Estimation of natural mortality coefficients for Antarctic minke whales through VPA studies

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ABSTRACT

Virtual population analyses were performed to infer natural mortality coefficients for Antarctic minke whales in Area IV and V using catch-at-age data from both commercial whaling (1971-1986) and scientific whaling (JARPA 1987/88-2003/2004). Abundance estimates from the both surveys were used as tuning indices. A clear difference in the estimates of the natural mortality coefficients between Area IV and V was observed. Uncertainties in the estimates were lower than those in previous estimates derived by Butterworth *et al.* (1999, 2002) because longer series of catch-at-age and abundance estimates were used in the present study. Some sensitivity tests in the light of the estimation of the natural mortality coefficients were also performed. These analyses showed the estimate of the natural mortality coefficient in Area IV was slightly affected by both grouping of data such as 2-year-2-age and 3-year-3-age and an assumption of the maximum age used in the log-likelihood of the catch-at-age data, while the estimate in Area V was rather stable in these sense. In addition, the amount of bias in the abundance estimates due to g(0) affected to some extent the estimates of the natural mortality coefficient in Area IV. As expected, the amount of the additional variance did not impact the point estimates in the both areas while it made the uncertainty increase.

INTRODUCTION

Natural mortality coefficient, M, is one of the most important parameters to improve the stock management, and therefore the estimation of M is one of the major objectives of JARPA. The parameter M can be estimated using catch-at-age data. In fact, virtual population analysis (VPA) has been applied to catch-at-age data for Antarctic minke whales. Butterworth *et al.* (1999) conducted VPA studies using catch-at-age data of commercial whaling and JARPA (up to 1997/98) and abundance estimates from both IDCR and JAPRA in Area IV and V. Also, Butterworth *et al.* (2002) updated the results using the data up to 1999/2000 survey. In these analyses, the abundance estimates from JARPA were assumed to be biased because of the presence of skips in high density area, and therefore a bias correction factor was estimated as well as other parameters.

Recently, all the samples from JARPA (1987/88-1999/00) were re-aged. In addition, data from recent JAPRA (2000/01-2003/2004) can be utilized. Futhermore, updated JAPRA abundance estimates with bias correction are also available (Hakamada *et al.* 2005). Therefore, it is possible to re-evaluate estimates of M using such newly available data sets. As known well, VPAs are inherently sensitive to both scenario of population dynamics and tuning factors. In this paper, we show preliminary estimates of the natural mortality coefficients for Antarctic minke whales in Area IV and V through VPA studies and also assess the sensitivity of the estimates of M.

MATERIALS AND METHODS

The present VPA studies use catch-at-age matrices and abundance estimates as data sets. The so-called pulse fishing are assumed as population dynamics. Parameters in the population dynamics are estimated by the maximum likelihood method. In this section, we describe the data utilized, population dynamics assumed, details of estimation method, and sensitivity tests for VPA.

Data set - Catch-at-age data and abundance estimates -

Catch-at-age matrices constructed from the data of commercial catches from 1971/72 to 1986/87 and scientific catches from 1987/88 to 2003/04 are used. The procedures of the construction of the catch-at-age matrices are same as in Butterworth *et al.* (1999).

In this paper, the catch-at-age data are grouped in terms of the combinations of 3-year and 3-age as described in Butterworth *et al.* (1999, 2002) to reduce the uncertainty in the observed catch-at-age matrices. The combination of 2-year and 2-ages is also used to assess the sensitivity of such groupings. Table 1 provides the catch-at-age matrices for Area IV and V by 3-year grouping.

As tuning factors for VPA, we used the abundance estimates of the both IDCR and JARPA surveys and their coefficient of variations (CVs) given in Table 2. These estimates were derived by the standard method and may have severe downward biases because $g(0)$ could be less than 1. However, no reliable estimates of $g(0)$ are available at this stage. For this reason, we assumed that $g(0) = 1$ and the abundance estimates are unbiased for the sake of convenience. The effect of the underestimation of abundance on the estimation of M is examined by sensitivity tests.

Population dynamics

In this section, we illustrate the population dynamics assumed in this paper in terms of 3-year grouping. Descriptions for 2-year grouping are essentially same as those for 3-year grouping, and therefore we omit them. In this paper, we assume that the population dynamics model is common to the two areas except for values of parameters.

As in Butterworth *et al.* (1999, 2002), we assume the pulse fishing model as follows. Let $N_{y,a}$ be the number of minke whales of age group a at the start of year y and $C_{y,a}$ be the number of whales of age group a caught in year y. Also, let M_a denote the natural mortality coefficient for age group a. Then, the following equation is assumed as population dynamics:

$$N_{a+3,y+3} = (N_{y,a} - C_{y,a})e^{-M_a}. \tag{1}$$

The actual fishing rate is defined by

$$F_{y,a} = \frac{C_{y,a}}{N_{y,a}}. \tag{2}$$

Taking the uncertainty in aging older whales into consideration, we assume that the maximum age group is fixed at 44, which is the same treatment in Butterworth *et al.* (1999, 2002). In this sense, the natural mortality coefficient for the age group greater than 41 is assumed to be infinity. Also, we suppose the natural mortality coefficient is age-independent for $a \leq 41$.

Now, we assume the separability in the expected fishing mortality rates as follows:

$$E[C_{y,a}] = \begin{cases} S_a^C F_y^E N_{y,a} & \text{if } 71 \leq y \leq 86, \\ S_a^S F_y^E N_{y,a} & \text{if } 89 \leq y \leq 04, \end{cases} \tag{3}$$

where $E[C_{y,a}]$ is the expected catch of whales of age group a in year y, S_a^C and S_a^S are the selectivities of age group a for commercial and scientific whaling, respectively, and F_y^E is the fishing mortality rate in year y. The selectivities at the age group m, S_m^C and S_m^S, are fixed at 1 for the identifiability of parameters.

Probability distributions of catch-at-age data

Let $C_{y,a}^*$ be the number of whales actually aged as age group a among those caught in year y. We assume that the maximum age group used in the likelihood of catch-at-age (say m) is set at 29 as a baseline case, Furthermore, as in Butterworth *et al.* (1999, 2002), the selectivities $S_a^C (a = 2, 5, \ldots, 14)$ in the period of commercial whaling is assumed to be 0. We, therefore, construct the likelihood using the catch-at-age data of age group $17 \leq a \leq m$ for commercial whaling and that of $2 \leq a \leq m$ for scientific whaling.

Let C_y^* be the total number of aged whales used in the likelihood :

$$C_y^* = \begin{cases} \sum_{a=17}^{m} C_{y,a}^* & \text{if } 71 \leq y \leq 86, \\ \sum_{a=2}^{m} C_{y,a}^* & \text{if } 89 \leq y \leq 04. \end{cases} \tag{4}$$

The expected proportion of whales of age group a in year y is given by

$$\begin{aligned} \rho_{y,a}^C &= \frac{S_a^C N_{y,a}}{\sum_{a=2}^{m} S_a^C N_{y,a}}, \qquad 71 \leq y \leq 86, \\ \rho_{y,a}^S &= \frac{S_a^S N_{y,a}}{\sum_{a=2}^{m} S_a^S N_{y,a}}, \qquad 89 \leq y \leq 04. \end{aligned} \tag{5}$$

(a) Multinomial models The distribution of $(C_{y,17}^*, \ldots, C_{y,m}^*)$ $(y \leq 86)$ and $(C_{y,2}^*, \ldots, C_{y,m}^*)$ $(y \geq 89)$ given C_y^* are usually assumed to be the multinomial distribution as follows:

$$\begin{aligned} (C_{y,17}^*, \ldots, C_{y,m}^*)|_{C_y^*} &\sim Multi(C_y^*;\ \rho_{y,17}, \ldots, \rho_{y,m}^C), \qquad 71 \leq y \leq 86, \\ (C_{y,2}^*, \ldots, C_{y,m}^*)|_{C_y^*} &\sim Multi(C_y^*;\ \rho_{y,2}, \ldots, \rho_{y,m}^S), \qquad 89 \leq y \leq 04. \end{aligned} \tag{6}$$

The log-likelihood for the catch-at-age data is represented as

$$\log L_1 \propto \sum_{y=71}^{86} \sum_{a=17}^{m} C^*_{y,a} \log \rho^C_{y,a} + \sum_{y=89}^{04} \sum_{a=2}^{m} C^*_{y,a} \log \rho^S_{y,a}. \tag{7}$$

(b) Dirichlet-multinomial models with overdispersion In multinomial models, an observed variance often exceeds the theoretical variance because of correlation or heterogeneities among samples. This kind of phenomenon is called overdispersion. To take the overdipersion into account, Butterworth *et al.* (1999) incorporate a multiplier as a quasi-likelihood manner to reduce the contribution of the likelihood of the catch-at-age data.

Instead, in this paper, we assume the Dirichlet multinomial distribution with the same mean as that of the multinomial distribution above and the covariance,

$$\mathrm{Cov}[C^*_{y,a}, C^*_{y,a'}] = \{1 + (C^*_y - 1)\phi^{C/S}_y\}\ C^*_y\ \rho^{C/S}_{y,a}\ \rho^{C/S}_{y,a'}, \tag{8}$$

where ϕ^C_y, ϕ^S_y are parameters related to the degree of the overdispersion. In this model, actual levels of the overdispersion depend on the samples size as well as the parameters ϕ^C_y, ϕ^S_y. Using the genuine likelihood of this model, we can objectively compare the multinomial model with the overdispersion model by a model selection criterion, AIC.

Probability distributions of abundance estimates

Let $\hat{N}_y$ and CV_y be an abundance estimate and its CV, respectively, and the distribution of $\hat{N}_y$ is assumed to be the log-normal distribution as follows:

$$\log \hat{N}_y - \log\{g(0)N_y\} \sim N(0, CV_y^2), \tag{9}$$

where N_y is the 1+population defined as

$$N_y = \sum_{a=2}^{44} N_{y,a}.$$

Then, the log-likelihood for the catch-at-age data is represented as

$$\log L_2 \propto \sum_y \left\{ -\frac{(\log \hat{N}_y - \log\{g(0)N_y\})^2}{2CV_y^2} \right\}. \tag{10}$$

We assumed these abundance estimates are unbiased, which means $g(0)$ is fixed at 1. The effect of the underestimation of abundance on the estimation of M is examined by sensitivity tests.

When the additional variance is taken into consideration, the distribution of $\hat{N}_y$ is represented as

$$\log \hat{N}_y - \log\{g(0)N_y\} \sim N(0, CV_y^2 + CV_{add}^2), \tag{11}$$

where CV_{add} is a coefficient of variation deriving from the additional variance.

Baseline scenario and parameters to be estimated

We assume the following scenario as baseline, which is essentially same as that in Butterworth *et al.* (1999, 2002):

1. terminal F: $F_{m,71} = F_{m-3,71}$ in Area IV and $F_{m,74} = F_{m-3,74}$ in Area V are assumed; the other terminal F's are unknown and estimated;
2. selectivity for the period of commercial whaling: $S_a^C = 0 (2 \leq a \leq 14)$; $S^C = S_{17}^C = S_{20}^C$ is unknown and estimated; $S_a^C = 1$ $(23 \leq a \leq m)$;
3. selectivity for the period of commercial whaling: $S^S = S_2^S = S_5^S$ is unknown and estimated; $S_a = 1$ $(a \geq 8)$;
4. the natural mortality M is constant up to age group 44 and unknown;
5. year-grouping: 3-year and 3-age combination;
6. the maximum age group m is set at 29;
7. $g(0) = 1$;
8. no additional variance: $CV_{add}^2 = 0$.

All the unknown parameters are estimated by maximizing the log-likelihood, $\log L_2 + \log L_1$, using the quasi-Newton algorithm in the statistical software R. Confidence intervals for the parameters are mainly obtained using a bootstrap method with 999 bootstrap samples. For some sensitivity tests, we use the standard errors derived from the inverse Fisher information matrix in place of the bootstrap method.

Sensitivity tests

The estimation of M through VPA depends on scenario as well as tuning indices. To assess the effects of changes of scenarios, we conduct some sensitivity tests in the following four aspects:

- Year-grouping: 3-year and 3-age grouping and 2-year and 2-age grouping;
- The maximum age group m: m=29, 35;
- g(0): g(0) is known, common to the both surveys, and set at the value less than 1;
- The additional variance: CV_{add}^2 is positive and known.

RESULTS

Table 3 shows the results of model selection in catch-at-age distributions for the baseline case. This table indicates that the amount of overdispersion is small and, as a result, the multinomial model is selected by AIC in each area. In fact, the estimate of M is almost unchanged in each area. We, therefore, conclude that there is no overdispersion in the catch-at-age data in the both areas.

The estimates of the natural morality coefficients in Area IV and V for the baseline scenario were 0.0788 (/year) and 0.0497 (/year), respectively. Table 4 provides the estimated numbers-at-age matrices in Area IV and V for the baseline scenario. Plots of the estimated total population size with the tuning indices are shown in Figure 1.

The results of sensitivity tests in terms of the year-grouping and the maximum age m are shown in Table 5. Also, the results of sensitivity tests in terms of g(0) and the additional variance are shown in Figure 2 and 3, respectively.

DISCUSSION

Table 4 shows there is a clear difference in M between Area IV and V. This result is consistent with the previous result in Butterworth *et al.* (2002), although the current estimate for the baseline scenario in Area IV is slightly greater than that in the paper.

Our estimates of the natural mortality coefficient M were estimated using longer series of catch-at-age and abundance estimates compared to Butterworth *et al.* (1999, 2002). Because of this, uncertainties in our estimates were lower than those in previous estimates.

Sensitivity analyses showed the estimate of M in Area V was rather stable. On the other hand, the estimate in Area IV was slightly affected by both the grouping of data and the assumption of the maximum age. Furthermore, the value of g(0) affects the estimates of M in Area IV. The trend of abundance estimates plays a key role in the estimation of M. In fact, if omitting the IDCR estimates in 78/79, then the trend in Area IV becomes flatter, and the estimate of M for each scenario becomes small (e.g. $\hat{M} = 0.0549$ for the baseline). In this sense, one IDCR estimates in 78/79 has a great impact on the estimation of M in Area IV. In other words, the estimate of M is not robust to the change of the 78/79 estimate.

As we expected, the amount of the additional variance did not impact the point estimates in the both area while it made the uncertainty increase. The inter-annual change between two areas may occur, and therefore there might be a positive amount of additional variance. In this sense, it is necessary to assess the additional variance in the abundance estimates from JAPRA as well as IDCR/SOWER in order to evaluate the uncertainty in the estimate of M.

In this paper, we assumed only spatial difference in M. However, the decline of abundance may change the value of M yearly. Detection of such temporal changes in M is a difficult task as well as estimating age-dependent M. Further successive scientific whaling is needed to accomplish these researches.

A lot of parameters such as the terminal F's must be estimated in VPA although the amount of data and information are limited. Instead of estimating these parameters independently, assuming a smoothness constraint among them may be helpful to reduce the burden to estimate them. Bayesian modeling is a promising way to incorporate the smoothness into the VPA model. For example, a smoothness prior for the terminal F's can be assumed as follows:

$$\begin{aligned} F_{Y,a-2}|_{F_{Y,a-1},F_{Y,a}} &\sim N(-2F_{Y,a-1} + F_{Y,a}, \tau^2), \\ F_{y-2,m}|_{F_{y-1,m},F_{y,m}} &\sim N(-2F_{y-1,m} + F_{y,m}, \gamma^2), \end{aligned} \tag{12}$$

where Y is the terminal year, and τ^2, γ^2 are parameters related to the amount of smoothness. The posterior means of parameters can be obtained using Markov chain Monte Carlo (MCMC) methods. Furthermore, if the marginal likelihood can be derived, the posterior probability of each scenario can be evaluated. It is one of challenging issues in the future work.

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Table 1. Catch-at-age matrices of whales in Area IV and V in terms of 3-year grouping

(a) Area IV

Cya	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	47	50	53	Total
1971	121	256	314	310	352	319	284	235	146	95	99	45	30	25	3	7	17	4	2663
1974	820	1508	1773	1716	1423	1261	895	723	470	345	170	110	92	18	15	13	7	0	11358
1977	80	329	437	633	618	529	283	234	125	79	48	11	25	6	0	2	6	0	3444
1980	213	493	626	730	776	751	596	469	294	228	138	117	64	47	36	23	18	0	5617
1983	235	499	606	808	709	886	664	506	346	216	84	47	34	32	7	7	3	0	5689
1986	68	181	330	478	598	676	598	539	358	234	116	92	51	20	15	6	0	0	4359
1989	63	97	80	47	44	61	61	33	45	27	12	13	7	6	1	0	0	0	598
1992	39	39	39	24	20	21	18	12	16	20	15	9	7	2	2	2	1	1	288
1995	92	82	79	93	48	42	36	28	43	24	27	24	13	6	4	10	5	4	660
1998	87	36	36	27	20	19	14	17	10	10	15	13	10	2	5	6	0	1	328
2001	83	81	75	52	54	52	48	34	24	33	26	27	27	18	15	7	1	1	660
2004	39	30	45	21	28	30	23	16	12	13	18	8	18	7	8	8	4	1	330

(b) Area V

Cya	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44	47	50	53	Total
1974	21	62	129	133	131	89	74	48	30	3	10	4	0	0	0	0	0	0	734
1977	38	279	374	488	502	439	320	188	146	98	40	34	9	13	12	0	0	2	2982
1980	58	179	323	344	395	464	264	246	259	198	84	81	37	23	26	25	0	0	3006
1983	117	382	479	584	700	678	527	376	285	150	103	60	34	23	11	6	2	1	4518
1986	61	151	202	307	357	497	426	314	275	164	75	64	15	14	3	4	2	3	2936
1989	13	34	27	28	39	25	21	15	8	10	5	5	5	0	0	0	0	0	236
1992	26	59	69	65	62	58	63	60	55	36	35	25	19	5	7	7	0	0	650
1995	32	23	44	35	39	31	28	20	21	17	11	16	8	4	0	0	0	0	330
1998	60	37	55	61	78	51	48	42	56	39	36	33	22	19	8	6	7	0	659
2001	16	26	29	31	33	42	9	26	28	21	19	16	15	2	6	3	4	4	330
2004	22	33	28	37	33	37	29	22	22	16	19	8	8	3	5	2	3	1	330

Table 2. Abundance estimates and their coefficient variations (CVs) in Area IV and V used as tuning factors

(a) Area IV

Survey	Estimates	CV
IDCR 1978/79	134,304	0.179
IDCR 1988/89	60,207	0.184
JARPA 1989/90	54,539	0.215
JARPA 1991/92	54,959	0.243
JARPA 1993/94	41,934	0.215
JARPA 1995/96	42,134	0.220
JARPA 1997/98	32,656	0.252
JARPA 1999/00	49,867	0.169
JARPA 2001/02	68,503	0.167
JARPA 2003/04	47,858	0.358

(b) Area V

Survey	Estimates	CV
IDCR 1980/81	257,768	0.280
IDCR 1985/86	290,675	0.136
IDCR 1991/92	190,044	0.180
JARPA 1990/91	195,743	0.210
JARPA 1992/93	122,048	0.229
JARPA 1994/95	168,566	0.268
JARPA 1996/97	171,332	0.261
JARPA 1998/99	198,423	0.233
JARPA 2000/01	179,796	0.210
JARPA 2002/03	226,884	0.161

Table 3. Results of model selection in terms of overdispersion for the baseline scenario in Area IV and V

Case	ϕc	ϕs	M	relative AIC
Area IV				
$\phi c=0$, $\phi s=0$	0	0	0.0788	min AIC
$\phi c>0$, $\phi s=0$	0.000360	0	0.0788	2.00
$\phi c=0$, $\phi s>0$	0	5.84	0.0791	1.08
$\phi c>0$, $\phi s>0$	0.000250	5.84	0.0791	3.52
Area IV				
$\phi c=0$, $\phi s=0$	0	0	0.0497	min AIC
$\phi c>0$, $\phi s=0$	4.84	0	0.0500	1.24
$\phi c=0$, $\phi s>0$	0	7.60	0.0501	0.92
$\phi c>0$, $\phi s>0$	4.77	4.54	0.0503	2.18

Table 4. The estimated numbers-at-age matrices in Area IV and V for the baseline scenario

(a) Area IV

Nya	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44
1971	28512	27196	22558	16794	11988	7954	6114	4219	3028	1976					
1974	21562	22533	21358	17616	13040	9195	6027	4597	3138	2268	1478				
1977	14926	16462	16668	15509	12577	9179	6263	4046	3051	2098	1511	1028			
1980	11887	11783	12791	12854	11768	9450	6828	4714	3003	2303	1587	1149	799		
1983	11973	9265	8950	9634	9590	8686	6866	4914	3343	2131	1631	1139	811	577	
1986	13077	9316	6949	6608	6982	7018	6157	4891	3471	2358	1505	1215	858	611	428
1989	9499	10325	7242	5242	4849	5044	5006	4383	3427	2449	1670	1092	883	634	464
1992	8857	7489	8109	5672	4109	3797	3933	3899	3426	2661	1904	1303	848	688	494
1995	8024	6999	5906	6391	4468	3231	2980	3087	3061	2682	2076	1484	1017	661	539
1998	10644	6295	5484	4614	4982	3492	2518	2321	2409	2374	2089	1610	1148	788	515
2001	6726	8379	4962	4314	3629	3921	2742	1974	1815	1888	1858	1630	1255	894	618
2004	6047	5272	6578	3871	3371	2824	3054	2124	1528	1409	1458	1440	1259	965	688

(b) Area V

Nya	2	5	8	11	14	17	20	23	26	29	32	35	38	41	44
1974	35786	37191	37061	31211	25888	20127	13608	12629	6823	705					
1977	30518	35374	35728	34575	28307	22825	17275	11352	10266	5393	542				
1980	26882	30147	33771	33098	31047	24639	19300	14221	9110	8035	4091	388			
1983	22962	26530	28837	31313	29833	27162	20842	15966	11405	7027	6054	3094	238		
1986	28102	22595	25162	26549	27989	25816	22833	17040	12722	8829	5312	4596	2344	157	
1989	23771	27735	21597	23367	23901	24486	21829	18794	13649	9882	6693	4045	3501	1799	111
1992	17049	23498	26655	20194	21258	21146	21088	18291	15325	10830	7625	5165	3120	2700	1389
1995	19339	16836	22555	24890	18334	18782	18180	17635	14878	12123	8338	5863	3971	2395	2082
1998	20253	19095	16179	21074	22638	16211	16166	15226	14375	11795	9350	6432	4516	3061	1847
2001	17648	19972	18339	15095	19140	19992	13932	13519	12391	11368	9081	7195	4943	3471	2349
2004	15136	17439	19193	17141	13720	16932	17200	11678	11011	9815	8765	7000	5545	3806	2679

Tables 5. Sensitivity in estimates of the natural mortality rates *M* (/year) in Area IV and V

(a) Area IV

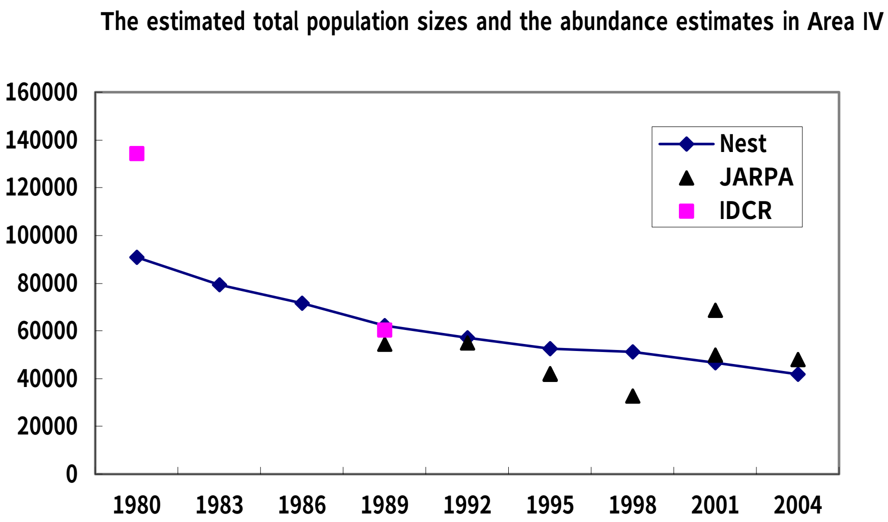
Groping	m	Esimates of M (/year)	Esimates of M (/year) in SC/54/IA25
3 years	30	0.0788 (0.0621, 0.0957)	0.070 (0.036, 0.093)
	36	0.0753 (0.0514, 0.0944)	-
2 years	30	0.0734 (0.0573, 0.0895)	-
	36	0.0695 (0.0534, 0.0856)	-

(b) Area V

Groping	m	Esimates of M (/year)	Esimates of M (/year) in SC/54/IA25
3 years	30	0.0497 (0.0335, 0.0644)	0.0480 (0.011, 0.095)
	36	0.0507 (0.0349, 0.0689)	-
2 years	30	0.0506 (0.0337, 0.0675)	-
	36	0.0517 (0.0348, 0.0686)	-

The values in parentheses show 90% confidence intervals. The value *m* is the maximum age used in the log-likelihood for catch-at-age. The estimates in SC/54/IA25 were obtained using the data up to 2001 in Area IV and 1998 in Area V.

(a) Area IV



(b) Area V

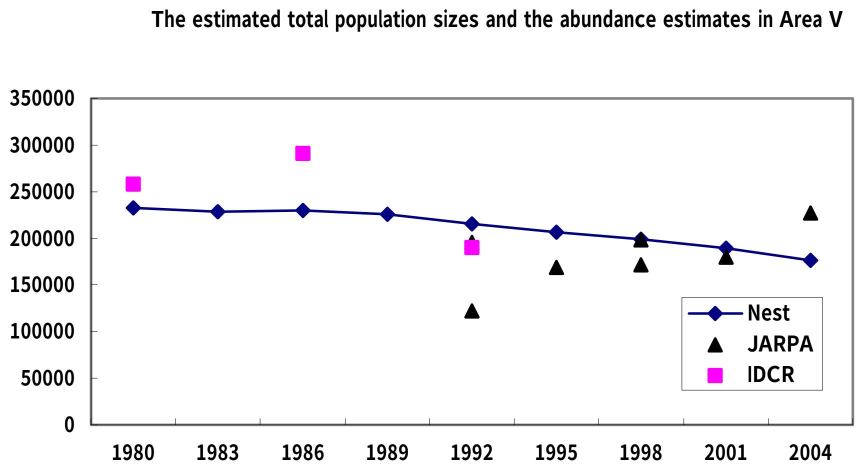


Figure 1. Plots of the total population size estimated by VPA with the abundance estimates used as tuning factors in Area IV and V for the baseline case.

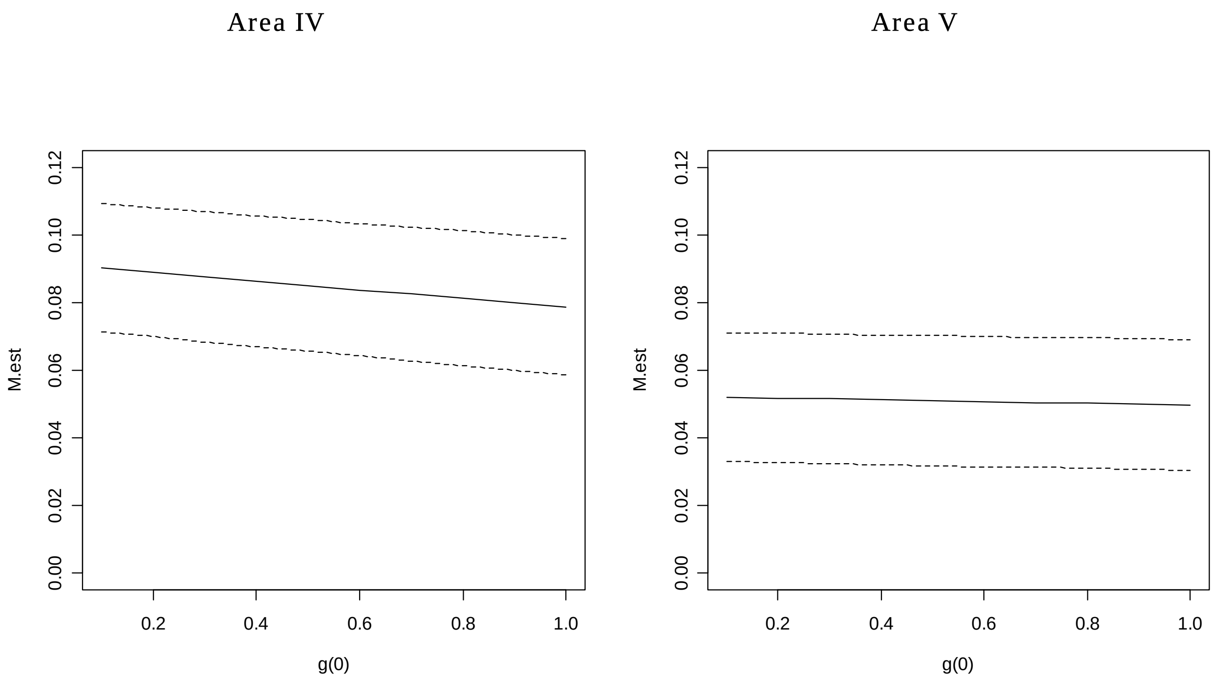


Figure 2. Sensitivity to the change in g(0) for the baseline scenario. Solid line: estimate of M; dashed line: 95% limits.

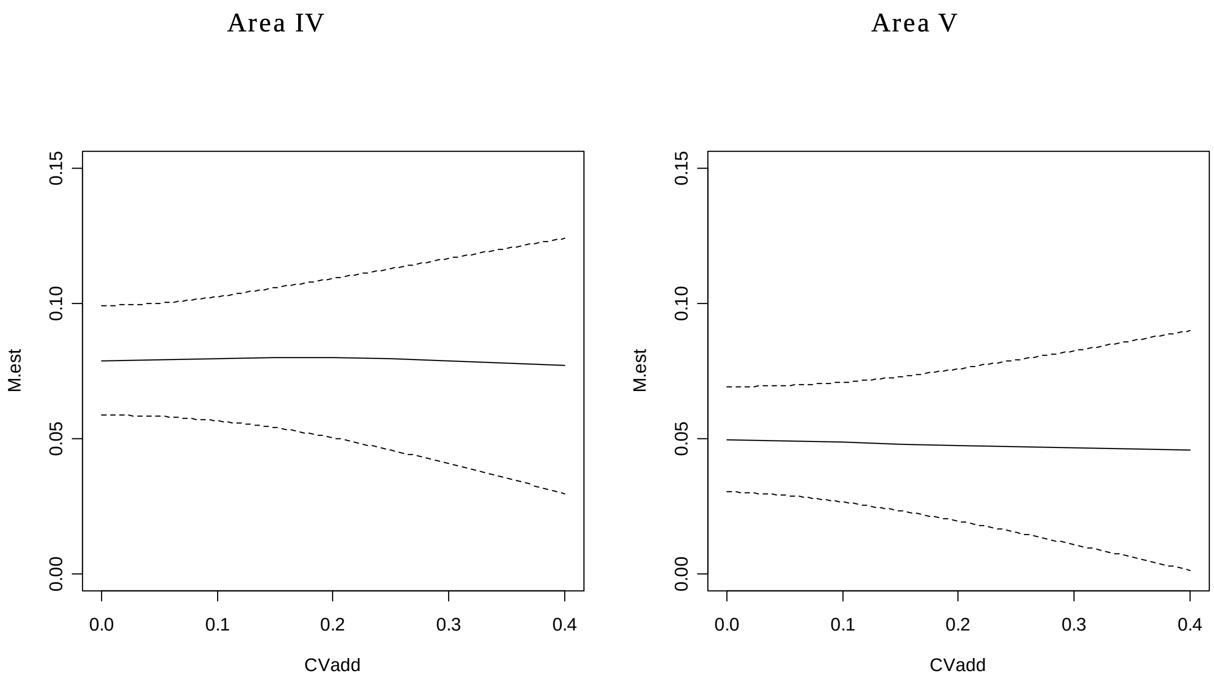


Figure 3. Sensitivity to the change in the amount of the additional variance for the baseline scenario. Solid line: estimate of M: dashed line: 95% limits for the baseline scenario.