Assessment of Antarctic minke whales using statistical catch-at-age analysis (SCAA)

ANDRÉ E. PUNT[1], TAKASHI HAKAMADA[2], TAKEHARU BANDO[2] AND TOSHIHIDE KITAKADO[3]

Contact e-mail: aepunt@uw.edu

ABSTRACT

Statistical catch-at-age analysis (SCAA) is applied to data for Antarctic minke whales. The SCAA model is spatially-structured, can model multiple stocks of minke whales, and can utilise several data types for parameter estimation. The application to Antarctic minke whales considers two stocks (I and P) in five areas which cover Antarctic Areas III–E to VI–W. The parameters of the model (annual deviations about the stock-recruitment relationship, changes over time in carrying capacity, density-dependence parameters related to productivity and carrying capacity, and the parameters which determine growth by stock, age-specific natural mortality by stock, and vulnerability by area and 'fleet') are estimated by fitting the model to data on catches, catch-at-length, conditional age-at-length, and estimates of absolute and relative abundance. A reference case analysis is selected, and sensitivity explored using retrospective analyses and by varying the assumptions on which the reference case analysis is based. The reference case analysis is able to mimic all of the data sources adequately. Most of the analyses (reference and sensitivity) indicates that Antarctic minke whales in the assessed area increased from 1930 until the mid-1970s and have declined thereafter, with the extent of the decline greater for minke whales in Antarctic Areas III–E to V–W than for those further east. Natural mortality is consistently estimated to be higher for younger and older individuals than for individuals of intermediate age. Estimates of $MSYR_{1+}$ (the exploitation rate on animals 1 and older at which sustainable yield is maximised) are presented, but are unreliable owing to the lack of contrast.

KEYWORDS: CATCH-AT-AGE, ANTARCTIC MINKE WHALE, POPULATION MODEL; SOUTHERN HEMISPHERE; SURVEY-VESSEL; MODELLING; MSY RATE; ANTARCTIC; MORTALITY RATE; SCIENTIFIC PERMITS

INTRODUCTION

One of the fundamental tasks of the Scientific Committee of the International Whaling Commission (IWC) is to conduct 'assessments' to determine the status (e.g. relative to carrying capacity), trends and productivity of whale populations. Most of these assessments are based on fitting population dynamics models to estimates of absolute and relative abundance from surveys (e.g. Johnston *et al.*, 2011; Müller, 2011; Punt and Polacheck, 2006). In contrast, best practice for fishery assessments, which are conducted for largely the same purposes as IWC assessments, involve fitting population models to catch-at-age (CAA) and length-frequency data as well as to abundance indices (Maunder and Punt, 2013). Southern Hemisphere minke whales (*Balaenoptera bonaerensis*) are unique among cetacean stocks in that there is a long history and CAA and length frequency data have been collected.

In the early 1980s, the Scientific Committee's recommendations on catch limits for these minke whales followed from the Committee's acceptance that Antarctic minke whale numbers had been increasing prior their exploitation to any substantial extent. Amongst the evidence taken to point towards these conclusions, until these came under question in 1983 (IWC, 1984), were estimates of the slope of the descending limb of minke whale catch curves (Oshumi, 1979). Concern was expressed regarding assessments of minke whales based on CAA data (e.g. Sakuramoto and Tanaka, 1985; 1986) given difficulties estimating natural mortality and in particular how natural mortality changes with age (e.g. Chapman, 1983; Cooke, 1985; de la Mare, 1985a; 1985b), because trends in population size for minke whales are sensitive to the value for natural mortality (Butterworth *et al.*, 1999). The 'Japanese Whale Research Programme under Special Permit in the Antarctic' (or JARPA) stated that its primary objective was to estimate the age-specific natural mortality coefficient for minke whales in response to this situation (Government of Japan, 1987), although this was later changed to estimation of average (over age) natural mortality (Government of Japan, 1992).

Two classes of stock assessment method have recently been proposed for application to Antarctic minke whales (see Punt (2014) for a summary of recent applications of age-structured assessment models to Antarctic minke whales). One of these (ADAPT-VPA; Butterworth *et al.*, 2002; Butterworth *et al.*, 1999; Butterworth *et al.*, 1996) is based on the assumption that the CAA data are measured with limited error compared to the indices of abundance used to estimate the values for the parameters of the model. The other is Statistical catch-at-age Analysis (SCAA; Punt, 2011; Punt, 2014; Punt *et al.*, 2013; Punt and Polacheck, 2005; 2006; Punt and Polacheck, 2007; 2008). In contrast to ADAPT-VPA, SCAA does not assume that the age-structure of the catches is measured with limited error, and can account for both sampling error and age-reading error[4]. The specific SCAA model developed for Antarctic minke whales can account for multiple stocks in the assessed area, time-varying growth, multiple areas, fleet-specific vulnerabilities,

[4]Age-reading error has been quantified for Antarctic minke whales by Kitakado *et al.* (2013).

[1] *School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA.*
[2] *Institute of Cetacean Research, Toyomi 4-5, Chuo-ku, Tokyo 104-0055, Japan.*
[3] *Tokyo University of Marine Science and technology, Konan 4-5-7, Minato-ku, Tokyo 104-8477, Japan.*

changes over time in the proportion of each stock in each area and changes over time in vulnerability.

The range of issues which have motivated the analyses using these methods has increased over time in response to the needs and priorities of the Scientific Committee and the Commission. One specific issue was understanding the cause for the decline in estimates of abundance for minke whales from the 2nd to the 3rd circumpolar surveys of minke whales conducted as part of the International Decade of Cetacean Research (IDCR)/Southern Ocean Whale and Ecosystem Research (SOWER) programmes. Butterworth and Punt (1999) identified several hypotheses for a decline in minke whale recruitment including 'super-compensation', increased competition from other krill predators, poorer environmental conditions and bias in the estimation method. (IWC, 2002; 2003) identified further hypotheses which could address the reasons for the decline. IWC (2005) noted that population modelling could provide a way to address the plausibility of the hypothesis that the decline in recruitment is related to competition and other population dynamic-related factors. It considered that a SCAA modelling approach would provide the most appropriate modelling framework to address the population dynamics-related issue because a SCAA could allow *inter alia* for errors in CAA data, more than a single stock, environmental covariates, fleet-specific vulnerabilities (IWC, 2005)[5] and changes over time in vulnerabilities to be addressed and explored within a single model framework.

SCAA (Fournier and Archibald, 1982) involves developing a population dynamics model and fitting it by maximising an objective function (which under some circumstances can be interpreted as a likelihood function). Two key differences between original ADAPT-VPA approach of, for example, Butterworth *et al.* (1999) and SCAA analysis are that the latter does not assume that the age-composition data are known exactly (although it often makes fairly strong assumptions regarding age- (or length-) specific vulnerability and how it changes over time) and can calculate numbers-at-age for years for which catch age-composition data are not available.

The reference case model considers five areas (Antarctic Areas III–E, IV, V–W, V–E, and VI–W), selected primarily because of the availability of data. The hypothesis on stock structure used in this study is that there are two stocks: the I (Indian) stock – assumed to be found in Areas III–E, IV, and V–W, and the P (Pacific) stock – assumed to be found in Areas V–E and VI–W. The hypothesis of at least two stocks is based on the genetic (mtDNA and microsatellite) and non-genetic (morphometric, biological parameters) analyses based on JARPA data (IWC, 2008; Pastene, 2006) and has been corroborated by the genetic analysis of JARPA II data (Pastene *et al.*, 2014). The specific stock structure hypothesis follows from the assumption that the core of each stock is the western (Area III–E and IV–W) and eastern (Area V–E and VI–W) parts of the area surveyed by JARPA/JARPA II. These stocks could be related to breeding areas in lower latitude waters off the eastern Indian Ocean and western South Pacific where high sighting densities have been reported in October (Kasamatsu *et al.*, 1995).

This paper applies SCAA to data for the Antarctic minke whales in Management Areas III–E, IV, V, and VI–W. It first outlines the mathematical specifications for the model and its associated estimation scheme. The paper then provides specifications for a 'reference' case analysis which uses all of the available index, catch length-composition and conditional age-at-length data. Full results for this reference case are provided based on suggestions for model outputs and fit diagnostics by the Scientific Committee. A series of sensitivity tests are outlined which examine the sensitivity of the results to the assumptions of the model, including that carrying capacity may have changed over time, and the weights assigned to each of the many data sources and penalties.

MATERIALS AND METHODS

Mathematical specifications for the population model and likelihood function

The population dynamics model (Appendix A) considers multiple stocks, and represents each stock using an age- and sex-structured population dynamics model. The model includes 15 'fleets' consisting of three whaling types (Japan before 1987/88, Japan from 1987/88, and ex-Soviet Union) in each of the five areas considered in the model. Two Japanese whaling types are considered so that the data for commercial and Scientific Permit catches can be treated separately. Each 'fleet' can have a different length-specific vulnerability pattern (the combined effects of harvest selectivity and availability), which may change over time. Similarly growth, which depends on stock and sex, can change over time. Appendix B outlines the negative of the log-likelihood function which is minimised to find the best estimates for the parameters.

Data utilised

The data used when conducting assessments of the Antarctic minke whales consist of catches, abundance estimates, length frequency data, and conditional age-at-length data. The data include the catches and sighting survey information from the 2011/12 austral summer season.

Catches and length-frequency data

Catches are available by fleet and sex for two nations (Japan and ex-Soviet Union) and five Management Areas (III–E, IV, V–W, V–E, and VI–W). The catches prior to 1971/72 are not allocated to fleet because these catches were taken by several nations. There is no information on the length-frequency of these catches so the vulnerability patterns for the years prior to 1971/72 are assumed to be equal to that for in 1971/72, and the pre-1971/72 catches for Area V are split equally between Areas V–W and V–E. The results are unlikely to be sensitive to these assumptions given the small magnitude of the catches concerned.

Age-composition data

Age-composition data and hence conditional age-at-length data are only available for the Japanese catches. Earplugs from both sides of the whale were collected on the vessel and preserved in a 10% formalin solution. At the laboratory,

[5]Often also referred to as 'selectivities' by the Scientific Committee. Vulnerability combines the effect of age- (or length)-specific selectivity by the whalers with the relative probability of whalers encountering a whale of a given age or length given the spatial and temporal distribution of the whaling effort.

the plug surfaces were cut longitudinally to the centre, and the age of each whale determined by counting the growth layers using a stereoscopic microscope. One growth layer was assumed to be deposited each year (i.e. one pair of dark and pale laminae per year) based on Best (1982) and Lockyer (1984). Age-reading was conducted without knowledge of biological information. Four scientists participated in the reading of earplugs. Ages from whales captured in the period 1971/72–1979/80 (commercial whaling) were determined by reader-M (Y. Masaki). Ages from whales captured in the period 1980/81–1989/90 (commercial whaling and JARPA), and 1992/93 (JARPA) were determined by reader-K (H. Kato). Reader-Z (R. Zenitani) conducted age readings for whales captured in the period 1990/91–1991/92 and 1993/94–2004/05 (JARPA) and reader-B (T. Bando) conducted age readings for whales captured in the period 2005/06–2011/12 (JARPA II).

Indices of abundance

Table 1 lists the estimates of absolute abundance from the IDCR program (Okamura and Kitakado, 2012) and the indices of abundance based on the JARPA/JARPA II programme. The latter indices are corrected for $g(0)$. However, there may be biases which are not fully accounted for so the JARPA/JARPA II estimates of abundance are treated as indices, except for one sensitivity test where they are treated as estimates of absolute abundance.

The methods used for the abundance estimation for the JARPA/JARPA II surveys are outlined by Hakamada *et al.* (2013). The estimates of abundance and their coefficients of variation were estimated by stratum and survey mode (closing and passing) (Haw, 1991), using the 'standard methodology' of Branch and Butterworth (2001). The Okamura and Kitakado (2012) and Bravington and Hedley (2012) approaches for estimating minke whale abundance using IDCR/SOWER data resulted in estimates of $g(0)$ which were less than 1, especially for schools of size 1. However, these approaches cannot be applied directly to the sightings data from JARPA/JARPA II. Consequently $g(0)$ for these surveys is based on a regression model which provides relationship between $g(0)$ and mean school size by stratum (Hakamada *et al.*, 2013). AIC was used to choose amongst log-linear models for the effects of survey mode and survey timing. Weighted averages of abundance estimates over survey modes were calculated, where the weights were chosen to minimise the associated variances. The nominal abundance estimates needed to be adjusted using factors estimated from the model selected before the weighted average was taken.

Table 1a

The estimates of abundance (with CVs in parenthesis) – IDCR estimates.

Year	Estimate	Year	Estimate
Area III–E		**Area IV**	
1987/88	11,782 (0.440)	1988/89	46,763 (0.169)
1994/95	34,659 (0.237)	1998/99	55,873 (0.341)
Area V–W		**Area V–E**	
1985/86	105,951 (0.159)	1985/86	154,658 (0.189)
2001/02	43,640 (0.139)	2003/04	136,457 (0.134)
Area VI–W			
1990/91	20,438 (0.271)		
1995/96	48,206 (0.177)		

The reference case analysis

The reference case analysis ignores the length-frequency data for the ex-Soviet Union fleet because of concerns regarding the reliability of these data (there are no age-composition data for this fleet) and vulnerability for the ex-Soviet Union and the Japanese fleet are assumed to be the same. This latter assumption was made given information on

Table 1b

The estimates of abundance (with CVs in parenthesis) – JARPA/JARPA II indices of relative abundance.

Year	Estimate	Year	Estimate	Year	Estimate
Area III–E		**Area IV**		**Area V–W**	
1995/96	7,305 (0.655)	1989/90	50,736 (0.323)	1990/91	91,870 (0.305)
1997/98	4,362 (0.792)	1991/92	55,878 (0.448)	1992/93	61,918 (0.288)
1999/00	10,311 (0.975)	1993/94	44,286 (0.271)	1994/95	31,972 (0.385)
2001/02	53,619 (0.811)	1995/96	48,751 (0.371)	1996/97	41,475 (0.409)
2003/04	19,402 (0.717)	1997/98*	30,637 (0.331)	1998/99	133,867 (0.620)
2005/06	42,535 (0.440)	1999/00	87,345 (0.294)	2000/01	43,038 (0.885)
2007/08	10,952 (0.319)	2001/02	91,811 (0.289)	2002/03	122,469 (0.394)
		2003/04	53,434 (0.374)	2004/05	34,026 (0.411)
		2005/06	46,628 (0.464)	2005/06	119,437 (0.510)
		2007/08	40,243 (0.331)	2006/07	98,346 (0.409)
				2007/08	85,943 (0.478)
				2008/09	143,255 (0.450)
Area V–E		**Area VI–W**			
1990/91	132,914 (0.583)	1996/97	26,703 (0.682)		
1992/93	63,837 (0.371)	1998/99	39,866 (0.220)		
1994/95	152,534 (0.395)	2000/01	48,532 (0.640)		
1996/97	231,597 (0.500)	2002/03	25,483 (0.713)		
1998/99	67,442 (0.355)	2004/05	42,453 (0.605)		
2000/01	160,411 (0.311)	2006/07	36,540 (0.756)		
2002/03	65,040 (0.300)	2008/09	40,565 (0.271)		
2004/05	99,155 (0.235)				
2006/07	16,384 (0.379)				
2008/09	58,483 (0.468)				

*Survey covered only a small part of Prydz Bay.

possible misreporting of catch length distributions by the ex-Soviet Union (IWC, 2011). Vulnerability for the Japanese fleets (before 1987/88) is assumed to be a time-varying double-normal function of length in which a separate length-at-50%-vulnerability is estimated for each year (see Equation App.A.D.4c), while vulnerability for the JARPA/JARPA II fleet is assumed to be a logistic function of length and to be constant over space.

The other specifications of the reference case are:

(1) an age-specific availability factor, $\tilde{S}_a$, is estimated for age 1 (see Equation App.A.D.2);

(2) values for the change in growth rate ($\kappa_y^{g,s}$) are estimated for each year from 1963/64 until 2011/12 (see Equation App.A.E.3);

(3) there is no survey bias for the IDCR/SOWER estimates (i.e. χ = 1 for the IDCR estimates) (See Equation App.B.B.1);

(4) separate survey bias parameters are estimated for the JAPRA / JARPA II indices in each of the five areas included in the analysis (see Equation App.B.B.1);

(5) the minus- and plus-group ages when fitting to the conditional age-at-length data, $a_{\min,y}$ and $a_{\max,y}$, are set to 1 and 45yr respectively (see Equation App.B.D.1);

(6) the minus- and plus-group lengths, $l_{\min,y}$ and $l_{\max,y}$ for females are set to 25ft and 32ft for the period of commercial whaling, and 17ft and 32ft for JARPA / JARPA II, and for males are set to 25ft and 31ft for the period of commercial whaling and 17ft and 31ft for JARPA / JARPA II. [These choices were made to avoid fitting the model to length-classes with few data] (See Equations App.B.C.1 and App.B.D.1);

(7) many of the parameters of the population dynamics model (the deviations in births, distribution, growth, carrying capacity, and vulnerability) are essentially random effects. The ideal way to estimate these parameters is within the context of a random effects formulation, in which the likelihood is integrated over the random effects. However, this is computationally infeasible for this model so a penalised likelihood estimation formulation is adopted instead. Punt (2014) investigated whether the method developed by Thompson and Lauth (2012) for estimating the variance of a random effect which does not involve maximising the marginal likelihood could be applied in this case but this method failed to provide reliable estimates. Consequently, the values for random effects standard deviations are pre-specified (Table 2) and sensitivity explored to alternative plausible values; and

(8) the ages at which natural mortality changes with age are set to 3, 10, 20 and 40. The justification for this particular selection is given in the first section under 'Results'.

Table 3 lists the estimable parameters of the reference case model.

Data weighting

The length-frequency and conditional age-at-length data are assumed to be multinomially distributed when fitting the model to the data (see Appendix B). Use of this likelihood function requires that the effective sample sizes be specified. Setting these sizes to the actual numbers of animals measured and aged would over-estimate the information content of these data sets because of a lack of independence between adjacent length-/age-classes. Previous applications of the SCAA have been based on setting the effective sample sizes as a pre-specified fraction of the observed numbers of animals measured and aged using the approach of McAllister and Ianelli (1997), which compares the variance of the standardised residuals about the fits to the data with the variance of the standardised residuals expected had the data been multinomially distributed. This approach has been criticised by Francis (2011) who noted that the residuals about the fits to length and conditional age-at-length data tend to be correlated between length-classes and ages given length. Francis (2011) proposed an alternative approach in which the effective sample size is based on how well the model mimics the mean lengths (and means ages given length for the conditional age-at-length data).

Fig. 1 summarises the application of the method of Francis (2011) given the other specifications for the reference case analysis. The model run on which this application is based

Table 2

Values for the parameters which determine the extent of the penalties on the deviation parameters.

Parameter	Value
Extent of variation in births, σ_R	0.3
Extent of variability in the vulnerability deviations, σ_S	10
Extent of variability in the proportion of each stock in each area, σ_P	0.3
Extent of variability in growth rate, σ_K	0.02
Extent of variability in carrying capacity, σ_K	0.05

Table 3

The estimable parameters of the population dynamics model and the objective function.

Parameter	Number of parameters: Stock I	Number of parameters: Stock P
Carrying capacity in 1930, $\tilde{K}_{1930}^{1+,s}$	1	1
Natural mortality: M^s by stock, γ, δ	4	
Resilience, A	1	1
Recruitment deviation, ε_y	83	83
Expected proportion in each Area, $\overline{P^{s,A}}$	2	1
Annual deviations about the expected proportions in each area, φ_y^a	69	26
Exploitation rate by year, sex and fleet, $F_y^{g,f}$	291	125
Inter-annual deviations in carrying capacity, v_y^s	82	82
Parameters of the growth curve, L_∞^g, k^g, t_0^g, σ_γ^g	8	8
Inter-annual deviations in growth rate, υ_y	98	98
Parameters to define vulnerability, $L_{50,y}^{g,f}$, $L_{\text{diff}}^{g,f}$, $L_{\text{left}}^{g,f}$, $L_{\text{right}}^{g,f}$	22	12
Age-specific vulnerability, $\tilde{S}_a$	1	1
Inter-annual deviations in vulnerability, $\delta_y^{g,f}$	72	22
JARPA survey bias, χ	3	2
Total	1,199	

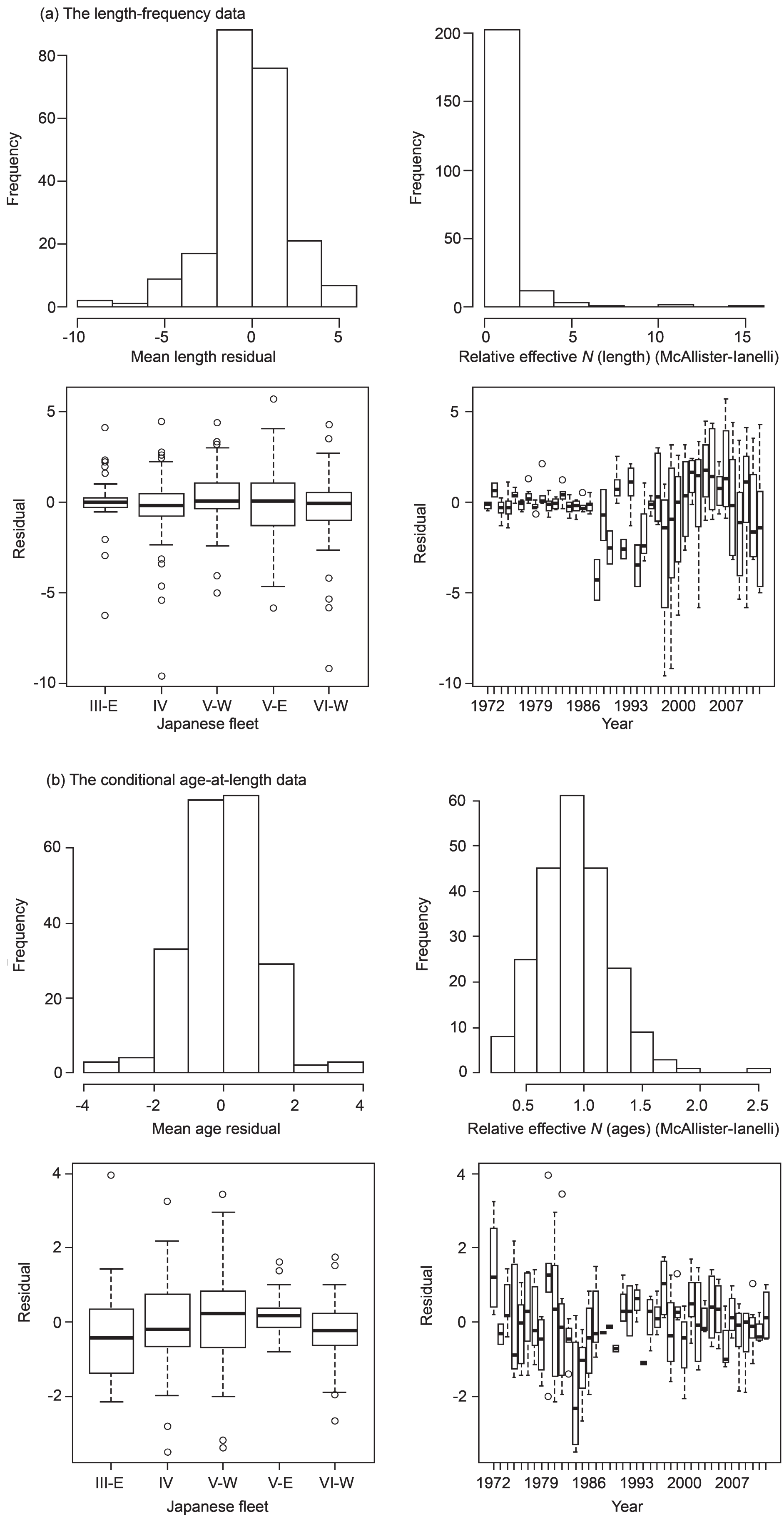

Fig. 1. Histograms of standardised residuals for the Japanese fleets about the mean length/ages (upper left panel), the ratio of the annual effective sample sizes to the observed numbers measured/aged based on the McAllister-Ianelli method (upper right panel), and the standardised residuals about the mean length/ages by area and year (lower panels).

set the effective sample sizes to the observed sample sizes. The residuals exhibit more variance than would be expected if the observed sample sizes reflect the effective sample sizes. Specifically, the ratio of the effective sample sizes to the observed sample sizes under the McAllister-Ianelli method (upper right panels of Figs 1a and 1b) also confirm

Table 4

The summary statistics and plots.

(a) Statistics

$b_{rec,1945–68}$ – slope of the linear regression of the estimates of the logarithms of the numbers of recruits (age 1 animals) on time (1945–68).
$b_{rec,1968–88}$ – slope of the linear regression of the estimates of the logarithms of the numbers of recruits on time (1968–88).
$b_{rec,1988–End}$ – slope of the linear regression of the estimates of the logarithms of the numbers of recruits on time (1988–last year).
$N_{tot,1945–68}$ – slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1945–68).
$N_{tot,1968–88}$ – slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1968–88).
$N_{tot,1988–Endr}$ – slope of the linear regression of the estimates of the logarithms of the numbers of 1+ animals on time (1988–last year).
$N_{\mathrm{End}–5,1}/N_{1968,1}$ – ratio of the number of recruits in 2007 to that in 1968.
K_{1930} – carrying capacity in 1930.
K_{1960}/K_{1930} – ratio of K in 1960 to that in 1930.
K_{2000}/K_{1960} – ratio of K in 2000 to that in 1960.
Natural mortality (ages 3, 15, 35).
Average proportions in each management area.
Survey q for JARPA.
MSYR (1+).

(b) Plots

Assessment outputs
Total (1+) population size versus year (by stock and by area).
Age 1 animals (recruits) versus time.
Carrying capacity versus year.
Natural mortality versus age.
Body growth coefficient versus year.

Diagnostic plots
Survey estimates of abundance from IDCR with the associated model predictions (by area).

Table 5

The sensitivity tests.

Run	Description Reference case
Related to the population dynamics model	
A1	Siler natural mortality (Equation App. A.B.2).
A2	Autoregressive natural mortality deviations (Equation App. A.B.3).
A3	The proportion of each stock in each area is time-invariant.
A4	No time-varying growth.
A5	Carrying capacity (K) is time-invariant.
A6	Ignore ageing error.
Related to vulnerability patterns	
B1	JARPA/JARPA II vulnerability is constant.
B2	JARPA/JARPA II vulnerability is constant (and time-invariant); carrying capacity is time-invariant.
B3	JARPA/JARPA II abundance estimates are absolute.
B4	IDCR/SOWER estimates are assumed to be negatively biased, $g(0) = 0.60$.
B5	IDCR/SOWER estimates are assumed to be negatively biased, $g(0) = 0.80$.
B6	Time-invariant fishery vulnerability.
B7	Separate vulnerability patterns for JARPA/JARPA II.
B8	Time-varying declining vulnerability.
Related to data selection and data weighting	
C1	Decrease σ_s by 50%.
C2	Increase σ_s by 50%.
C3	Decrease σ_K by 50%.
C4	Increase σ_K by 50%.
C5	Decrease σ_p by 50%.
C6	Increase σ_p by 50%.
C7	Decrease σ_κ by 50%.
C8	Increase σ_κ by 50%.
C9	Decrease σ_R by 50%.
C10	Increase σ_R by 50%.
C11	Double weight on length data.
C12	Halve weight on length data.
C13	Double weight on conditional age-at-length data.
C14	Halve weight on conditional age-at-length data.
C15	All years of age and length data weighted equally.
C16	Increase cut-off lengths by 2ft.
C17	The length frequency and age composition data for the years until 1973/74 are down-weighted by 90%.

that the data are overdispersed relative to the multinomial. The residuals about mean length are higher for the period of JARPA /JARPA II (Fig. 1a, lower right panel), while the residuals for mean age given length are higher for the pre-JARPA period (Fig. 1b, lower right panel). There is no strong evidence for between-fleet differences in residual variance (Figs 1a and b, lower left panels). Consequently, the factor used to adjust the observed sample sizes to compute effective sample sizes are set to 1 for the commercial length-frequency data and 0.15 for the JARPA/ JARPA II length-frequency data. Furthermore, the factor used to adjust the observed sample sizes to compute effective sample sizes are set to 0.5 for the commercial conditional age-at-length data and 1 for the JARPA/ JARPA II conditional age-at-length data. 0.5 and 0.15 are rounded standard deviations of the residuals about mean length/age in Fig. 1.

Diagnostic statistics

Table 4 outlines the diagnostic statistics and plots. The statistics and some of the plots were originally selected by the Scientific Committee, but subsequently modified based on requests for additional analyses. The plots either summarise the key outputs from the assessments or aid understanding of those outputs somewhat better.

Sensitivity tests

Table 5 lists the specifications for the sensitivity tests. These sensitivity tests explore sensitivity to the weight assigned to the various data sources and penalties, the assumptions related to vulnerability, natural mortality and catchability, and to the use or otherwise of the JARPA/JARPA II index data. Results for the sensitivity tests are restricted to a set of 'core' statistics to keep the volume of results to minimum.

RESULTS

Modelling natural mortality

Table 6 and Fig. 2 contrast the results of analyses in which natural mortality is assumed to take the Siler form ('Siler', sensitivity test A1), in which natural mortality for ages 2–50

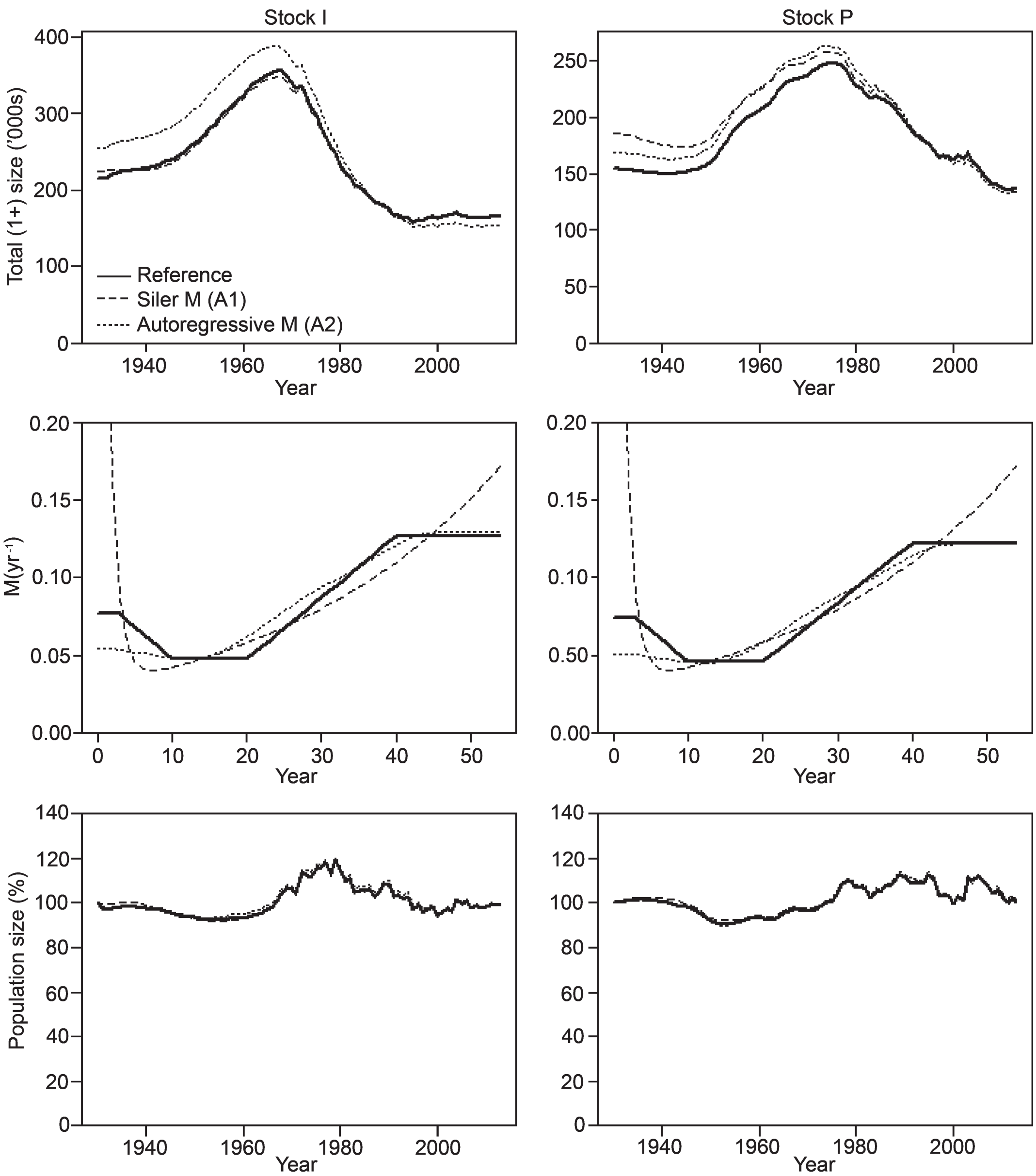

Fig. 2. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for three ways to model natural mortality (the Siler model, autoregressive and piecewise linear).

Table 6a – Stock I

Results of the reference case analysis and the analyses to examine the sensitivity of the results to modifying some of the assumptions of the analysis method. The asymptotic standard errors for the estimates for natural mortality are given in parenthesis. The average proportions by area are given above the estimates for the JARPA χs (the numbers in parenthesis).

	b_{rec}			N_{tot}							Natural mortality (ages)			Mean proportion $\overline{b}^N$ (upper)/ JARPA χ^A (lower)			
Case	1945–68	1968–88	1988–End	1945–68	1968–88	1988–End	$N_{End-5,1}/N_{1968,1}$	K_{1930}	K_{1960}/K_{1930} (%)	K_{2000}/K_{1960} (%)	3	15	35	III–E	IV	V–W	MSYR (1+)
Reference	1.282	–2.931	0.956	1.912	–3.718	–0.168	0.539	214,922	162.1	49.2	0.077	0.048	0.107	0.156	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.658)	(0.947)	(1.013)	
A1	1.234	–2.905	0.880	1.933	–3.667	–0.114	0.527	224,852	153.1	50.0	0.089	0.042	0.094	0.157	0.376	0.468	0.218
											(0.03)	(0.004)	(0.004)	(0.692)	(1.009)	(1.077)	
A2	0.527	–3.400	1.141	1.539	–4.143	–0.439	0.517	253,935	151.9	41.3	0.054	0.049	0.107	0.150	0.371	0.479	0.221
											(0.009)	(0.006)	(0.007)	(0.707)	(0.989)	(1.008)	
A3	0.845	–3.565	0.908	1.581	–4.216	–0.391	0.495	228,085	149.6	42.1	0.072	0.053	0.110	0.214	0.344	0.442	0.221
											(0.017)	(0.005)	(0.005)	(0.565)	(1.276)	(1.265)	
A4	2.134	–1.810	–1.152	2.060	–2.549	–1.192	0.445	219,538	100	100	0.212	0.033	0.100	0.147	0.389	0.464	0
											(0.015)	(0.003)	(0.002)	(0.656)	(0.806)	(0.917)	
A5	1.775	–2.427	0.697	1.543	–3.178	0.108	0.627	219,047	100	100	0.055	0.039	0.106	0.156	0.375	0.469	0.002
											(0.013)	(0.003)	(0.002)	(0.631)	(0.926)	(0.979)	
A6	1.808	–5.272	0.572	2.245	–4.852	0.087	0.342	281,011	170.6	43.2	0.166	0.072	0.141	0.153	0.395	0.452	0.235
											(0.011)	(0.005)	(0.005)	(1.29)	(1.703)	(1.961)	
B1	1.309	–2.926	0.922	1.936	–3.683	–0.204	0.534	211,002	162.6	49.5	0.069	0.047	0.107	0.156	0.376	0.469	0.218
											(0.014)	(0.005)	(0.005)	(0.627)	(0.904)	(0.963)	
B2	1.829	–2.434	0.609	1.558	–3.156	0.060	0.605	217,579	100	100	0.062	0.039	0.106	0.156	0.375	0.469	0.001
											(0.013)	(0.003)	(0.002)	(0.619)	(0.907)	(0.96)	
B3	1.191	–2.983	1.000	1.836	–3.813	–0.156	0.541	225,183	159.7	47.9	0.088	0.049	0.108	0.126	0.381	0.494	0.220
											(0.018)	(0.005)	(0.005)	(1)	(1)	(1)	
B4	1.315	–2.300	0.970	1.951	–3.198	–0.083	0.601	299,225	164.0	54.7	0.082	0.047	0.106	0.158	0.369	0.473	0.219
											(0.016)	(0.005)	(0.005)	(0.419)	(0.628)	(0.648)	
B5	1.308	–2.629	0.954	1.938	–3.469	–0.124	0.567	245,298	163.3	51.9	0.080	0.047	0.107	0.157	0.372	0.471	0.219
											(0.016)	(0.005)	(0.005)	(0.541)	(0.796)	(0.837)	
B6	0.992	–3.332	0.337	1.917	–4.399	–0.470	0.983	272,981	163.9	42.7	0.192	0.050	0.109	0.152	0.385	0.462	0.224
											(0.012)	(0.005)	(0.005)	(0.951)	(1.260)	(1.414)	
B7	1.248	–2.953	1.605	1.888	–3.758	0.100	0.630	218,029	161.6	49.1	0.083	0.048	0.107	0.156	0.383	0.461	0.219
											(0.017)	(0.005)	(0.005)	(0.725)	(0.973)	(1.095)	
B8	1.042	–3.069	0.809	1.767	–4.143	0.189	0.587	242,359	169.6	47.3	0.216	0.053	0.106	0.159	0.385	0.456	0.226
											(*)	(*)	(*)	(1.216)	(1.739)	(1.964)	
Reference	1.282	–2.931	0.956	1.912	–3.718	–0.168	0.539	214,922	162.1	49.2	0.077	0.048	0.107	0.156	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.658)	(0.947)	(1.013)	
C1	1.314	–2.903	0.928	1.927	–3.697	–0.166	0.538	213,477	162.5	49.6	0.079	0.047	0.107	0.156	0.377	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.655)	(0.943)	(1.009)	
C2	1.277	–2.936	0.958	1.910	–3.721	–0.168	0.539	215,098	162.1	49.2	0.077	0.048	0.107	0.156\	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.658)	(0.948)	(1.013)	
C3	1.742	–2.329	1.197	1.946	–3.131	0.256	0.666	220,982	149.3	60.2	0.061	0.041	0.105	0.151	0.391	0.458	0.215
											(0.014)	(0.004)	(0.003)	(0.56)	(0.763)	(0.865)	
C4	1.277	–2.934	0.963	1.909	–3.721	–0.167	0.540	215,138	162.0	49.2	0.077	0.048	0.107	0.156	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.659)	(0.949)	(1.014)	
C5	1.155	–3.218	0.873	1.789	–3.960	–0.318	0.499	212,021	156.8	45.6	0.076	0.049	0.108	0.193	0.350	0.452	0.219
											(0.016)	(0.005)	(0.005)	(0.583)	5(1.13)	(1.154)	
C6	1.328	–2.691	0.986	1.957	–3.520	–0.102	0.567	231,531	164.1	51.7	0.078	0.047	0.106	0.127	0.400	0.467	0.218
											(0.016)	(0.005)	(0.005)	(0.726)	7(0.78)	(0.918)	
C7	1.479	–2.654	0.482	2.096	–3.530	–0.459	0.480	199,409	172.2	49.4	0.099	0.046	0.105	0.155	0.376	0.468	0.218
											(0.017)	(0.005)	(0.005)	(0.66)	(0.933)	(1.000)	
C8	1.197	–3.030	1.128	1.841	–3.785	–0.051	0.580	220,632	158.2	49.4	0.063	0.048	0.108	0.155	0.37	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.655)	6(0.945)	(1.008)	
C8	1.199	–2.953	0.939	1.871	–3.754	–0.207	0.531	220,187	160.7	48.5	0.078	0.048	0.107	0.155	0.376	0.468	0.219
											(0.016)	(0.005)	(0.005)	(0.662)	(0.946)	(1.008)	
C10	1.438	–3.051	0.962	1.979	–3.660	–0.129	0.522	205,653	163.5	50.3	0.071	0.047	0.106	0.157	0.376	0.467	0.218
											(0.016)	(0.005)	(0.005)	(0.643)	(0.935)	(1.003)	
C11	1.444	–2.846	0.563	2.020	–3.605	–0.480	0.528	208,700	167.4	48.7	0.102	0.046	0.106	0.154	0.377	0.469	0.218
											(0.017)	(0.005)	(0.005)	(0.704)	(0.977)	(1.053)	
C12	1.139	–3.086	1.319	1.825	–3.798	0.096	0.564	219,679	157.9	49.4	0.054	0.049	0.108	0.157	0.375	0.468	0.219
											(0.017)	(0.005)	(0.005)	(0.625)	(0.929)	(0.979)	
C13	0.835	–3.294	1.125	1.610	–4.017	–0.117	0.527	254,363	154.0	44.9	0.045	0.053	0.111	0.155	0.379	0.465	0.221
											(0.012)	(0.005)	(0.005)	(0.615)	(0.88)	(0.948)	
C14	1.750	–2.585	0.664	2.167	–3.373	–0.267	0.556	184,671	167.1	53.5	0.102	0.042	0.103	0.155	0.372	0.472	0.216
											(0.018)	(0.006)	(0.005)	(0.698)	(1.007)	(1.058)	
C15	1.938	–2.700	0.429	2.069	–3.366	–0.885	0.538	211,783	164.0	48.0	0.124	0.039	0.108	0.148	0.379	0.473	0.216
											(0.01)	(0.005)	(0.004)	(0.728)	(0.942)	(1.027)	
C16	1.209	–3.060	1.313	1.938	–3.685	0.076	0.595	204,153	163.4	51.4	0.053	0.049	0.107	0.157	0.375	0.468	0.218
											(0.017)	(0.005)	(0.005)	(0.646)	(0.95)	(1.007)	
C17	1.354	–3.154	0.915	2.068	–3.712	–0.182	0.548	205,748	167.9	49.8	0.081	0.048	0.106	0.156	0.377	0.468	0.219
											(0.017)	(0.005)	(0.005)	(0.663)	(0.952)	(1.02)	

Table 6b – Stock P

Results of the reference case analysis and the analyses to examine the sensitivity of the results to modifying some of the assumptions of the analysis method. The asymptotic standard errors for the estimates for natural mortality are given in parenthesis. The average proportions by area are given above the estimates for the JARPA χs (the numbers in parenthesis).

	b_{rec}			N_{tot}							Natural mortality (ages)			Mean proportion $\overline{b}^N$ (upper)/ JARPA χ^A (lower)		
Case	1945–68	1968–88	1988–End	1945–68	1968–88	1988–End	$N_{End-5,1}$/ $N_{1968,1}$	K_{1930}	K_{1960}/ K_{1930} (%)	K_{2000}/ K_{1960} (%)	3	15	35	V–E	VI–W	MSYR (1+)
Reference	1.958	–2.957	–0.298	2.127	–0.779	–1.612	0.345	154,239	143.5	73.9	0.074	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.685)	(1.190)	
A1	1.704	–3.044	–0.542	1.76	–0.947	–1.721	0.343	185,636	128.2	68.8	0.089	0.042	0.094	0.788	0.212	0.218
											(0.03)	(0.004)	(0.004)	(0.726)	(1.265)	
A2	1.689	–3.283	0.023	2.121	–1.009	–1.83	0.327	168,575	142.5	66.2	0.050	0.046	0.100	0.793	0.207	0.219
											(0.008)	(0.005)	(0.007)	(0.671)	(1.217)	
A3	1.956	–3.008	–0.202	2.189	–0.831	–1.632	0.347	156,638	145.8	72.4	0.067	0.049	0.102	0.791	0.209	0.218
											(0.016)	(0.005)	(0.005)	(0.683)	(1.27)	
A4	3.476	–1.367	–2.527	3.079	0.618	–1.382	0.331	82,732	181.1	116.1	0.185	0.029	0.087	0.783	0.217	0.210
											(0.016)	(0.004)	(0.004)	(0.65)	(1.093)	
A5	1.403	–1.637	0.697	0.667	–0.178	–0.449	0.650	167,899	100	100	0.051	0.036	0.098	0.779	0.221	0.004
											(0.012)	(0.002)	(0.002)	(0.638)	(1.017)	
A6	3.759	–3.757	–0.227	2.710	–1.133	–1.286	0.436	145,631	151.7	75.8	0.146	0.064	0.124	0.780	0.220	0.230
											(0.012)	(0.005)	(0.005)	(1.445)	(2.397)	
B1	1.995	–2.927	–0.317	2.143	–0.734	–1.619	0.344	153,032	143.1	74.7	0.066	0.046	0.103	0.789	0.211	0.217
											(0.013)	(0.005)	(0.005)	(0.646)	(1.126)	
B2	1.413	–1.625	0.644	0.668	–0.176	–0.460	0.643	167,575	100	100	0.057	0.035	0.098	0.779	0.221	0.004
											(0.012)	(0.002)	(0.002)	(0.622)	(0.991)	
B3	1.865	–3.044	–0.236	2.085	–0.889	–1.608	0.346	145,149	143.5	71.8	0.085	0.047	0.104	0.725	0.275	0.218
											(0.018)	(0.005)	(0.005)	(1)	(1)	
B4	1.948	–2.925	–0.329	2.118	–0.756	–1.602	0.346	255,302	143.5	74.2	0.079	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.417)	(0.723)	
B5	1.957	–2.942	–0.322	2.125	–0.765	–1.615	0.344	192,064	143.5	74.0	0.077	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.551)	(0.958)	
B6	1.923	–3.789	–0.667	2.136	–1.217	–1.576	0.325	154,436	153.8	69.4	0.182	0.047	0.104	0.781	0.219	0.221
											(0.016)	(0.005)	(0.005)	(1.055)	(1.77)	
B7	1.905	–2.994	0.359	2.101	–0.835	–1.425	0.392	155,601	143.4	73.2	0.080	0.047	0.104	0.791	0.209	0.218
											(0.017)	(0.005)	(0.005)	(0.712)	(1.302)	
B8	1.551	–3.262	–0.366	1.857	–1.507	–1.416	0.346	173,619	148.8	63.7	0.213	0.052	0.105	0.777	0.223	0.225
											(*)	(*)	(*)	(1.437)	(2.340)	
Reference	1.958	–2.957	–0.298	2.127	–0.779	–1.612	0.345	154,239	143.5	73.9	0.074	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.685)	(1.190)	
C1	1.957	–2.960	–0.329	2.123	–0.783	–1.638	0.341	154,824	143.4	73.5	0.076	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.683)	(1.191)	
C2	1.960	–2.955	–0.294	2.129	–0.777	–1.610	0.346	154,098	143.5	73.9	0.074	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.685)	(1.19)	
C3	1.902	–2.387	0.485	1.301	–0.409	–0.968	0.489	165,158	120.2	84.2	0.059	0.04	0.100'(0.0	0.784	0.216	0.214
											(0.013)	(0.003)	03)	(0.649)	(1.077)	
C4	1.959	–2.953	–0.291	2.129	–0.779	–1.605	0.346	154,111	143.5	74.0	0.074	0.046	0.103	0.788	0.212	0.217
											(0.016)	(0.005)	(0.005)	(0.685)	(1.19)	
C5	1.988	–2.942	–0.293	2.160	–0.763	–1.604	0.347	153,074	144.4	74.3	0.072	0.046	0.103	0.801	0.199	0.217
											(0.016)	(0.005)	(0.005)	(0.664)	(1.294)	
C6	1.971	–2.934	–0.257	2.132	–0.759	–1.574	0.350	159,794	143.6	74.6	0.075	0.046	0.103	0.699	0.301	0.217
											(0.016)	(0.005)	(0.005)	(0.783)	(0.751)	
C7	2.164	–2.716	–0.855	2.266	–0.566	–1.750	0.319	142,307	148.9	77.1	0.095	0.045	0.101	0.789	0.211	0.217
											(0.017)	(0.005)	(0.005)	(0.672)	(1.18)	
C8	1.852	–3.142	–0.143	2.056	–0.902	–1.545	0.36	160,772	140.6	72.5	0.061	0.047	0.104	0.788	0.212	0.217
											(0.015)	(0.005)	(0.005)	(0.685)	(1.188)	
C9	1.918	–2.987	–0.283	2.098	–0.828	–1.679	0.35	157,151	143.2	73.2	0.075	0.047	0.103	0.789	0.211	0.218
											(0.016)	(0.005)	(0.005)	(0.685)	(1.198)	
C10	2.051	–3.15	–0.325	2.207	–0.676	–1.552	0.334	149,854	143.5	74.2	0.069	0.045	0.102	0.788	0.212	0.217
											(0.015)	(0.005)	(0.005)	(0.669)	(1.161)	
C11	2.036	–2.905	–0.742	2.167	–0.690	–1.745	0.343	149,744	146.2	74.8	0.099	0.044	0.102	0.789	0.211	0.217
											(0.017)	(0.005)	(0.005)	(0.708)	(1.242)	
C12	1.920	–3.012	0.020	2.110	–0.824	–1.537	0.355	157,484	141.5	73.2	0.052	0.047	0.104	0.787	0.213	0.217
											(0.016)	(0.005)	(0.005)	(0.665)	(1.151)	
C13	1.816	–3.331	–0.116	2.479	–1.026	–1.690	0.311	153,933	152.4	68.9	0.043	0.050	0.105	0.788	0.212	0.219
											(0.011)	(0.004)	(0.005)	(0.667)	(1.164)	
C14	2.100	–2.529	–0.506	1.778	–0.437	–1.520	0.388	152,573	133.9	81.2	0.099	0.041	0.100	0.788	0.212	0.215
											(0.018)	(0.005)	(0.005)	(0.688)	(1.192)	
C15	2.444	–2.999	–1.147	2.390	–0.607	–2.058	0.372	144,813	150.9	74.2	0.122	0.039	0.107	0.792	0.208	0.216
											(0.011)	(0.004)	(0.004)	(0.700)	(1.253)	
C16	1.892	–3.236	–0.057	2.085	–0.908	–1.623	0.360	161,866	140.7	71.4	0.052	0.048	0.104	0.789	0.211	0.218
											(0.016)	(0.005)	(0.005)	(0.681)	(1.189)	
C17	1.905	–3.023	–0.405	2.116	–0.854	–1.680	0.334	157,087	144.0	72.0	0.079	0.047	0.103	0.788	0.212	0.218
											(0.017)	(0.005)	(0.005)	(0.693)	(1.209)	

is modelled using an autoregressive process ('Autoregressive M', sensitivity test A2), and in which natural mortality changes at ages of 3, 10, 20 and 40 ('Reference'). Treating natural mortality as an autoregressive series leads to higher estimates of 1+ abundance for the pre-1980 period compared to the other two analyses. The Siler M analysis also leads to higher estimates of pre-1980 1+ abundance for stock P. Age-specific natural mortality from the Siler-based analysis implies much higher rates of natural mortality for very young and old animals than the autoregressive formulation, unrealistically so for the young ages (Fig. 2, center panels).

The breakpoints for the reference case model were set so that the profile of M-at-age matches than from the autoregressive M analysis quite well. The remaining analyses of this paper are consequently based on modelling natural mortality as a piecewise linear function of age, with breakpoints at ages 3, 10, 20 and 40, given that this is more parsimonious than the autoregressive M approach and does not lead to unrealistically high values for M-at-age for the younger ages,

Reference case analysis

Both stocks are estimated to have increased from 1930 until the early 1970s, with both stocks having declined subsequently thereafter (Fig. 3). The increase in abundance is due primarily to an increase in recruitment owing in turn to an increase in carrying capacity (Fig. 3). Carrying capacity is estimated to have declined subsequently for both stocks, but the effect of this on recruitment and hence total population size is much smaller for stock P than for stock I (Fig. 3). The total (1+) population size is estimated to track carrying capacity quite closely. Stock I is estimated to have initially been larger than stock P, but stock P is currently the larger of the two stocks (Fig. 3, Table 6). The estimates of the recruitment deviations (Fig. 3) suggest that there have been periods of good and poor recruitment. The estimates of natural mortality indicate that natural mortality is highest for the youngest and (particularly) oldest animals (Fig. 3; Table 6). Natural mortality for stock I is estimated to be slightly higher at large age than for stock P (0.107yr^{-1} for animals of age 35, compared to 0.103yr^{-1}; Table 6). The CV for natural mortality is highest for young ages and approximately 10% for ages 10–30 (Fig. 3).

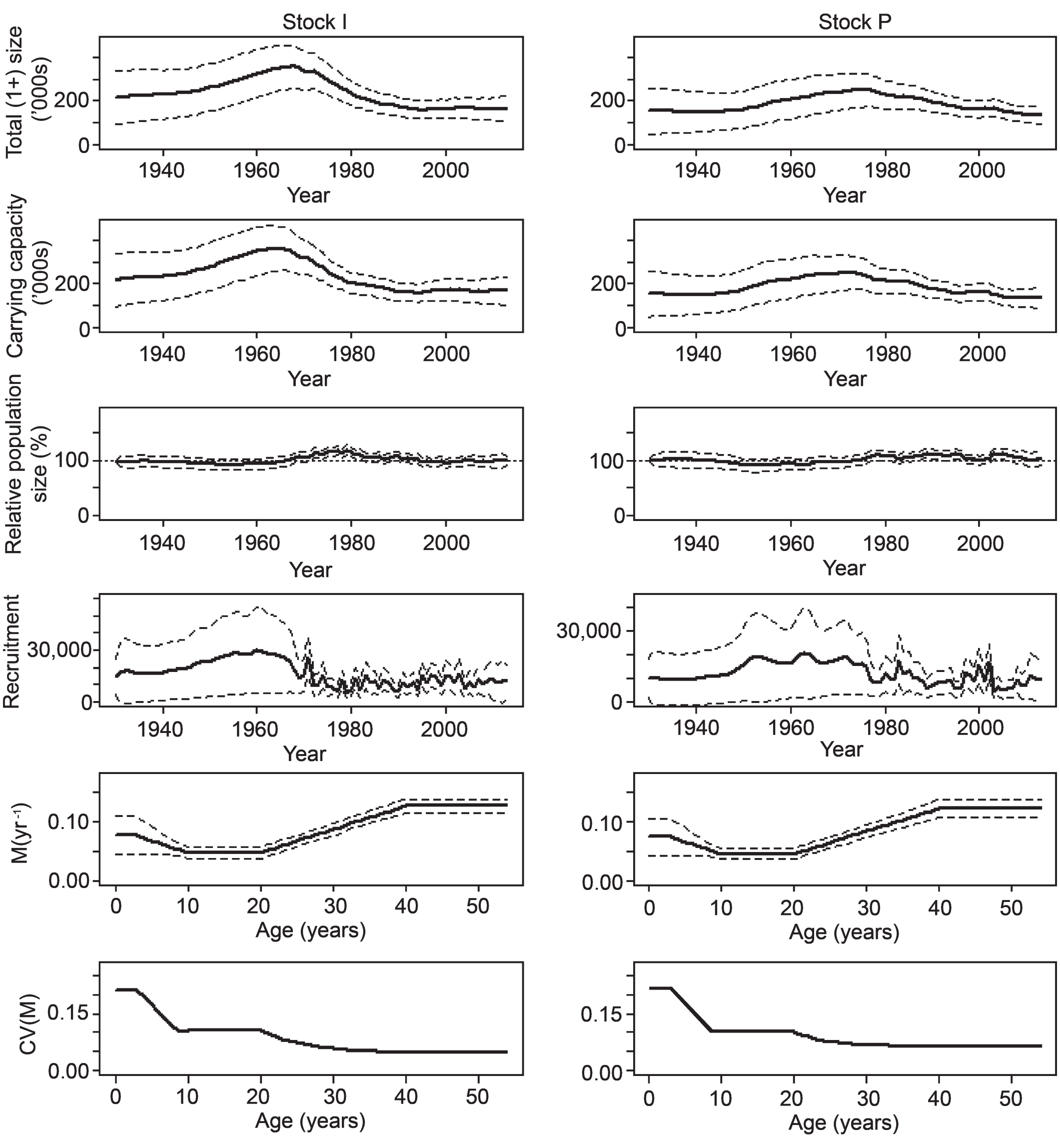

Fig. 3. Time-trajectories of total (1+) population size, carrying capacity, total (1+) population relative to carrying capacity, and recruitment (from 1930 and from 1975), and age-specific natural mortality by stock (estimates and CVs) for the reference case analysis. The dotted lines indicate 95% asymptotic confidence intervals.

The estimates of the proportions of the total population in each area changes over time, and vary inter-annually to better fit the abundance estimates, while there is also evidence for time-varying growth (Fig. 4). The initial declining trends in the proportion of the total population in Areas III–E, IV and V–W is due to the faster estimated rate of increase for the P stock. The von Bertalanffy growth rate is estimated to have peaked in the mid-1980s and to have declined thereafter (Fig. 4).

Figs 5 and 6 illustrate how well the model is able to mimic the estimates of absolute and relative abundance given the estimated changes in abundance as well as inter-annual variation in the proportion of the population in each area. The confidence intervals for the abundance estimates generally intersect the population trajectory, indicating that the extent of process error in the proportion of the stocks in each area is sufficient to capture additional variance.

Results are not shown for the fits to the length-frequency and conditional age-at-length data given the large number of associated plots. However, the fits to the commercial length-frequency data are generally excellent, except when sample sizes are very small. However (and expected from Fig. 1), the fits to the length-frequency data for JARRA/JARPA II are occasionally quite poor. Most of the poor fits occur when sample sizes are small. There are also no major concerns with the fits to the mean ages-at-length, suggesting that the extent of time-varying growth is sufficient to mimic the changes in growth over time.

Sensitivity tests

There are many sensitivity tests, and the results are generally insensitive to changes to specifications of the reference case analysis (Table 6). Consequently plots of results are only shown for 'interesting' cases. Not allowing for time-varying growth (sensitivity test A4) leads a markedly faster rate of increase for stock P and also to higher estimates of natural mortality for very young animals for both stocks (Fig. 7), but the fit of the model to the data is much poorer than for the reference case analysis (Table 7). As expected, the rate of increase is least over the initial years of the projection period when carrying capacity is constant (sensitivity tests A5 & B2, Fig. 7, 8). The results for stock I are very sensitive to whether allowance is made for age-reading error or not, with abundance for this stock increasing to much higher levels if age-reading error is ignored (sensitivity test A6). In terms of estimates of natural mortality, ignoring ageing error leads to higher rates of natural mortality.

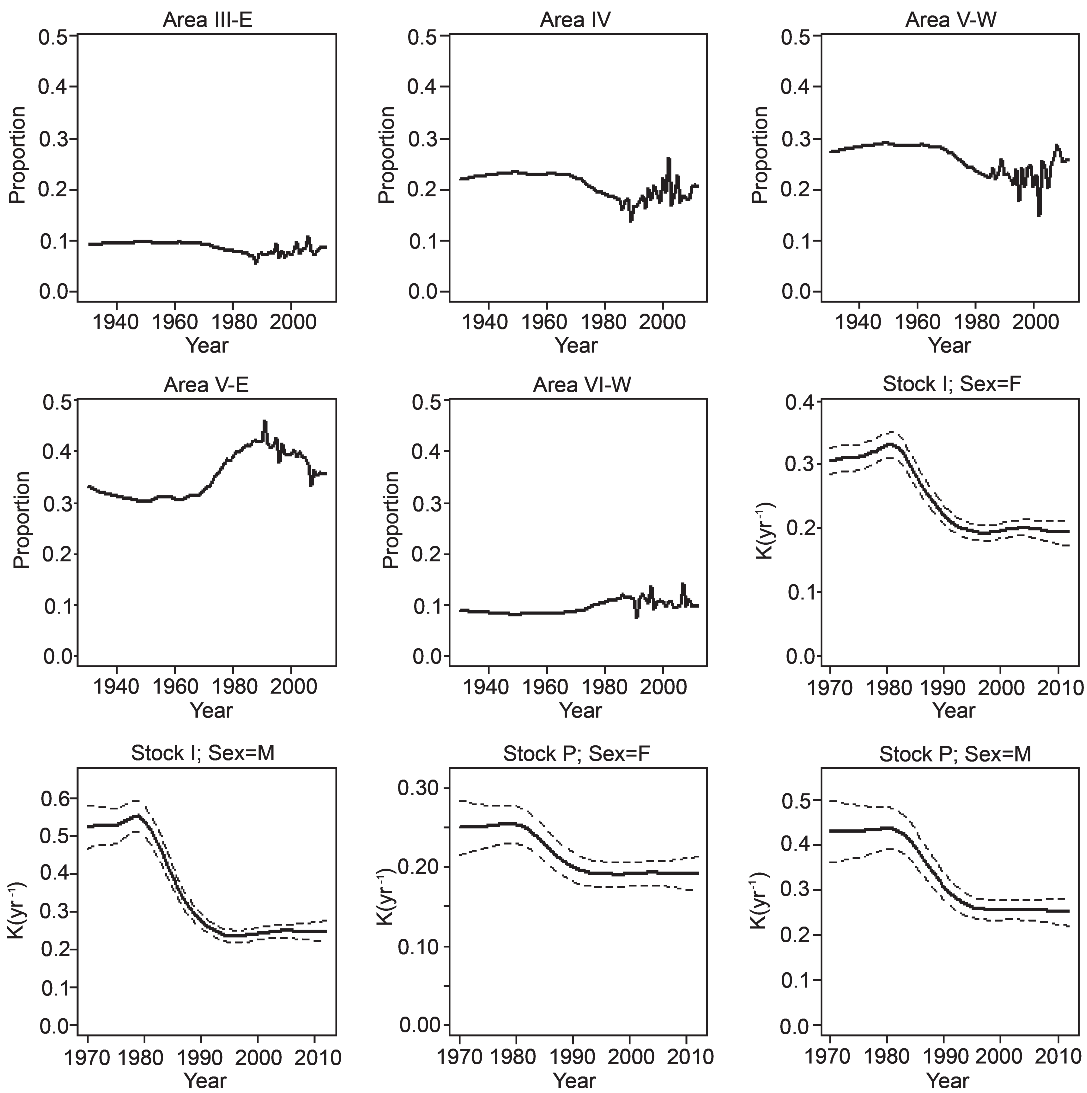

Fig. 4. Time-trajectories of the proportion of the total population in each of the five areas considered in the model as well as those of the growth rate parameter κ (by stock and sex) for the reference case analysis.

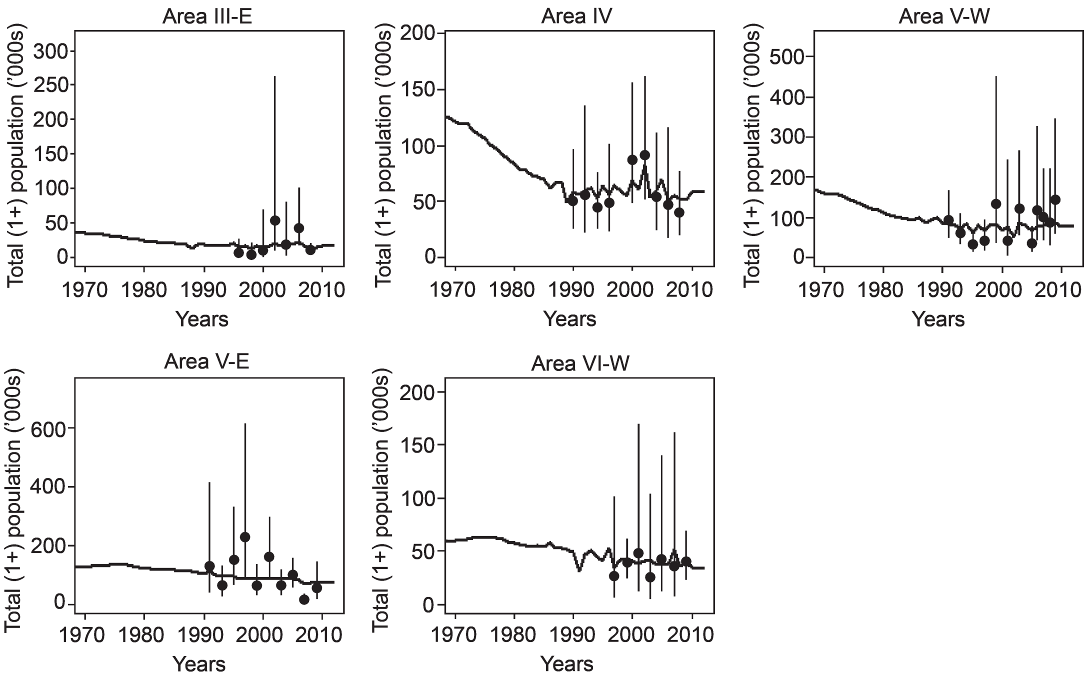

Fig. 5. Fits to the indices of relative abundance (from JARPA) for the reference case analysis. The bars indicate 95% confidence intervals based on the supplied sampling standard errors.

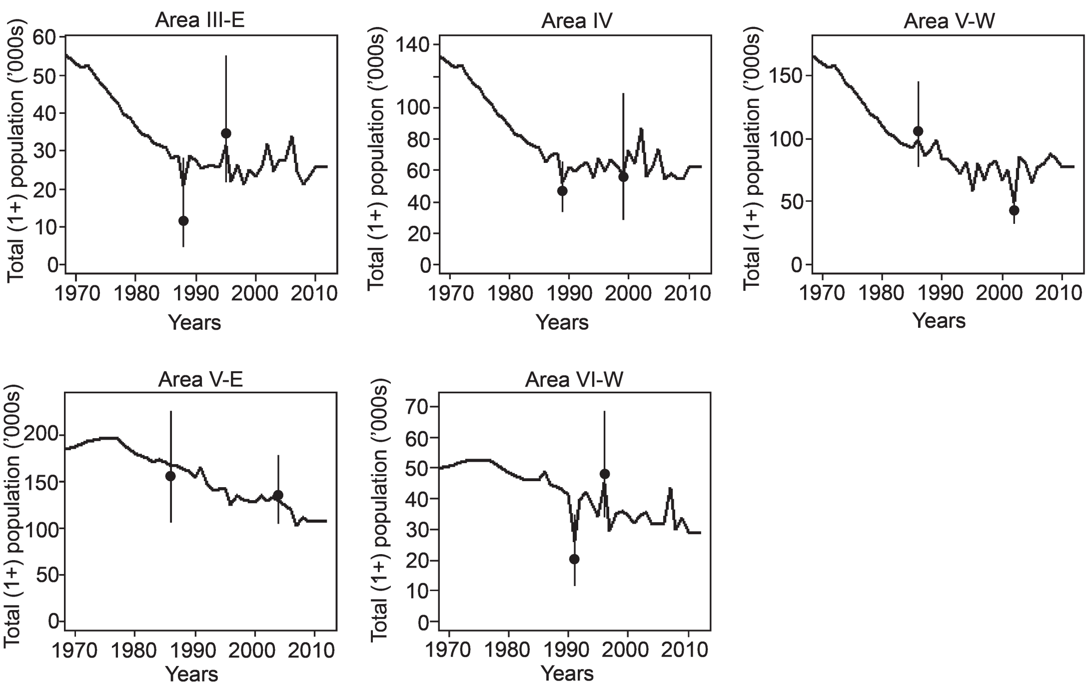

Fig. 6. Fits to the indices of absolute abundance (from IDCR) for the reference case analysis. The bars indicate 95% confidence intervals based on the supplied sampling standard errors.

As expected, assuming $g(0) = 0.8$ or 0.6 (sensitivity tests B4 & B5) leads to higher numbers in an absolute sense (Fig. 8), but the fits are hardly different in an AIC sense (Table 7). The numbers of animals in stock I are predicted to be higher before 1970 if vulnerability is time-invariant (sensitivity test B6), but not allowing for time-varying vulnerability leads to markedly poorer fits to the data. The numbers in stock I are also higher when allowance is made for time-varying declining vulnerability (sensitivity test B8) (and this is supported by AIC; Table 7). However, the Hessian matrix was not positive definite for this case, suggesting that the model is over-parameterised for this sensitivity test. Natural mortality for the younger animals is higher when vulnerability is assumed to be time-invariant and when allowance is made for time-varying declining vulnerability (but the lack of convergence for this case means the results should be interpreted with caution).

The time-trajectory of 1+ abundance and age-specific natural mortality are insensitive to treating the JARPA/JARPA II indices as absolute or relative indices of abundance (results not shown). The assumption $g(0) = 1$ for the IDCR surveys would have much stronger support if the JARPA/

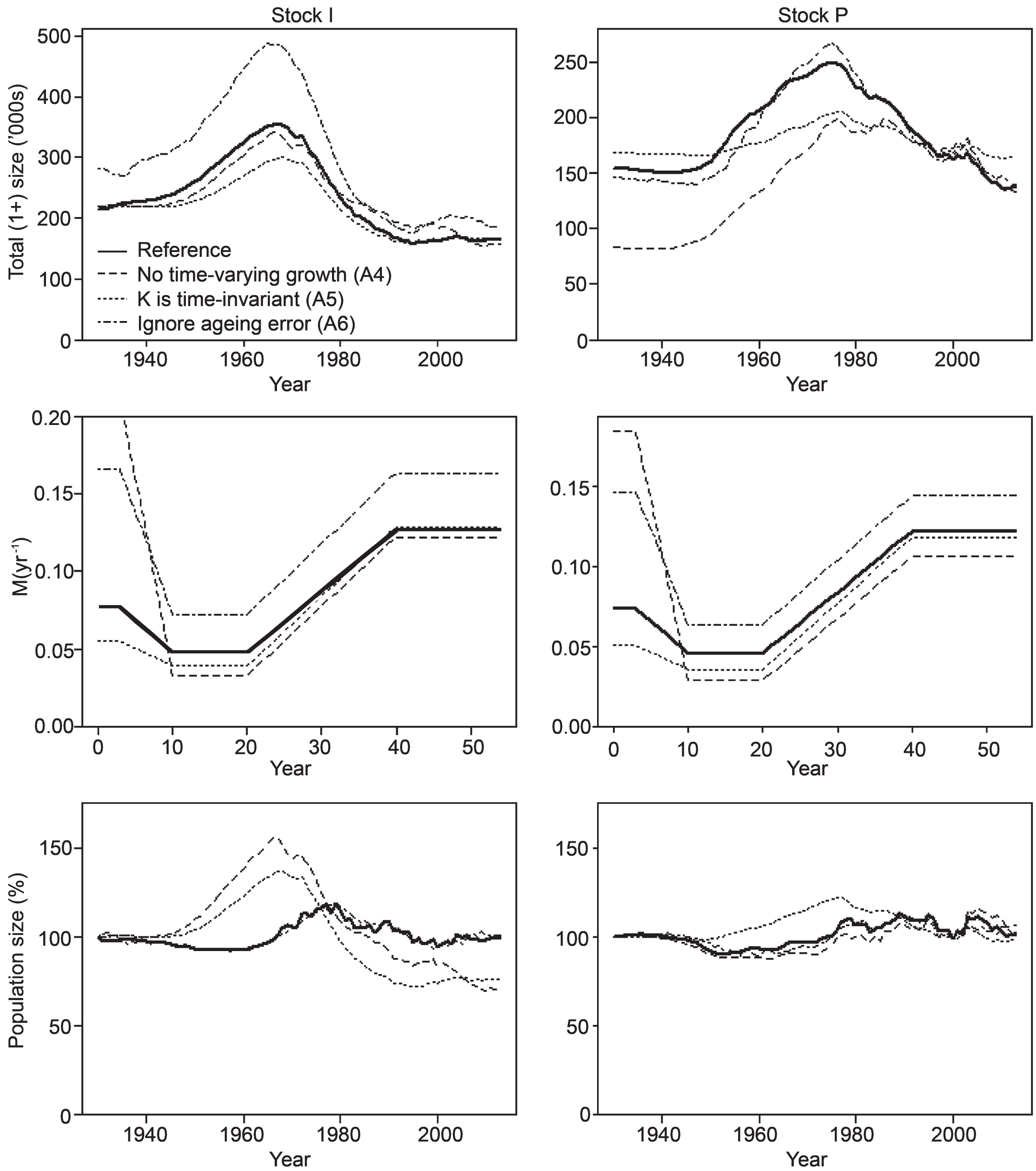

Fig. 7. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for the reference case analysis and a sub-set of the sensitivity tests.

Table 7

Number of parameters, AIC and ΔAIC (relative to the reference case) for the sensitivity tests which are comparable in terms of likelihood formulation with the reference case analysis.

Case	No. parameters	AIC	ΔAIC
Reference	1,199	34,332.8	0
A1	1,201	34,324.4	–8.4
A2	1,246	34,452.6	119.8
A3	1,104	34,182.8	–150
A4	1,003	35,487	1,154.2
A5	1,035	34,186	–146.8
A6	1,199	33,769.8	–563
B1	1,199	34,324.8	–8
B2	1,031	34,163.4	–169.4
B3	1,194	34,327.2	–5.6
B4	1,199	34,326	–6.8
B5	1,199	34,329.4	–3.4
B6	1,105	36,168.4	1,835.6
B7	1,203	34,338.2	5.4
B8	1,293	34,171.2	–161.6

JARPA II indices are assumed to be absolute indices of abundance.

Retrospective analyses

Fig. 9 shows the time-trajectories of 1+ population size and recruitment for the reference case analysis and for analyses in which the data for the last two, last four, etc. years are ignored. In general, the qualitative results are robust to ignoring recent data. However, leaving out historical data leads to higher numbers (recruitment and in total) before 1970 for stock I. The sensitivity of the results for stock P to ignoring recent data is more complicated, with lower numbers before 1970, but to higher numbers for recent years. The estimates of natural mortality, *M*, for ages 0–3 decline with increasing years of data from $0.101yr^{-1}$ for stock I when the data set is restricted to the years 2002 and earlier to $0.077yr^{-1}$ for the reference case while they decline from $0.095yr^{-1}$ to $0.074yr^{-1}$ for stock P. The estimates of *M* for ages

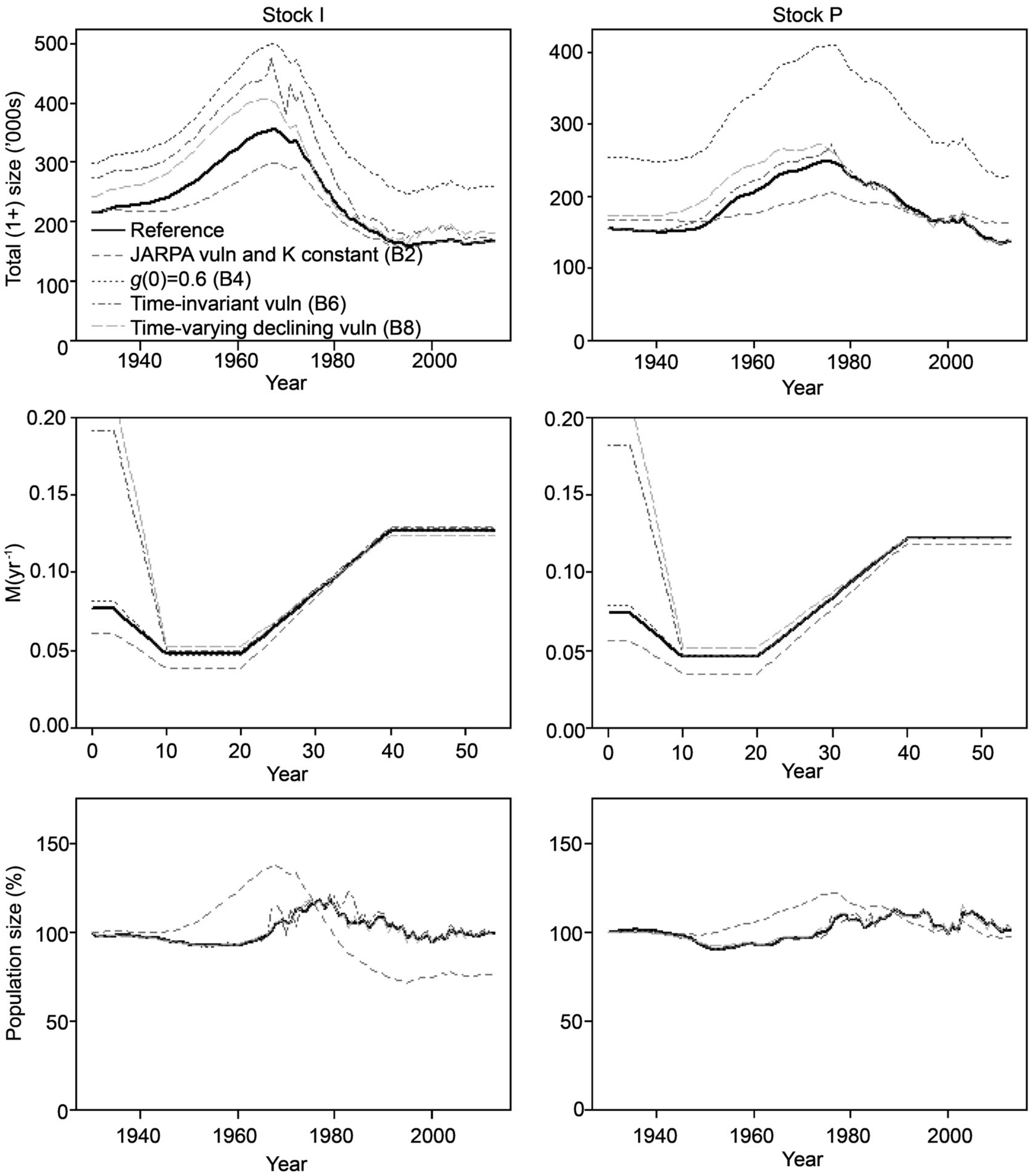

Fig. 8. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for the reference case analysis and a sub-set of the sensitivity tests.

10+ are, however, insensitive to leaving data out of the analysis. The standard error of the estimate of M for age 3 declined from 0.020yr^{-1} when the data set is restricted to the years 2002 and earlier to 0.016yr^{-1} for the reference case.

Ignoring the JARPA/JARPA II data

Dropping the JARPA/JARPA II length-frequency and conditional age-length data means that it is not possible to estimate vulnerability for the period of scientific catches. Consequently, the sensitivity tests in this section are based on setting the vulnerability pattern for the JARPA / JARPA II catches to that estimated for the reference case analysis. This assumption has no impact for the analyses which ignore both the age and length data because it is impossible to estimate vulnerability without composition data. However, this assumption will give some additional information to the analyses which ignore either, but not both, of the conditional age-at-length and length-frequency data.

Fig. 10 shows 1+ abundance (as a function of time), natural mortality (as a function of age), and total (1+) population size relative to carrying capacity for the reference case analysis and analyses in which the JARPA/JARPA II conditional age-at-length, length-frequency and index data are ignored. As suggested by Punt (2014) the results are very insensitive to ignoring the JARPA/JARPA II abundance estimates. However, results for stock I are very sensitive to the ignoring the JARPA/JARPA II conditional age-at-length data, while ignoring the JARPA/JARPA II length-frequency and conditional age-at-length data simultaneously lead to a qualitative change to the time-trajectory of 1+ abundance for stock P.

DISCUSSION

Population status and trends

All of the analyses indicate that Antarctic minke whales in the assessed area increased from 1930 until the mid-1970s and, with the exception of the analysis in which growth rates do not change over time (sensitivity A4 in Table 6), declined

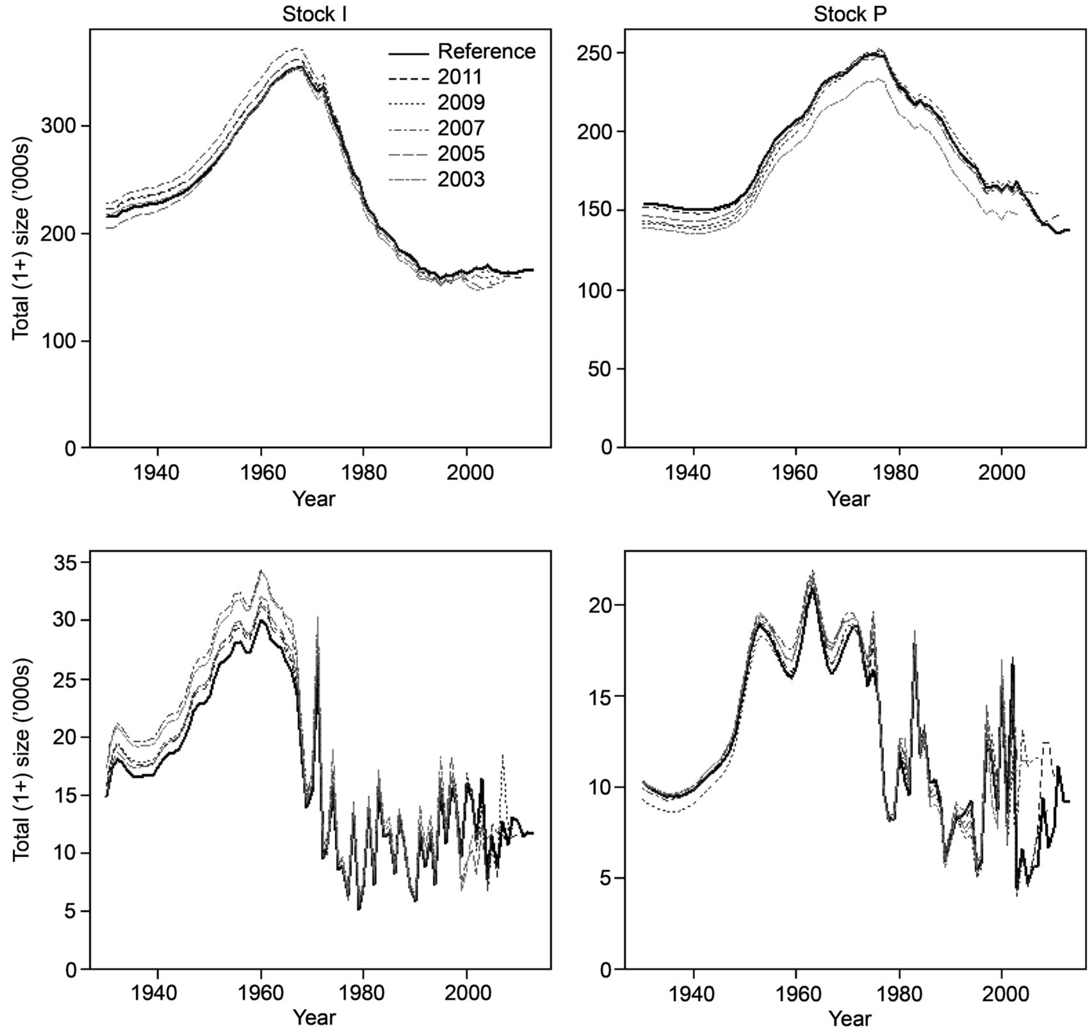

Fig. 9. Time-trajectories of 1+ population size and recruitment for the reference case analysis and for analyses when the data series are ignored after the indicated year.

over the period from the mid-1970s until 1988. The increase rate for total abundance size is 1.9% (SE 0.7%) annually for stock I and 2.1% (SE 1.1%) for stock P (Table 6). The extent of increase from 1945 to 1968 is estimated to be higher for stock P (Antarctic Areas V–E to VI–W) than for stock I (Antarctic Areas III–E to V–W). This result is robust to changes to the assumptions of the assessment. The recent (1988 onwards) trend in total abundance from the reference case analysis is downward (–0.2% (SE 0.5%) annually for stock I and –1.6% (SE 0.5%) for stock P). The conclusion that abundance is declining for stock P is robust to the changes to the assumptions, but the trend estimate for stock I for recent years is not statistically different from zero and some of the sensitivity tests for stock I (A5, A6, B2, B7, B8) suggest a slightly increasing trend (in point estimate terms).

The trends in recruitment mimic those in the total population size. However, given the time-lags involved in the model, even though total population size is estimated to be declining for stock I according to the reference case analysis, recruitment during 1988 onwards for this stock is estimated to be increasing by about 1% annually across almost all of the sensitivity tests.

With the exceptions of the trials in which carrying capacity is assumed to be time-invariant (A5 and B2), the analyses suggest that carrying capacity was higher in 1960 than in 1930 (reference case 162% (SE 28%) for stock I and 144% (SE 34%) for stock P), while carrying capacity in 2000 was about half (stock I) and 75% (stock P) of that in 1960. Consequently, carrying capacity in 2000 is estimated to be about 80% of that in 1930 for stock I and 110% of that in 1930 for stock P.

Parameter estimation

Natural mortality can be estimated with high precision (reference case: CVs of 20% for the youngest animals and 5% for the older ages, Fig. 3). Analyses conducted by Punt (2014) based on a previous version of the SCAA showed that this high precision is not a result of using an asymptotic method to estimate standard errors. Natural mortality is consistently estimated to be higher for younger and (particularly) older individuals. The functional form for natural mortality was forced to follow a piecewise linear formulation which should reduce the variance of the estimates of natural mortality. However, even allowing natural mortality to follow an auto-regressive process (sensitivity test A2) did not lead to markedly less precise estimates of natural mortality.

The Siler model for natural mortality was expected to be a parsimonious way to model age-specific natural mortality rather than pre-specifying breakpoints in the relationship

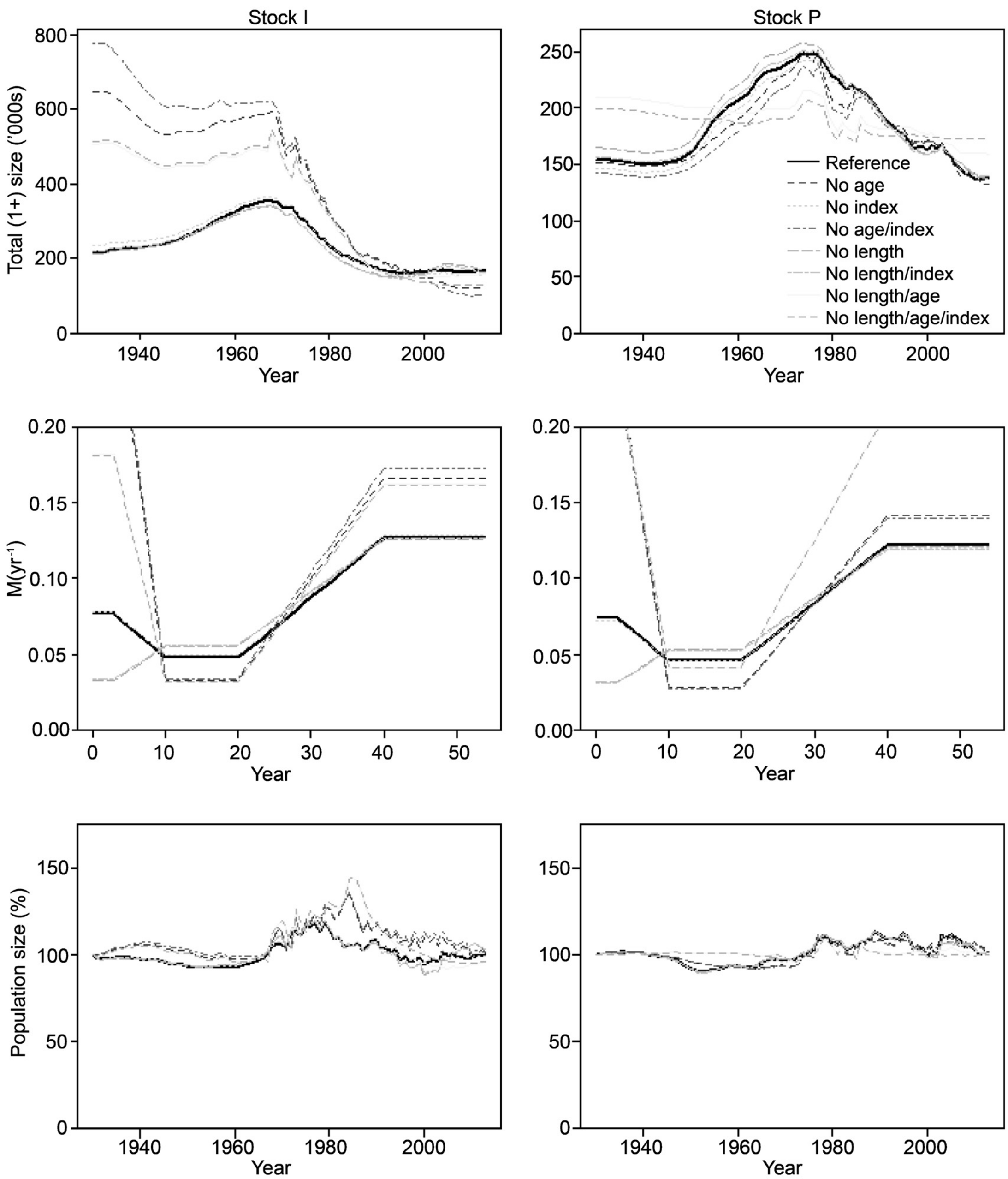

Fig. 10. Time-trajectories of total (1+) population size (upper panels), age-specific natural mortality (center panels), and total (1+) population size relative to carrying capacity (lower panels) for the reference case analysis, and variants thereof in which various combinations of the JAPRA/JARPA II index, the JAPRA/JARPA II conditional age-at-length and JAPRA/JARPA II length-frequency data are ignored when fitting the model.

between natural mortality and age. However, the estimates of natural mortality for very young animals based on the Siler relationship are unrealistically high (Fig. 2). Age-0 animals are not recorded while age-1 animals are poorly selected. Consequently the high natural mortality predicted for very young animals is an extrapolation based on natural mortality estimated for older animals.

The reference case estimates of $MSYR_{1+}$[6] are generally very high (>0.2), but some of the sensitivity tests led to estimates of $MSYR_{1+}$ which are essentially zero. A primary reason for the inability to estimate $MSYR_{1+}$ is that the stock is estimated to be close to carrying capacity throughout the assessment period (Figs 3, 7, and 8) for most of the analyses. It is noteworthy that $MSYR_{1+}$ is estimated to be essentially zero when carrying capacity is assumed to be a piecewise linear function of time (as was the case for previous SCAA configurations).

[6]The exploitation rate at which maximum sustainable yield is achieved when vulnerability is uniform on all animals aged one year and older.

Value and impact of JARPA/JARPA II data

Fig. 10 shows that the results are insensitive to dropping the JARPA/JARPA II abundance estimates while retaining other JARPA/JARPAII data. This contrasts with the results by Butterworth and Punt (1990) who highlighted the value of index data to reduce uncertainty regarding estimate of natural mortality. The JARPA/JARPA II abundance estimates are, however, not ignored (even though they are fairly imprecise; Table 1) because replacing the actual estimates by artificial data which exhibit strong trends in abundance resulted in estimated time-trajectories of population size which differed markedly from those for the reference case analysis (results not shown). This suggests that the JARPA/JARPA II abundance data are providing similar information on trends in abundance to the other data sources.

In contrast to the abundance indices, the results of the SCAA are very sensitive to simultaneously ignoring the JARPA / JARPA II length-frequency and conditional age-at-length data (Fig. 10), which suggests that these data are the primary reason that it is possible to resolve between different trends in abundance and values for natural mortality, a fact also expected from the analysis of Butterworth and Punt (1990). In addition, the standard errors for the estimates of natural mortality are higher (by up to 75% for the young ages and 40% for age 15) when the JARPA/JARPA II age and length data are ignored (results not shown).

Caveats and model structure issues

The model on which the assessment is based is very complicated because it explicitly models five areas and two stocks, allows for time-varying vulnerability, and consequently has over 1,100 parameters. The complexity arises because: (1) some of the parameters (those related to natural mortality) are shared between stocks, necessitating that the two stocks are modelled simultaneously; and (2) the estimates of absolute abundance from IDCR are area-specific, which implies that the proportion of the population in each area needs to be modelled. In principle, the IDCR data could have been treated as relative indices of abundance, but then a constraint would have had to have been imposed on the survey catchability coefficients so that they sum to 1 over all areas in which a stock is found. Explicit allowance for spatial structure would also be needed if mixing of stocks was desired.

The analyses are based on many assumptions, several of which have been explored in the tests of sensitivity. In general, the results are robust to those assumptions. Assumptions which could not be explored in detail in this study related to stock structure are perhaps of greatest concern. In particular, the analyses of this paper assume that there are two stocks of minke whales in Antarctic Areas III–E through VI–W and that there are no areas of mixing.

The application of SCAA in this case is unusual because the fishing mortality rates are generally very small, and the population dynamics are driven primarily by the impact of changes in year-class strength. In this situation, the availability of estimates of absolute abundance is essential. Without such data, it would be impossible to determine the 'scale' of the population. This is evident from sensitivity tests B4 and B5 which vary a key parameter which determines the scale of the population ($g(0)$ for the IDCR estimates of abundance) but the change in AIC is fairly small (Table 7).

Future analyses

Although the SCAA-based assessment is 'mature' in that it has been under development for almost a decade and has been refined through the suggestions and advice of the Scientific Committee, there remain areas for future work. Most of these either require information not yet available or are computationally prohibitive (at least at present). Some key areas where future work could focus on are as follows:

(1) The analyses are based on a somewhat simple stock structure hypothesis, namely that there are two stocks with a hard boundary between them. Other stock hypotheses are worth considering in future work, including a single stock with an isolation-by-distance structure (IWC, In press) and two stocks that mix with each other in part of Area V–W (Pastene, 2006). Further, analyses that used genetic and non-genetic data from JARPA and JARPA II suggested that the spatial distribution of the two stocks has a soft boundary in Areas IV–E and V–W, which depends on year and sex (Kitakado *et al.*, 2014). The analyses by Kitakado *et al.* (2014) have yet to be finalised so could not be used in this paper. In any case, accounting for sex-specific mixing patterns would require a fairly substantial change to the model.

(2) Evaluating the performance of the estimation method using simulations. Some preliminary simulation-estimation analyses were undertaken by Punt and Polacheck (2008). However, the structure of the model as well as the method of parameter estimation has changed substantially since those analyses were undertaken. If simulation testing of the assessment method is desired, it would be sensible to drop the area-structure and move to a parameterisation in which the catchability coefficients for IDCR add to 1 over space as this should substantially speed up the time it takes to fit the model.

(3) Considering alternative likelihood functions for the length-frequency and conditional age-at-length data. The approach of Francis (2014) in particular warrants consideration in this regard.

(4) Basing the analysis on Bayesian techniques. While currently computationally infeasible, use of Bayesian methods should allow the parameters controlling the variance of the random effects for calf survival, growth, spatial distribution, etc. to be estimated rather than being pre-specified.

(5) Analysing the estimates of deviations in calf survival rate to identify the likelihood of possibly causal mechanisms for the changes in recruitment over time. This exercise should, however, be conducted carefully because evidence from fisheries is that relationships between measures of recruitment success and environmental variables can be spurious and can disappear given additional information (e.g. Howell *et al.*, 2013; Myers, 1998). Haltuch and Punt (2011) provide a framework to assess the likelihood of spurious correlations and ways to structure an evaluation of which environmental variables are indeed related to recruitment success.

Can the reason or reasons be determined for the decline in abundance of Antarctic minke whales?

In simple terms, the answer to this question is no. However, some progress has been made. In particular, the results point to the possibility that carrying capacity has changed over time (first increasing then decreasing). However, 'carrying capacity' in the model relates to trends in at least four processes: pregnancy rates, infant survival rates, age-0 survival rates and changes in maturity – the data included in the current paper do not allow these processes to be distinguished. Even if this could be achieved, it would be a substantial undertaking to link any driving process to the underlying environmental cause. One of the original motivations for the development of an SCAA model was to evaluate the hypothesis of competition effects (IWC, 2005). The changes in carrying capacity may reflect such effects, but the model is not structured to test this hypothesis directly.

As noted above, the results of the paper do provide the types of data (deviations in age-1 abundance from the expectations given the number of mature females – under the assumption that maturity has not changed over time) which could allow an evaluation of which biological and environmental factors may have driven the changes in recruitment success.

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APPENDIX A

SPECIFICATIONS FOR THE POPULATION DYNAMICS MODEL

A. The population dynamics model

Under the assumption that harvesting occurs instantaneously at the start of the year, the number of animals of stock *s*, sex *g* and age *a* at the start of year *y*, $N^{g,s}_{y,a}$, is given by:

$$N^{g,s}_{y,a} = \begin{cases} 0.5\,\tilde{N}^{s}_{y,0} & \text{if } a = 0 \\ (N^{g,s}_{y-1,a-1} - C^{g,s}_{y-1,a-1})e^{-M^{s}_{a-1}} & \text{if } 1 \le a \le x-1 \\ (N^{g,s}_{y-1,x-1} - C^{g,s}_{y-1,x-1})e^{-M^{s}_{x-1}} + (N^{g,s}_{y-1,x} - C^{g,s}_{y-1,x})e^{-M^{s}_{x}} & \text{if } a = x \end{cases} \quad \text{(App.A.A.1)}$$

where $\tilde{N}^{s}_{y,0}$ is the number of births to stock *s* at the start of year *y* (see Equation App.A.C.1, here the sex-ratio at birth is assumed to be 50:50), $C^{g,s}_{y,a}$ is the catch of animals of stock *s*, sex *g* and age *a* during year *y*, calculated as the sum of the catch of such animals over all fleets i.e.:

$$C^{g,s}_{y,a} = \sum_{f} C^{g,s,f}_{y,a} \quad \text{(App.A.A.2)}$$

$C^{g,s,f}_{y,a}$ is the catch of animals of stock *s*, sex *g* and age *a* by fleet *f* during year *y*, M^{S}_{a} is the instantaneous rate of natural mortality on animals of stock *s* and age *a* (assumed to be time-invariant), and *x* is the plus-group (set equal to 54).

B. Natural mortality-at-age

The relationship between natural mortality and age is taken to be piecewise linear, with natural mortality for stock I assumed to be a constant proportion of that for stock P:

$$M^{s}_{a} = \begin{cases} \delta M^{s} & \text{if } a \le a_1 \\ M^{s}[\delta + (1-\delta)\dfrac{(a-a_1)}{(a_2-a_1)}] & \text{if } a_1 < a < a_2 \\ M^{s} & \text{if } a_2 \le a \le a_3 \\ M^{s}[1 + (\gamma-1)\dfrac{(a-a_3)}{(a_4-a_3)}] & \text{if } a_3 < a < a_4 \\ \gamma M^{s} & \text{if } a \ge a_4 \end{cases} \quad \text{(App.A.B.1)}$$

where σM^S is the rate of natural mortality for animals of stock s aged a_1 and younger, M^S is the rate of natural mortality for animals of stock s aged between a_2 and a_3, and γM^S is the rate of natural mortality for animals of stock s aged a_4 and older.

Sensitivity is explored to alternative formulations for natural mortality as a function of age. The Siler (Siler, 1979) relationship between natural mortality and age is:

$$M_a^s = \tilde{M}_1 e^{-\tilde{M}_2 a} + M^s + \tilde{M}_3 e^{-\tilde{M}_4 a/x} \quad \text{(App.A.B.2)}$$

where $\tilde{M}_1$, $\tilde{M}_2$, $\tilde{M}_3$, and $\tilde{M}_4$, are the parameters of the Siler relationship between natural mortality and age.

The second alternative model for the relationship between natural mortality and age is an AR(1) relationship, i.e.

$$\varepsilon_a^M = \varepsilon_{a-1}^M + \phi_a^M \quad \text{(App.A.B.3a)}$$

$$M_a^s = M^s e^{\varepsilon_a^M} \quad \text{(App.A.B.3b)}$$

where ε_a^M is the log of the deviation in the natural mortality between ages a and a–1 (the ϕ_a^M are subject to a normal penalty with standard deviation 0.05).

C. Births

The number of births to stock s during year y depends on the number of females that have reached the age-at-first-parturition at the start of year y and the extent of density-dependence in pregnancy rate and infant survival[1]:

$$\tilde{N}_{y,0}^s = 0.5\, f_0^s B_y^{\mathrm{F},s}\, e^{A^s(1-B_y^{1+,s}/K_y^{1+,s})}\, e^{\varepsilon_y^s} \quad \text{(App.A.C.1)}$$

where $B_y^{\mathrm{F},s}$ is the number of females of stock s that have reached the age-at-first-parturition at the start of year y, i.e.:

$$B_y^{\mathrm{F},s} = \sum_{a=1}^{x} \beta_a N_{y,a}^{g,s} \quad \text{(App.A.C.2)}$$

$B_y^{1+,s}$ is the number of animals aged 1 and older in stock s at the start of year y:

$$B_y^{1+,s} = \sum_g \sum_{a=1}^{x} N_{y,a}^{g,s} \quad \text{(App.A.C.3)}$$

$K_y^{1+,s}$ is the carrying capacity of stock s (expressed in terms of the size of the 1^+ component of the population) at the start of year y, β_a is the proportion of animals of age a that have reached the age-at-first-parturition, f_0^s is the pregnancy rate / infant survival rate in absence of harvesting for stock s, A^s is the resilience parameter for stock s, ε_y^s is the logarithm of the ratio of the expected to actual number of births for stock s during year y. The values for the ε_y^s are not treated as estimable parameters because Equation App.A.C.1 can lead to more calves than mature females for some values for ε_y^s. Therefore, a parameter θ_y^s is estimated for each year and stock, and the number of calves defined as:

$$\tilde{N}_{y,0}^s = 0.5 \tfrac{\exp(\theta_y^s)}{1+\exp(\theta_y^s)} B_y^{\mathrm{F},s} \quad \text{(App.A.C.4)}$$

The values for the ε_y^s are then computed as:

$$\varepsilon_y^s = \ell n\left(\tfrac{\exp(\theta_y^s)}{1+\exp(\theta_y^s)} / (f_0^s e^{A^s(1-B_y^{1+,s}/K_y^{1+,s})})\right) \quad \text{(App.A.C.5)}$$

β_a is defined by a logistic curve where 50% of animals reach first parturition at 8.5 years and 95% by 11.5 years. The first age at which an animal may reach first parturition is set equal to 3 years. These specifications were made for consistency with the analyses conducted by Butterworth and Punt (1999).

Allowance is made for the possibility that carrying capacity has changed over time as an autocorrelated time-series, i.e.:

$$K_y^{1+,s} = K_{1930}^{1+,s}\, e^{\xi_y^s} \quad \text{(App.A.C.6a)}$$

$$\xi_y^s = \xi_{y-1}^s + v_y^s \quad \text{(App.A.C.6b)}$$

where v_y^s is the extent to which the logarithm of carrying capacity changes from year y–1 to year y for stock s.

D. Catches and vulnerability

The model-estimate of the catch of animals of stock s, sex g and age a by fleet f during year y depends on the number of animals of stock s, sex g and age a, the exploitation rate by fleet f on animals of sex s during year y, the proportion of animals of stock s in the area where fleet f operates, and the relative vulnerability of animals of sex g and age a during year y to fleet f (assumed to be independent of stock). $C_{y,a}^{g,s,f}$ is computed using the formula:

$$C_{y,a}^{g,s,f} = \sum_l C_{y,a,l}^{g,s,f} \quad \text{(App.A.D.1)}$$

where $C_{y,a,l}^{g,s,f}$ is the catch during year y by fleet f of animals of stock s, sex g and age a that are in length-class l:

$$C_{y,a,l}^{g,s,f} = \tilde{S}_a S_{y,l}^{g,f} F_y^{g,f} X_{y,a,l}^{g,s} P_y^{A,s} N_{y,a}^{g,s} \quad \text{(App.A.D.2)}$$

[1]As calves are not harvested, this formulation for density-dependence conceptually encompasses density-dependent effects in the survival rate of calves.

$S_{y,l}^{g,f}$ is the vulnerability of animals of sex g and length l to fleet f during year y, $\tilde{S}_a$ is a factor to reduce the availability of animals of certain (younger) ages to the fishery, $F_y^{g,f}$ is the exploitation rate due to fleet f on fully-selected (i.e. $S_{y,l}^{g,f}\rightarrow 1$) animals of sex g during year y, $P_y^{A,s}$ is the proportion of stock s that is in the area A (where fleet f is found in area A) during year y (the model assumes that there is no sex- or age-structure to distribution):

$$P_y^{A,s} = \overline{P^{A,s}} e^{\varphi_y^{A,s}} / \sum_{A'} e^{\varphi_y^{A',s}} \qquad \text{(App.A.D.3)}$$

$\overline{P^{A,s}}$ is the expected proportion of stock s that is in area A, $\varphi_y^{A,s}$ is the deviation from the expected proportion for stock s in area A during year y, and $X_{y,a,l}^{g,s}$ is the proportion of animals of stock s, sex g and age a that are in length-class l during year y.

Vulnerability by fleet is assumed to be a function of length, fleet and sex. The model has options which allow vulnerability to be uniform (Equation App.A.D.4a), logistic (Equation App.A.D.4b), or domed-shaped (Equation App.A.D.4c), and to vary over time:

$$S_{y,l}^{g,f} = 1 \qquad \text{(App.A.D.4a)}$$

$$S_{y,l}^{g,f} = (1 + e^{-\ell n 19(L_l - L_{50,y}^{g,f})/L_{\text{diff}}^{g,f}})^{-1} \qquad \text{(App.A.D.4b)}$$

$$S_{y,l}^{g,f} = \begin{cases} \exp(-(L_l - L_{50,y}^{g,f})^2 / L_{\text{left}}^{g,f}) & \text{if } L_l \le L_{50,y}^{g,f} \\ \exp(-(L_l - L_{50,y}^{g,f})^2 / L_{\text{right}}^{g,f}) & \text{otherwise} \end{cases} \qquad \text{(App.A.D.4c)}$$

where $L_{50,y}^{g,f}$ is the length-at-50%-vulnerability (logistic vulnerability) / length-at-full-vulnerability (dome-shaped vulnerability) for fleet f during year y for animals of sex g:

$$L_{50,y}^{g,f} = L_{50,y-1}^{g,f} + \delta_y^{g,f} \qquad \text{(App.A.D.5)}$$

$\delta_y^{g,f}$ is the 'vulnerability deviation' during year y for fleet f for animals of sex g, $L_{\text{diff}}^{g,f}$ is the width of the length-specific vulnerability ogive for fleet f for animals of sex g, $L_{\text{left}}^{g,f}$ and $L_{\text{right}}^{g,f}$ are the parameters that determine the extent of dome-shapedness for the length-specific vulnerability ogive for fleet f for animals of sex g, and L_l is the length (in ft) corresponding to the mid-point of length-class l.

Time-dependence in vulnerability is modelled by allowing the length-at-50%-/full-vulnerability to change from one year to the next, i.e. the shape of the vulnerability given is the same each year, but the point at which vulnerability first equals 1 change. Time-dependence in vulnerability was modelled in this way to avoid the over-parameterization that might occur if allowance was also made for time-dependence in the parameters that determine the shape of the vulnerability give (this possibility is explored in one of the tests of sensitivity in which $L_{\text{left}}^{g,f}$ changes over time according to Equation App.A.D.5.).

E. Growth

The proportion of animals of stock s and sex g in age-class a that are in length-class l during y, $X_{y,a,l}^{g,s}$, is given by:

$$X_{y,a,l}^{g,s} = \int_{L_l-\Delta L}^{L_l+\Delta L} \frac{1}{\sqrt{2\pi}\sigma_\gamma^{g,s}} e^{-\frac{(L-\bar{L}_{y,a}^{g,s})^2}{2(\sigma_\gamma^{g,s})^2}} dL \qquad \text{(App.A.E.1)}$$

where ΔL is half of the width of each length-class (0.5 ft), $\sigma_\gamma^{g,s}$ is the extent of variability about the growth curve for sex g for animals of stock s, $\bar{L}_{y,a}^{g,s}$ is the expected length of an animal of stock s, sex g and age a during year y, assuming that length-at-age is governed by a von Bertalanffy growth curve and that the growth rate parameter $\kappa_y^{g,s}$ varies over time:

$$\bar{L}_{y,a}^{g,s} = \begin{cases} L_0^{g,s} & \text{if } a = 0 \\ L_\infty^{g,s} - (L_\infty^{g,s} - \bar{L}_{y-1,a-1}^{g,s}) e^{-\kappa_{y-1}^{g,s}} & \text{otherwise} \end{cases} \qquad \text{(App.A.E.2)}$$

$L_\infty^{g,s}$ is the asymptotic length for animals of stock s and sex g, $\kappa_y^{g,s}$ is the value of the Brody growth coefficient for animals of stock s and sex g during year y:

$$\kappa_y^{g,s} = \kappa_{y=1}^{g,s} e^{\upsilon_y^s} \qquad \text{(App.A.E.3)}$$

$L_0^{g,s}$ is the length of an animal of age zero for animals of stock s and sex g, and υ_y^s is the extent to which the growth rate changes from year y–1 to year y for stock s.

F. Initial conditions

The initial conditions (y_1 = 1930) correspond to a population at its unexploited equilibrium level:

$$N_{y_1,a}^{g,s} = \begin{cases} 0.5\,\tilde{N}_{y,0}^s & \text{if } a = 0 \\ N_{y_1,a-1}^{g,s} e^{-M_{a-1}^s} & \text{if } 1 \le a \le x-1 \\ N_{y_1,x-1}^{g,s} e^{-M_{x-1}^s} / (1 - e^{-M_x^s}) & \text{if } a = x \end{cases} \qquad \text{(App.A.F.1)}$$

where $\tilde{N}_{y,0}^s$ is the expected number of calves in the absence of exploitation for stock s.

The value of the parameter f_0^s is chosen so that the population remains in balance in the absence of exploitation:

$$f_0^s = \left[\sum_{a=1}^{x-1} \beta_a \, e^{-\sum_{a'=0}^{a-1} M_{a'}^s} + \beta_x e^{-\sum_{a'=0}^{x-1} M_{a'}^s} / (1 - e^{-M_x^s}) \right]^{-1} \quad \text{(App.A.F.2)}$$

APPENDIX B

SPECIFICATIONS FOR THE REFERENCE CASE OBJECTIVE FUNCTION

The objective function contains contributions from the data and from penalties on some of the parameters:

$$L = \sum_i O_i \, \ell n L_i + \sum_j PEN_j \quad \text{(App.B.1)}$$

where $\ell n L_i$ is the contribution of the i^{th} data source to the objective function, PEN_j is the contribution of the j^{th} penalty term to the objective function, and O_i is a factor to account for overdispersion.

The data included in the assessment are the annual catches (by fleet and sex), the estimates of abundance (IDCR and JARPA/JARPA II), the catch length-frequency data and the conditional age-at-length data, while there are penalties on the magnitudes of the deviations from the expected number of births (Equation App.A.C.1), on the inter-annual deviations in the carrying capacity (Equation App.A.C.6b), on the inter-annual deviations in the growth rate (Equation App.A.E.3), on the inter-annual variation in the proportion of the population in each area (see Equation App.A.D.3), and on the inter-annual deviations in vulnerability (Equation App.A.D.5). Each of these contributions is discussed in turn below. The equations listed below assume that data for each data-type are available for every year, and for all areas and fleets. This is not the case in reality, and the equations are modified appropriately in the absence of data for specific years, areas and fleets.

A. Catches

The contribution of the catches to the objective function is based on the assumption that any errors when measuring the catch are log-normally distributed[1]:

$$\ell n L_1 = \sum_y \sum_g \sum_f \left\{ \frac{1}{2\sigma_C^2} \sum_y (\ell n \tilde{C}_y^{g,f} - \ell n C_y^{g,f})^2 \right\} = Const \quad \text{(App.B.A.1)}$$

where $\tilde{C}_y^{g,f}$ is the actual catch by fleet f of animals of sex g during year y, $C_y^{g,f}$ is the model-estimate of total catch by fleet f of animals of sex g during year y:

$$C_y^{g,f} = \sum_s \sum_a C_{y,a}^{g,s,f} \quad \text{(App.B.A.2)}$$

σ_C quantifies the extent of variation in catches.

B. Estimates of abundance

The contribution of the estimates of abundance to the objective function is based on the assumption that sampling error is log-normally distributed:

$$\ell n L_2 + \sum_A \sum_y \left\{ \frac{1}{2(\tilde{\sigma}_y^A)^2} (\ell n V_y^A = \ell n(\chi^A B_y^{\text{Surv},A}))^2 \right\} = Const \quad \text{(App.B.B.1)}$$

where V_y^A is the estimate of abundance for area A and year y, χ^A is the uncorrected bias factor for area A, $\tilde{\sigma}_y^A$ is the measurement error standard deviation, determined from the observation error standard deviation and the extent of additional variance:

$$(\tilde{\sigma}_y^A)^2 = \tau^2 + (\phi_y^A)^2 \quad \text{(App.B.B.2)}$$

τ^2 is the extent of additional variance (set to 0 for the calculations of this paper), ϕ_y^A is the coefficient of variation of V_y^A, $V_y^{\text{Surv},A}$ is the model-estimate of the total (1+) abundance in area A at the start of year y:

$$B_y^{\text{Surv},A} = \sum_s \sum_g \sum_{a>0} \sum_l P_y^{A,s} X_{y,a,l}^{g,s} S_{y,l}^{g,f^*} N_{y,a}^{g,s} \quad \text{(App.B.B.3)}$$

f^* is the fleet to which the abundance estimates pertain (set to the post-1987 Japanese fleet for the JARPA / JARPA II indices; set to uniform selectivity for the IDCR indices).

[1]Note that very high weight is assigned to this component of the objective function so the model effectively replicates the actual catches exactly.

C. Length-frequency data

The contribution of the length-frequency data to the objective function is based on the assumption that the catch by sex and fleet is taken multinomially from the vulnerable population:

$$\ell n L_3 = -\sum_y \sum_f \sum_g M_y^{g,f} \sum_{l=l_{\min,y}}^{l_{\max,y}} \rho_{y,l}^{g,f} \, \ell n(\hat{\rho}_{y,l}^{g,f} / \rho_{y,l}^{g,f}) + Const \qquad \text{(App.B.C.1)}$$

where $M_y^{g,f}$ is the effective sample size for the length-frequency data for animals of sex g taken by fleet f during year y (set equal to the number of animals of sex g taken by fleet f during year y for which information on length is available, potentially multiplied by an year-specific overdispersion factor), $\rho_{y,l}^{g,f}$ is the observed fraction of the catch of animals of sex g taken by fleet f during year y that is in length-class l, $\hat{\rho}_{y,l}^{g,f}$ is the model-estimate of the fraction of the catch of animals of sex g taken by fleet f during year y that is in length-class l:

$$\hat{\rho}_{y,l}^{g,f} = \frac{\sum_s \sum_a C_{y,a,l}^{g,s,f}}{\sum_{s'} \sum_{a'} \sum_{l'} C_{y,a',l'}^{g,s',f}} \qquad \text{(App.B.C.2)}$$

Lengths $l_{\min,y}$ and $l_{\max,y}$ define the plus and minus groups for the length-frequency data for year y (data and model-predictions for animals with length less than $l_{\min,y}$ are pooled in the $l_{\min,y}$ length-class while data and model-predictions for animals with length greater than $l_{\max,y}$ are pooled in the $l_{\max,y}$ length-class).

D. Conditional age-at-length data

The age data are included in the objective function under the assumption that sampling for age is multinomial conditioned on length:

$$\sim n L_4 + \sum_y \sum_f \sum_g \sum_{l=l_{\min,y}}^{l_{\max,y}} \tilde{M}_{y,l}^{g,f} \sum_{a=a_{\min,y}}^{a_{\max,y}} \theta_{y,a,l}^{g,f} \sim n\left(\hat{\theta}_{y,a,l}^{g,f} / \theta_{y,a,l}^{g,f}\right) + Const \qquad \text{(App.B.D.1)}$$

where $\tilde{M}_{y,l}^{g,f}$ is the effective sample size for the age breakup of the animals of sex g in length-class l taken by fleet f during year y (set equal to the number of animals of sex g in length-class l taken by fleet f during year y for which information on length and age is available, potentially multiplied by a year-specific overdispersion factor), $\theta_{y,a,l}^{g,f}$ is the observed fraction of the catch of animals in length-class l of sex g taken by fleet f during year y that were aged to be age a, $\hat{\theta}_{y,a,l}^{g,f}$ is the model-estimate of the fraction of the catch of animals in length-class l of sex g taken by fleet f during year y that were aged to be age a:

$$\hat{\theta}_{y,a,l}^{g,f} = \frac{\sum_s \tilde{C}_{y,a,l}^{g,s,f}}{\sum_{s'} \sum_{a'} \tilde{C}_{y,a',l}^{g,s,f}} \qquad \text{(App.B.D.2)}$$

$\tilde{C}_{y,a,l}^{g,s,f}$ is the model-estimate of the number of animals of sex g and stock s in length-class l caught by fleet f during year y that would have been aged to be age a:

$$\tilde{C}_{y,a,l}^{g,s,f} = \sum_{a'} Y_{a,a',y} C_{y,a',l}^{g,s,f} \qquad \text{(App.B.D.3)}$$

$Y_{a,a',y}$ is the fraction during year y of animals of sex g and age a' that are aged to be age a (the age-reading error matrix):

$$Y_{a,a',y} = \int_{a-0.5}^{a+0.5} \frac{1}{\sqrt{2\pi}\sigma''_{a',y}} e^{-\frac{(\lambda-\beta_{a',y})^2}{2(\sigma_{a',y})^2}} d\lambda \qquad \text{(App.B.D.4)}$$

$\tilde{\beta}_{a,y}$ is the expected age based on age-readings for an animal of true age a during year y, and $\sigma''_{a,y}$ is the standard error of the age-estimate for an animal of true age a during year y. The year-dependence of $\tilde{\beta}_{a,y}$ and $\sigma''_{a,y}$ is related to the ager who conducted the age-readings in year y (Table App.B.1), while age-dependence is modelled by allowing and $\sigma''_{a,y}$ to change linearly with age.

$$\tilde{\beta}_{a,y} = \tilde{\beta}_{L,y} + (\tilde{\beta}_{H,y} - \tilde{\beta}_{L,y})\frac{a}{70}; \quad \sigma''_{a,y} = \sigma''_{L,y} + (\sigma''_{H,y} - \sigma''_{L,y})\frac{a}{70} \qquad \text{(App.B.D.5)}$$

Table App. B.1

Parameters which determine the age-reading error matrix. These values correspond to the 'Lockyer unbiased' analysis of Kitakado *et al.* (2013). The values for L and H are 0 and 70 respectively.

Year	Reader	$\tilde{\beta}_L$	$\tilde{\beta}_H$	σ''_L	σ''_H
1971/72–1979/80	Masaki	3.0837	58.7940	1.5531	1.5531
1980/81–1989/90	Kato	2.4545	56.0060	0.5391	7.3718
1990/91–1991/92	Zenitani	1.0300	62.8530	0.4637	3.6614
1992/93	Kato	2.4545	56.0060	0.5391	7.3718
1993/94–2004/05	Zenitani	1.0300	62.8530	0.4637	3.6614
2005/06–2011/12	Bando	1.6355	63.6440	0.6588	3.4128

Ages $a_{\min,y}$ and $a_{\max,y}$ define the plus and minus groups for the ageing data for year y, i.e. data and model-predictions for animals with age greater than $a_{\max,y}$ are pooled at age $a_{\max,y}$[2] and those with age less than $a_{\min,y}$ are pooled at age $a_{\min,y}$.

E. Penalties

The penalty on the deviations from the expected number of births is based on the assumption that these deviations are log-normally distributed:

$$PEN_1 = \tfrac{1}{2\sigma_R^2}\sum_s\sum_y(\varepsilon_y^s)^2 \qquad \text{(App.B.E.1)}$$

where σ_R is the standard deviation of ε_y^s.

The penalty on the changes over time in the vulnerability deviations is based on the assumption that these deviations are normally distributed:

$$PEN_2 = \tfrac{1}{2\sigma_S^2}\sum_g\sum_y\sum_f(\delta_y^{g,f})^2 \qquad \text{(App.B.E.2)}$$

where σ_S is the extent of inter-annual variation in the age-at-50%-vulnerability.

The penalty on the annual deviations in the proportion of each stock in each area is based on the assumption that these deviations are normally distributed:

$$PEN_3 = \tfrac{1}{2\sigma_P^2}\sum_s\sum_y\sum_A(\varphi_y^{A,s})^2 \qquad \text{(App.B.E.3)}$$

where σ_P is the extent of variation in the distribution of the stock.

The penalty on the inter-annual changes in the von Bertalanffy growth rate parameter is based on the assumption that these deviations are normally distributed:

$$PEN_4 = \tfrac{1}{2\sigma_\kappa^2}\sum_s\sum_y(\upsilon_y^s)^2 \qquad \text{(App.B.E.4)}$$

where σ_κ is the extent of variation in changes in growth rate.

The penalty on the inter-annual changes in the logarithm of carrying capacity is based on the assumption that these deviations are normally distributed:

$$PEN_5 = \tfrac{1}{2\sigma_K^2}\sum_s\sum_y(\nu_y^s)^2 \qquad \text{(App.B.E.5)}$$

where σ_k is the extent of variation in changes in carrying capacity.

[2]Note that the evaluation of the impact of age-reading error is determined before the application of the plus-group.