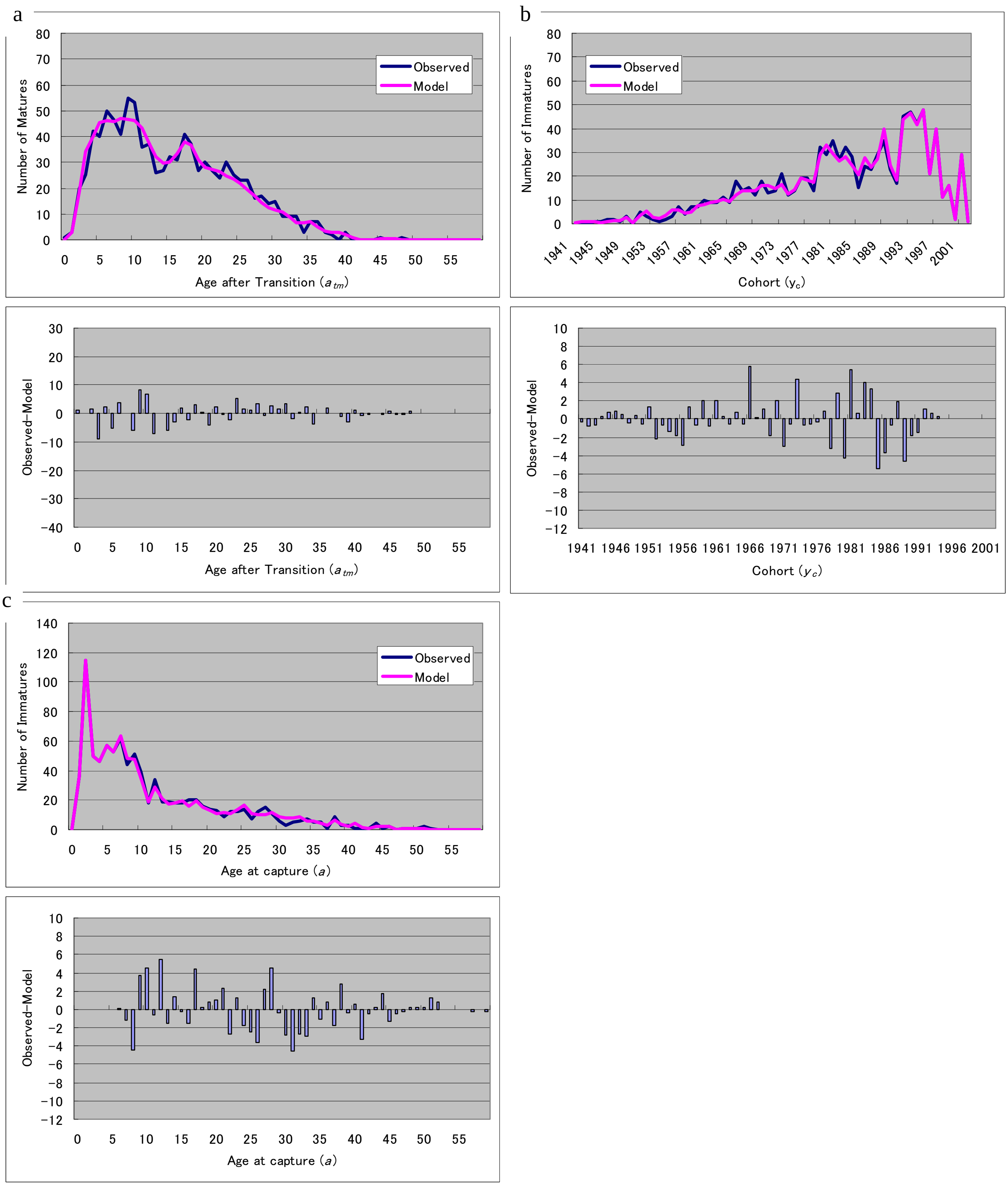


Figure 9. Observed and model-predicted distributions of age after transition (a_{tm}) for the complete dataset (upper plot), and residuals for this fit (lower plot) for **Model 2** without "learning" are shown in (a). Similar representations for the number of "immatures" against cohort and against age are shown in (b) and in (c), respectively [results are for the **P-stock**].