An initial examination of possible inferences concerning MSYR for Southern Hemisphere minke whales from recruitment trends estimated in catch-at-age analyses[1]

D.S. BUTTERWORTH* AND A.E. PUNT†

Contact e-mail: dll@maths.uct.ac.za

ABSTRACT

A slightly modified version of the BALEEN II population dynamics model, which makes allowance for time trends in carrying capacity K, is fitted to the recruitment time series provided by the base-case ADAPT VPA assessment of the catch-at-age and survey abundance data for minke whales in Area IV reported in Butterworth *et al.* (1999). The initial increasing trend of these recruitment estimates from 1944-1968 is well fitted by the model, yielding an estimate of $MSYR_{mat}$ of some 13% (or $MSYR_{1+}$ of about 6%) which is reasonably robust to changes in a number of assumptions such as variation in the period over which K is assumed to increase. The post-1970 drop in recruitment indicated by the base-case ADAPT VPA assessment cannot be explained by the effects of catches and super-compensation alone, and requires the additional assumption of a recent decline in K. However, the need for this last assumption diminishes if allowance is made for likely negative bias in the absolute abundance estimates from the IWC surveys input to the ADAPT VPA assessments.

KEYWORDS: MINKE WHALE; INDEX OF ABUNDANCE; TRENDS; MODELLING; MSY RATE; RECRUITMENT RATE

INTRODUCTION

Butterworth *et al.* (1999) present estimates of trends in recruitment (strictly 2 year olds, given the three-year, three-age grouping system for catch-at-age data which they consider) for minke whales in Areas IV and V of the Antarctic[2], based upon the joint analysis of catch-at-age and survey abundance data. Their base-case estimator for Area IV reflects an increasing trend in recruitment of 5.5% per annum over the 1947-68 period. A further feature of their results is the marked drop in recruitment indicated from 1970 to the mid-1980s.

Butterworth *et al.* (1999) comment that this increasing trend in recruitment relates to the matter of a range of plausible values for MSY rate (*MSYR*[3]) for minke whales, which is a key input to the Revised Management Procedure *Implementation Simulation Trials*[4] (IWC, 1993; 1994; 1995), and suggest that the trend may reflect an increase in carrying capacity for minke whales linked, perhaps, to the concurrent heavy depletion of populations of large baleen whales in the Southern Ocean. They further speculate that a possible explanation for the subsequent drop in recruitment after 1970 might be the phenomenon of super-compensation (Holt, 1985; Butterworth and Best, 1990). This is a reduction in the absolute recruitment level as a population nears its carrying capacity, as illustrated, for example, in the stock-recruitment plots of Fig. 1 for $MSYR_{mat}$ values of 4% or greater.

This paper presents an initial quantitative examination of these suppositions by fitting a modified version of the BALEEN II population model (de la Mare, 1989; Punt, 1996) to the time series of recruitment estimates from two of the Area IV minke whale ADAPT VP A assessments of Butterworth *et al.* (1999). These fits are based on maximising a likelihood function. A variety of alternative parametrizations of the time-dependence in carrying capacity are examined. The primary purposes are to draw inferences about the possible value of *MSYR,* and to ascertain whether the combined effects of catches (which effectively commenced in 1970, and contribute to a reduction in recruitment through the removal of some adult females) and super-compensation are alone sufficient to explain the post-1970 recruitment trends evident in the results of the ADAPT VPA analyses.

METHODS

Modifications to the population dynamics model

Two modifications have been made to the standard BALEEN II model (de la Mare, 1989; Punt, 1996) for these analyses. These involve (i) the function relating the number of births to the number of mature females; and (ii) the time-dependence of carrying capacity.

The number of births in the BALEEN II model is governed by the equation[5]:

$$N_{y,0}^{m/f} = \begin{cases} f_{-\infty} P_y^M (1+A) & \text{if } P_y^D = 0 \\ \max(0, f_{-\infty} P_y^M (1 + A(1-(P_y^D / K_y^D)^z)) & \text{otherwise} \end{cases} \quad (1)$$

where: $N_{y,0}^{m/f}$ is the number of male/female calves at the start of year y;

$f_{-\infty}$ is the pregnancy rate at carrying capacity;

P_y^M is the number of females which have reached the age at first parturition (termed here the 'mature' females, for convenience) at the start of year y;

A is the resilience parameter (which is the primary determinant of the *MSYR*);

[1] An earlier version of this paper was submitted to the IWC Scientific Committee as SC/49/SH22.

[2] Area IV = 70ºE-130ºE and Area V = 130ºE-170ºW; see Donovan (1991).

[3] The ratio of *MSY* to the population level, *MSYL*, at which it is achieved. The value depends upon the component of the population considered to be under harvest, as detailed later in the paper.

[4] This is because procedure performance in such trials is critically dependent on the population's productivity level, which is not well known for minke whales.

[5] Allowance is made here for the possibility that the component of the population to which density-dependence is functionally related becomes zero even though some mature females remain.

* *Department of Mathematics and Applied Mathematics, University of Cape Town, Rondebosch 7701, South Africa.*

† *Division of Marine Research, CSIRO Marine Laboratories, GPO Box 1538, Hobart, Tas 7001, Australia.*

z is the degree of compensation;

P_y^D is the size, at the start of year y, of the component of the population to which density dependence is functionally related (taken here to be the number of 'mature' females P_y^M); and

K_y^D is the carrying capacity, at the start of year y, for the component of the population to which density dependence is functionally related.

This relationship is illustrated in the top panel of Fig. 1 for various values of the *MSYR* in terms of the mature component of the population ($MSYR_{\text{mat}}$). As this figure shows, it leads to zero births for sizes of the pertinent component of the population larger than $(1 + A^{-1})^{1/z}K_y^D$. If the population overshoots carrying capacity, or if carrying capacity declines rapidly over time, the number of births drops quickly to zero for relatively little overshoot, which seems unrealistic biologically. To eliminate this problem, if the number of 'mature' females exceeds their (current) carrying capacity, the assumption is made here that the number of births is equal to the number expected at carrying capacity, i.e.:

$$N_{y,0}^{m/f} = \begin{cases} f_{-\infty} P_y^M (1+A) & \text{if } P_y^D = 0 \\ f_{-\infty} P_y^M (1 + A(1-(P_y^D / K_y^D)^z)) & \text{if } 0 < P_y^D < K_y^D \\ f_{-\infty} K_y^M & \text{if } P_y^D \geq K_y^D \end{cases} \quad (2)$$

as illustrated in the lower panel of Fig. 1.

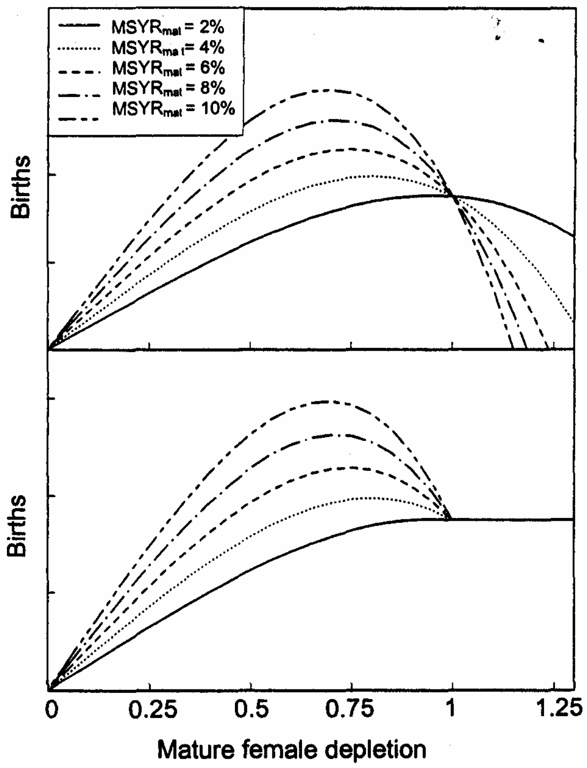

Fig. 1. The upper panel shows plots of births as functions of mature female depletion for the standard BALEEN II model, as given by Equation (1). The plots are evaluated for the values of biological parameters specified in the text, and shown for different values of $MSYR_{\text{mat}}$. The lower panel shows the modification adopted for this paper (Equation 2), for which the number of births remains constant for depletions above 1 (i.e. for $P^D > K^D$).

The second modification to the BALEEN II model relates to the time-dependence of carrying capacity, K. The current version of BALEEN II allows K to change in a piecewise linear fashion where the years in which changes in K occur are pre-specified. This has been generalised here to allow K to change in a non-linear fashion between pre-specified years. For example, if K changes between the years y_i and y_{i+1}, the time dependence of K is given by:

$$K_y = a + by^{\beta} \qquad y_i \leq y \leq y_{i+1} \quad (3)$$

where a and b are chosen to effect continuity at the end points of this period.

Specification of a scenario regarding the time dependence of K therefore involves choosing a value for β and selecting the years in which the relationship between K and time changes (i.e. $\{y_i: i = 1,2,\ldots,m\}$). For simplicity, it is assumed that K is constant from the first year considered in the analysis (1920) to year y_1, and also constant from year y_m to the last year considered in the analysis (1996).

Likelihood function

The population dynamics model is fitted to the estimates of age 2 abundance from the ADAPT VPA assessments (Butterworth *et al.*, 1999) by assuming that these estimates are normally distributed about the modified BALEEN II model estimates[6]. Additive (normal) rather than multiplicative (log normal) error is assumed because bootstrap estimates of variance for these abundance estimates are more suggestive of the former - see fig. 10 of Butterworth *et al.* (1999). This leads to minimisation of the following negative log likelihood (after removal of constants) for $MSYR_{\text{mat}}$, K_{1920}^D and $\{K_i^D/K_1^D: i = 2,\ldots\}$[7]:

$$-\ell nL = n\ell n\hat{\sigma} + n/2 \quad (4)$$

where: $\hat{\sigma}$ is the 'residual' standard deviation, and is given by

$$\hat{\sigma} = \sqrt{\frac{1}{n}\sum_y (\tilde{N}_{y,2} - \tilde{N}_{y,2}^{VPA})^2} \; ; \quad (5)$$

$\tilde{N}_{y,2}^{VPA}$ is the ADAPT VPA estimate of the abundance of animals assigned to age 2 and year y under the three-year, three-age grouping system used by Butterworth *et al.* (1999);

$\tilde{N}_{y,2}$ is the model quantity corresponding to $\tilde{N}_{y,2}^{VPA}$

$$\tilde{N}_{y,2} = \sum_{y'=y-1}^{y+1} (R_{y',2}^f + R_{y',2}^m + U_{y',2}^f + U_{y',2}^m) \; ; \quad (6)$$

$R_{y,2}^{m/f}$ is the number of recruited males/females of age 2 at the start of year y;

$U_{y,2}^{m/f}$ is the number of unrecruited males/females of age 2 at the start of year y; and

n is the number of years for which ADAPT VPA estimates of age 2 abundance are available.

For the purposes of the preliminary examination, the estimates of $MSYR_{\text{mat}}$ are constrained to lie in the range [0, 15%] while the estimates of K_i^D/K_1^D are forced to lie in the range [0, 15].

[6] The information on abundance from the IWC cruises and from the JARPA programme are not included in the likelihood function, as they are already taken into account in the ADAPT VPA assessments used to obtain the estimates of age 2 abundance.
[7] By definition $K_{1920}^D = K_1^D$.

Catch data and biological parameter values

Analyses in this paper consider minke whales in Area IV and use the annual catch data for this Area. The (age- and sex-independent) rate of natural mortality, M, is set equal to 0.057 yr^{-1} (the value estimated for the base-case ADAPT VPA assessment of Butterworth *et al.* (1999), for which the corresponding estimates of age 2 abundance are given in Table 1). The proportion of 'mature' females 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. Density-dependence is assumed to act on the mature female component of the population.

It is necessary to account for the commercial and scientific take catches differently because the selectivity patterns for these two periods are quite different (see table 5(c) of Butterworth *et al.*, 1999). This has been achieved here by assuming that the commercial catches were taken uniformally from the mature component of the population, while the scientific catches were taken uniformally from the 1+ component of the population[8].

Variance estimation

Three alternative methods are used to quantify uncertainty. Two of these condition on the ADAPT VPA point estimates (the recruitment estimates and the (age-independent) value for M) while the third considers the imprecision in the ADAPT VPA output.

For the analyses conditioned on the ADAPT VPA point estimates, the (conditioned) parametric bootstrap approach is used to estimate coefficients of variation and, in conjunction with the percentile method, to estimate 95% confidence intervals. The (conditioned) parametric bootstrap approach is described in detail by Punt and Butterworth (1991), so that only the details of how the artificial datasets are generated will be outlined here. The age 2 abundance for year y and artificial data set U, $\tilde{N}_{y,2}^{VPA,U}$, is generated using the formula:

$$\tilde{N}_{y,2}^{VPA,U} = \hat{\hat{N}}_{y,2} + \varepsilon_y^U \qquad \varepsilon_y^U \sim N(0;\hat{\sigma}^2) \qquad (7)$$

where: $\hat{\hat{N}}_{y,2}$ is the estimate of $\tilde{N}_{y,2}^{VPA}$ obtained by fitting the model to the actual ADAPT VPA output; and

$\hat{\sigma}$ is the estimate of the residual standard deviation obtained by fitting the model to the actual ADAPT VPA output, and is sufficiently small compared to the recruitment estimates themselves, that the potential problem of Equation (7) generating negative values does not arise in practice.

The profile likelihood method (Press *et al.*, 1988; Venzon and Moolgavkor, 1988; Schnute, 1989) is also used to calculate a 95% confidence interval for $MSYR_{\text{mat}}$. This method is, however, not used for any other model outputs because it is highly intensive computationally (especially for model outputs which are not estimable parameters of the model).

The ADAPT VPA output upon which the estimation is conditioned is subject to considerable imprecision (see fig. 5 and table 11 of Butterworth *et al.*, 1999). The impact of this imprecision can be examined by applying the estimation procedure of Equation (4) above, to each of 100 ADAPT VPA bootstrap outputs. Each of these contain a time-series of recruitment estimates and a value of the (age-independent) rate of natural mortality. Coefficients of variation and 95% intervals for the estimated quantities can be calculated from the 100 sets of results obtained by fitting to the 100 sets of outputs.

[8] This reflects the maximum flexibility which the available computer code for the BALEEN II model admits.

Specification of analyses

In order to fully define an analysis, it is necessary to provide specifications for the following (the options considered in this paper are given in parenthesis).

(a) The number of years of ADAPT VPA age 2 abundance estimates to consider (1944-1968; 1944-1995). The rationale for considering these two periods is explained below.

(b) The value of the parameter in Equation (3) which determines the extent of non-linearity in the time-dependence of K over the period, $y_1 \leq y \leq y_2$, β (0.5, 1, 2). The choice $\beta = 1$ (i.e. linearity) has been made for the base-case on the basis of simplicity.

(c) The years in which the relationship between K and time changes (a variety of choices involving either two or three changes are considered).

(d) The value of $MSYL_{\text{mat}}$ (0.5, 0.6, 0.7, 0.8).

RESULTS AND DISCUSSION

Two ADAPT VPA assessments from Butterworth *et al.* (1999) are considered in this initial examination. The first corresponds to their base-case estimator, while the second is for the case when the absolute estimates of abundance (from dedicated IWC surveys) input to that estimator are doubled. There are two particular reasons for considering this second case. The first is that the IWC cruise abundance estimates are likely to be negatively biased to some extent (IWC, 1991, pp.58-9) as a result of factors such as the incomplete area coverage by these surveys, and the assumption in the analysis of their results that all whales on the trackline are seen (i.e. that $g(0) = 1$). For example, the 'equivalent northern boundaries' abundance estimates of Punt *et al.* (1997) used for the computations of Butterworth *et al.* (1999) pertain to open ocean areas south of latitude 60°S only, and furthermore to only portions of those regions (some 80% for Area IV and 60% for Area V). Secondly, the estimated recruitment trend after 1970 is notably different in this case, reflecting a much smaller drop in relative terms. The two ADAPT VPA recruitment series considered are listed in Table 1.

The analyses of the paper are conducted in two stages. In the first, only the initial increasing recruitment trend (over 1944-68) from the ADAPT assessment is fitted by the modified BALEEN II model, and under very simple assumptions concerning the time trend in K: constant to year y_1, increasing (usually linearly) until year y_2, and thereafter constant again at the higher value reached. The purpose of this exercise is twofold: first to see whether or not inferences about the value of $MSYR$ drawn from such model fits are robust to variations in the model assumptions, and this in circumstances where such $MSYR$ estimates are not perhaps biased by lack of fit for years subsequent to 1968 as a result of model misspecification; and secondly to examine how well such model fits are able to predict the post-1970 recruitment estimates provided by the ADAPT VPA assessments.

The results of this exercise for the base-case ADAPT VPA assessment are shown in Table 2a for various choices for y_1, y_2, $MSYL_{mat}$ and β (the parameter determining the linearity or otherwise of the increasing trend in K between years y_1 and y_2 - see Equation 3). Essentially variations are performed on a base-case specified by the choice of $MSYL_{mat}$ equal to the value of 0.6 conventionally assumed by the IWC Scientific Committee, $\beta = 1$ (linearity for simplicity), and $y_1 = 1930$, $y_2 = 1960$ corresponding roughly to the period of heavy harvesting of the other baleen whale species around Antarctica (e.g. see Allen, 1980).

The results for a fit are summarised in the tables by 12 statistics (13 if carrying capacity is assumed to change three times rather than twice during the period 1920-1996):

Table 1

Estimates of the abundance of age 2 animals in Area IV (pooled into three-year groupings) based on two of the ADAPT VPA analyses in Butterworth *et al.* (1999).

	Analysis	
Year	Base-case	Double abundance estimates
1944	5,494	8,652
1947	7,100	11,174
1950	8,327	13,111
1953	10,722	16,840
1956	12,041	18,942
1959	15,098	24,083
1962	18,083	29,764
1965	20,322	33,887
1968	20,913	36,226
1971	18,825	34,288
1974	15,468	29,439
1977	10,904	21,967
1980	8,756	18,371
1983	8,592	19,023
1986	11,942	27,102
1989	10,640	24,187
1992	10,486	23,945
1995	9,721	22,266

(a) $MSYR_{mat}$ - *MSYR* in terms of uniform-selectivity harvesting of the mature component of the population (expressed as a percentage);

(b) $MSYR_{1+}$ - *MSYR* in terms of uniform-selectivity harvesting of the 1+ component of the population (expressed as a percentage);

(c) K_i/K_1 - the ratio of the carrying capacity at the start of year y_i to that at the start of 1920;

(d) $-\ell nL$ - the negative log likelihood (see Equation 4);

(e) σ - the estimate of the residual standard deviation (see Equation 5);

(f) P_y^m/K_y^M - the ratio of number of mature females at the start of year y to the corresponding carrying capacity (presented for $y = 1968$, 1983 and 1995);

(g) N_y^{1+} - the total (1+) population size at the start of year y (presented for $y = 1968$ and 1995); and

(h) $N_{y,2}/N_{68,2}$ - the ratio of the age 2 abundance at the start of year y (see Equation 6) to that at the start of 1968 (presented for $y = 1983$ and 1995).

Note that values for statistics (g) and (h) are available for the ADAPT VPA results as reported in Butterworth *et al.* (1999), so that these values can be compared with those forthcoming from fitting the modified BALEEN II model.

The choice made for a base-case in fact provides one of the best of the fits to the data amongst those reported in Table 2a. The only variations which provide slight improvements are those which increase $MSYL_{mat}$ to 0.7 or have K increasing quadratically rather than linearly with time over the 1930-1960 period.

The base-case fit, and those for two other variants, are shown in Fig. 2. The instance where the increase in K commences in 1920 rather than 1930 results in a markedly misspecified fit - the worst of all the variants considered in

Table 2

Summary statistics for fits of the modified Baleen II model to the estimates of age 2 abundance (1944-1968) for minke whales in Area IV from ADAPT VPA. The row 'Observed' contains values for some of the summary statistics from the output of the ADAPT VPA analyses. Profile likelihood 95% confidence interval estimates for $MSYR_{mat}$ are given in square parentheses.

									P_y^M/K_y^M			N_y^{1+}		$N_{y,2}/N_{68,2}$	
y_1	y_2	$MSYL_{mat}$	β	K_2/K_1	$MSYR_{mat}$	$MSYR_{1+}$	$-\ell nL$	σ	1968	1983	1995	1968	1995	1983	1995
(a) Base-case recruitment estimates															
Observed												77,188*	57,063	0.411	0.465
1930	1960	0.6	1	10.79	13.36 [12.33 14.39]	6.02	108.04	245	0.784	0.851	1.093	80,131	82,859	0.778	0.503
1930	1960	0.5	1	14.63	13.12 [11.48 14.24]	5.97	111.88	304	0.648	0.811	1.029	79,925	92,155	0.893	0.645
1930	1960	0.7	1	8.45	13.42 [12.52 14.20]	6.02	107.39	237	0.899	0.798	1.152	80,328	83,036	0.841	0.439
1930	1960	0.8	1	6.95	13.32 [12.28 14.42]	5.98	113.17	326	0.987	0.779	1.178	80,581	79,692	0.953	0.393
1930	1960	0.6	0.5	11.35	13.40 [12.32 14.44]	6.03	108.65	254	0.785	0.851	1.093	80,106	82,821	0.777	0.502
1930	1960	0.6	2	9.08	13.30 [12.30 14.24]	6.00	106.91	230	0.786	0.849	1.092	80,290	83,027	0.782	0.505
1920	1960	0.6	1	14.98	9.99 [8.42 11.04]	4.89	128.21	752	0.692	0.832	1.063	81,140	93,400	0.940	0.613
1930	1955	0.6	1	11.28	13.29 [12.03 14.48]	6.00	111.19	292	0.779	0.857	1.092	80,103	82,868	0.774	0.505
1930	1965	0.6	1	11.45	14.93 [13.56 15.00+]	6.50	110.78	286	0.827	0.821	1.113	79,935	82,678	0.778	0.473
1930	1970	0.6	1	12.50	14.99+[13.74 15.00+]	6.52	114.18	345	0.787	0.911	1.106	80,003	82,110	0.763	0.520
(b) 'Double abundance estimates' recruitment															
Observed												127,346*	130,939	0.525	0.615
1930	1960	0.6	1	12.52	13.71 [12.36 15.00+]	6.13	120.00	477	0.731	1.033	0.967	132,132	128,473	0.496	0.653

* The ADAPT VPA computes this quantity for ages up to 27 only.

+ Constraint boundary.

terms of the σ values listed in Table 2 - and would therefore seem not to merit further consideration. Notable then is the fact that all the remaining variants considered yield $MSYR_{mat}$ estimates in excess of 13%, corresponding to $MSYR_{1+}$ estimates above 6%.

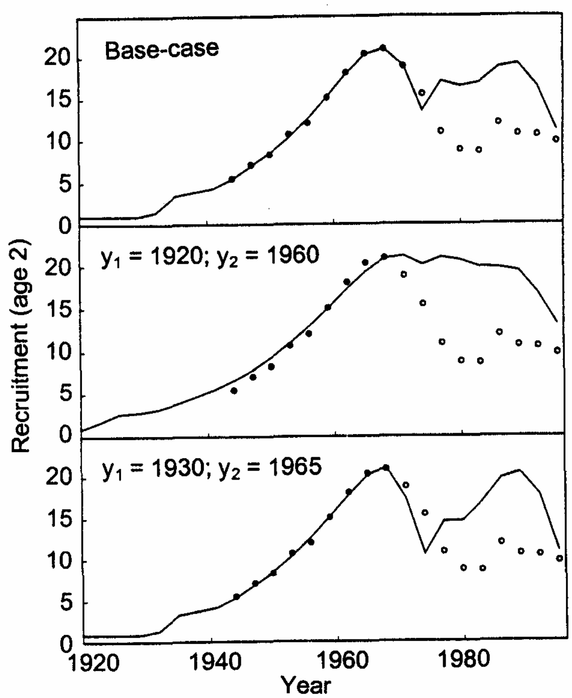

Fig. 2. Estimates of recruitment for minke whales in Area IV (age 2 abundance in thousands pooled into three-year groupings) from the base-case ADAPT VPA assessment (dots) and based on the results of fits of the BALEEN II model to the data (solid lines) The fits shown here take account of the ADAPT estimates from 1944-1968 (solid dots) only, omitting consideration of those from 1971-1995 (open dots). Results are shown for three alternative prescriptions for specifying time-dependence in carrying capacity K, which is constant to year y_1, increases to year y_2 and then is constant again (the values for y_1 and y_2 are shown in each panel).

Also apparent both from the fits shown in Fig. 2, and the tabulated values of $N_{y,2}/N_{68,2}$ in Table 2a, is that although the combination of the effect of catches and super-compensation (given the high $MSYR$ estimate) do result in a drop of recruitment in the modified BALEEN II model fits after 1970, these drops are not as large as the ADAPT VPA base-case assessment results suggest. However, in Table 2b which reports results for the ADAPT VPA assessment for which the absolute abundance estimates input are doubled, this marked lack of fit essentially disappears.

Table 3 reports bootstrap CVs and 95% confidence interval estimates for all the statistics of the base-case fit considered, while profile likelihood estimates of this confidence interval for $MSYR_{mat}$ are provided for all the variants considered in Table 2. The two methods for confidence interval estimation provide virtually identical results for $MSYR_{mat}$ for the base-case. All these results reflect high precision, but are based on point estimates of recruitment and M from the ADAPT VPA. When the imprecision of these last estimates is also taken into account, CV estimates increase markedly[9] – to 20% for $MSYR$ estimates, for example. Nevertheless the lower 5%-ile for $MSYR_{mat}$ remains notably large at 6.7%.

The second stage of this examination is even more preliminary, and considers what further changes in K after 1960 are necessary to have the modified BALEEN II model better reflect the post-1970 recruitment trends indicated by the ADAPT VPA assessment results. Clearly the large drop in recruitment for the base-case ADAPT assessment requires some decline in K after 1960 (the base-case choice for y_2 in Table 2). The further options considered are for this decline to continue to y_3 = 1980 or 1990, after which K again stays constant.

[9] The intervals calculated in this way are not strictly confidence intervals, as they do not take the imprecision arising from the fit of the modified BALEEN II model to a specific set of input values into account. However, as is evident from comparison of the results in Table 3, this source of imprecision is totally dominated by that related to the imprecision of the ADAPT VPA estimates of M and recruitment, so that these estimated intervals should be reasonably representative of the overall confidence interval, and hence are, for convenience, reflected as such in Table 3.

Table 3

Point estimates, bootstrap coefficients of variation and percentile method 95% confidence intervals (in square parentheses) for ten quantities of interest for the Area IV base-case analysis. A profile likelihood 95% confidence interval for $MSYR_{mat}$ is given in round parentheses. Results are shown both for analyses which ignore and which account for the imprecision in the ADAPT VPA estimates of recruitment and M.

Quantity	Point estimate	Ignore recruitment and M imprecision		With recruitment and M imprecision	
		CV	95% CI	CV	95% CI
K_2/K_1	10.79	0.041	[10.05 11.75]	0.491	[1.11 14.99*]
$MSYR_{mat}$	13.36	0.036	[12.36 14.32] (12.33 14.39)	0.197	[6.72 15.00*]
$MSYR_{1+}$	6.02	0.025	[5.70 6.32]	0.198	[3.34 6.70]
P^M_{68}/K^M_{68}	0.784	0.025	[0.742 0.819]	0.146	[0.600 0.997]
P^M_{83}/K^M_{83}	0.851	0.019	[0.817 0.879]	0.060	[0.729 0.932]
P^M_{95}/K^M_{95}	1.093	0.005	[1.084 1.103]	0.056	[0.904 1.149]
N^{1+}_{68}	80,131	0.006	[79,164 81,100]	0.332	[49,095 159,317]
N^{1+}_{95}	82,859	0.008	[81,886 84,317]	0.283	[61,583 160,059]
$N_{83,2}/N_{68,2}$	0.778	0.019	[0.752 0.808]	0.171	[0.563 1.122]
$N_{95,2}/N_{68,2}$	0.503	0.023	[0.483 0.529]	0.403	[0.176 1.012]

* Constraint boundary.

The results of this exercise are reported in Table 4a and also shown in Fig. 3. The choice $y3$ = 1980 reflects a marginally better fit. However $y3$ = 1990 seems biologically more realistic. Although difficult to establish any direct cause-effect relationship, it is not inconceivable that the carrying capacity for minke whales might have been decreasing over more recent decades, perhaps reflecting some combination of partial recovery of the larger baleen whale populations under protection, increases in other, possibly competing, predators (such as crabeater seals) or changes in the physical environment (IWC, 1997); but if so, a longer period for this decrease would seem more likely than this process having co e to a halt as early as 1980.

Results in Table 4a for the base-case ADAPT VPA assessment indicate that a drop of about 50% in K for minke whales since 1960 is necessary for the modified BALEEN II model to provide a satisfactory fit to the ADAPT recruitment trends. However, for the ADAPT variant for which absolute abundance estimates input are doubled, hardly any post-1960 change in K is necessary to provide a reasonable

Table 4

Summary statistics for fits of the modified BALEEN II model to the estimates of age 2 abundance (1944-1995) for minke whales in Area IV from ADAPT VPA. The analyses in this Table all assume that $MSYL_{mat}$ = 0.6, y_1=1930 and β=1. The row 'Observed' contains values for some of the summary statistics from the output of the ADAPT VPA analyses.

								P_y^M / K_y^M			N_y^{1+}		$N_{y,2} / N_{68,2}$	
y_2	y_3	K_2/K_1	K_3/K_1	$MSYR_{mat}$	$MSYR_{1+}$	$-\ell nL$	σ	1968	1983	1995	1968	1995	1983	1995
(a) Base-case recruitment estimates														
Observed											77,188*	57063	0.411	0.465
1960	1980	10.60	5.30	9.82 [8.09 11.53]	4.83	272.23	1,167	0.677	1.135	0.920	81,507	57,242	0.377	0.515
1960	1990	11.49	7.23	12.32 [10.83 14.03]	5.69	272.19	1,165	0.749	0.986	1.029	80,567	57,353	0.426	0.390
(b) 'Double abundance estimates' recruitment														
Observed											127,346*	130,939	0.525	0.615
1960	1980	11.35	12.80	13.92 [11.43 15.00+]	6.20	292.23	2,034	0.762	0.979	1.000	130,580	135,360	0.531	0.652
1960	1990	9.66	9.89	12.23 [10.87 14.80]	5.66	294.74	2,181	0.756	0.988	0.977	132,164	134,461	0.539	0.700

* The ADAPT VPA computes this quantity for ages up to 27 only.
+ Constraint boundary.

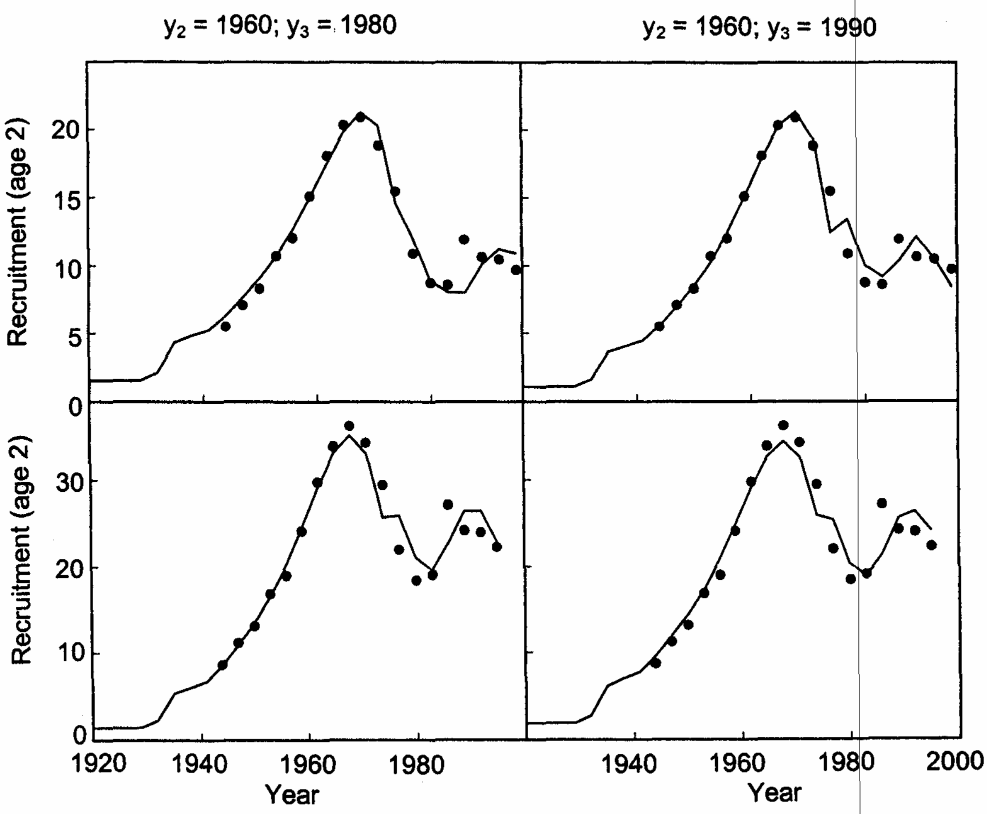

Fig. 3. Estimates of recruitment for minke whales in Area IV (age 2 abundance in thousands pooled into three-year groupings) based on ADAPT VPA assessments (solid dots) and on the results of fits of the BALEEN II model to the data (solid lines). Results are shown for fits to ADAPT VPA estimates based on two alternative analyses ('base-case' = upper panels and 'double abundance estimates' = lower panels), and for two alternative prescriptions for specifying the time-dependence in carrying capacity K, both of which have this first increasing from year y_1 = 1930 to year y_2, then decreasing to year y_3 after which it remains constant (the values for y_2 and y_3 are shown above the relevant panels).

fit (see Table 4b and Fig. 3). The results in Table 4 are reflective of $MSYR_{mat}$ estimates in the region of 10-14% (corresponding to $MSYR_{1+}$ of about 5-6%).

CONCLUSIONS

The most surprising result of what was conceived as no more than an exploratory exercise, is its substantial success as reflected by the good fits shown in Fig. 3, which are based only on relatively simple trends assumed for *K*. The base-case ADAPT VPA assessment results do require some downward trend in *K* in recent years to be fit adequately by the modified BALEEN II model, but the need for this adjustment is diminished if the quite plausible assumption of some negative bias in the IWC survey abundance estimates is admitted.

Thus, it seems that the post-1970 recruitment trends as estimated by the ADAPT VPA can largely (perhaps completely) be attributed to the effects of catches and super-compensation, and also that inferences can be drawn from these trends about likely values of *MSYR*.

ACKNOWLEDGEMENTS

The authors are appreciative of the comments of G. Stefansson (Marine Research Institute, Reykjavik, Iceland) and an anonymous reviewer on an earlier version of this paper.

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