MSYR - SHOULD THE INFORMATION WHICH HAS BECOME AVAILABLE SINCE SELECTIONS WERE MADE FOR RMP DEVELOPMENT IN 1987 HAVE CHANGED PERCEPTIONS ON THE LIKELY RANGE AND RELATIVE PLAUSIBILITIES OF VALUES FOR THIS PARAMETER FOR BALEEN WHALES?

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ABSTRACT

It is argued that continued attempts to estimate *MSYR* from accumulating data, to refine the plausible range of values for this parameter and relative plausibilities within this range, cannot be other than a crucial component of the process of development (and, in due course, refinement) of the Revised Management Procedure (RMP) and of the interpretation of the results of the associated *Implementation Simulation Trials* (*IST*s) for particular RMP applications. In 1987, when the range of *MSYR* values for RMP trials was first specified, four of the six independent sources of information available suggested definite "low" *MSYR* values (~1%). None of these four sources appears to have survived to the present. Estimates of *MSYR* for twenty populations have become available since 1987 - eleven based on population model fits and the balance on the relationship *MSYR* > *r*(0)/2. Two arguments advanced previously against the use of this last relationship are considered: the one is dismissed because it lacks support in empirical data, while the other appears negated by an analysis by Best (1993). In the fourteen cases where estimates of *MSYR* (in terms of uniform selectivity harvesting on the 1+ population) are determined with reasonable precision, most lie in the 2%-6% range, and only one of these has a lower 90 or 95% confidence/probability bound below 1%. Cases of low point estimates of *MSYR* show wide confidence intervals not incompatible with this 2-6% range. Thus, evidence forthcoming since 1987 (much of it subsequent to 1993 when the Scientific Committee last discussed this issue substantively) would seem to support a change in the Committee's perception at that time of the likely range of values for *MSYR* for baleen whale stocks, as well as informing judgments on the relative plausibilities of values within this range.

Note: This paper is an updated version of one with a similar title first presented 15 years previously: SC/44/O23. In 2003 it was updated (as SC/55/RMP10) to include information that had become available since the last occasion upon which the Scientific Committee had directly discussed the topic (IWC, 1994a), in particular as an aid to the determination of the relative plausibility of RMP *Implementation Simulation Trials* with differing *MSYR* values for the RMP *Implementation* for North Pacific minke whales under consideration at that time. It is further updated here to contribute to a review of the range of plausible *MSY* rates for baleen whales which the 2006 meeting of the Scientific Committee agreed be undertaken to inform the range to be used in management procedure evaluation (IWC, 2007a).

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INTRODUCTION

In 1987, when the Scientific Committee formally commenced development of the Revised Management Procedure (RMP), the first set of simulation trials developed encompassed *MSYR* values of 1% and 4% for an aggregated population model (IWC, 1989). During 1990, an *MSYR* value of 7% was added to this set; further, the aggregated model was changed to one with age-structure, and the decision was made that the *MSYR* values considered would apply to the mature (equivalent to recruited for the trials) component of the population (IWC, 1992a).

Since the RMP is intended to be robust to a wide range of possible dynamics for the resources to which it is applied, it is important to check that this range of *MSYR* values corresponds to that indicated by the available data. In particular, it seems pertinent to consider the evidence available in 1987 when the original 1%-4% range was chosen, and whether the status of this evidence has changed in the meantime. This paper attempts to outline such a consideration, together with a brief compilation of other information on *MSYR* which has become available since that time, and particularly since the Scientific Committee last discussed this issue in 1993 (IWC, 1994a), and further again briefly in 2003 in the context of the RMP *Implementation* for North Pacific minke whales (IWC, 2004, p.82-3).

The intent of this exercise is to provide a basis to assess whether the information forthcoming since 1987 is sufficient to warrant changing the perceptions at that time about *MSYR*, which were linked to the original *MSYR* range specified for the RMP trials. Clearly there may be differing opinions on the relevance of this to the RMP and its application. Holt (1992), responding to a further contribution by Best (1992) (later published as Best, 1993) on this subject, comments of this contribution that "while it recognises some of the difficulties of inferring *MSYR*s from increase rates of severely depleted stocks ... Best's paper addresses none of these substantively." Holt goes on to comment that: "The beauty of the approach to management [the RMP] launched by de la Mare .... is that [it] appeared to point a way out of the jungle of impossible parameter estimation... the Commission has accepted this approach ... if we now descend again into inconclusive arguments about ... parameter values, scientists may forfeit [the Commission's] trust."

It is perfectly true that the RMP differs philosophically from earlier approaches to management. It is structured to achieve performance that is reasonably robust to a wide range of alternative possible real situations, to take due account of inevitable uncertainties; it does not attempt to base catch limit recommendations on a "best" assessment (coupled perhaps to some *ad hoc* reduction for uncertainty), as was the case in the Scientific Committee in earlier years when, for example, implementing the NMP (New Management Procedure). Although the RMP's catch limit algorithm (IWC, 1994b) involves a Bayes-like *MSYR* estimation process, this does not mean that the primary aim of the procedure is to use the "best" current estimate of *MSYR* for the stock concerned.

However, it is certainly ***not*** true that the RMP has rendered the process of *MSYR* estimation redundant, as Holt's comments imply. Further, if, as his comments indicate, the Commission has this impression, this would seem to make it all the more important that the Scientific Committee endeavour to correct such a misapprehension. Reason for this is provided by Butterworth and Punt (1990), who show that the addition of an independent estimate of *MSYR*, even if relatively imprecise, can result in a substantial improvement in the performance of a whale stock management procedure. But a yet more important reason why Holt was incorrect relates to the robustness which the RMP seeks to achieve. It is impossible to design a procedure which is robust to every conceivable scenario. Some bounds have to be placed on the range of possibilities to which a procedure is to be robust, and these must sensibly be restricted to what can be defended as reasonably plausible, or such procedures will be rendered needlessly "inefficient" (a more "efficient" procedure is one which, for example, achieves a greater catch for the same perceived level of risk). Assessed procedure performance in a particular case is very sensitive to the plausibilities of possible different true values for *MSYR*; this is because perceptions of risks associated with the RMP have in the past all been based on trials for which the true *MSYR* of the stock harvested is 1% (in terms of the mature component of the population) (e.g. IWC, 1992b). Clearly therefore, it is important to consider whether such a value remains within the plausible range for this parameter, and even if it does, how plausible this value is when compared to others to be able to develop a realistic impression of risk.

Indeed, whether the Scientific Committee continues to hold the view that *MSYR*(mat)=1% is within the plausible range seems questionable, since it agreed in the context of the lowest value of *MSYR* that needed consideration in AWMP trials that *MSYR*(1+) = 1% was to be preferred to *MSYR*(mat) = 1%, as the former "more closely corresponded to biological reality" (IWC, 1998, p.87). At the time, AWMP attentions were focused primarily on the ENP gray and B-C-B bowhead populations, for which assessments had already indicated that *MSYR*(1+) clearly exceeded 1%, but recent use of this value as a lower bound for analyses for West Greenland minke whales reflects an extension to a population for which direct evidence on *MSYR* is lacking. Moreover, when considering results for RMP *Implementations* evaluated in more recent years, the *MSYR*(mat)=1% value has been retained, though accorded only a 'medium' plausibility ranking in comparison to *MSYR*(mat)=4% value accorded a 'high' ranking (IWC, 2004, p.83; IWC, 2007b).

Thus continued attempts to estimate *MSYR* from data, as they accumulate over time, to refine the plausible range and relative plausibilities of values for this parameter *cannot be other than a crucial component* of the process of development (and, in due course, refinement) of the RMP, and interpretation of the results of *Implementation Simulation Trials* (*IST*s) for particular applications, contrary to the implications of Holt's (1992) comments.

MSYR PERCEPTIONS IN 1987

Table 1 sets out the opinions which were current in 1987 concerning *MSYR* for baleen whales. Some of these estimates/inferences pertain to net recruitment rate, rather than to *MSYR per se*, and the *MSYR* estimates/inferences listed generally refer to the recruited components of the stocks concerned (having been based on analyses of CPUE data). This Table has been drawn from a more detailed compilation in Butterworth and Punt (1992a). It omits estimates for North Pacific Brydes and Southern Hemisphere sei whales which were each put forward on only one occasion, and do not appear to ever have been accorded particular import by the Scientific Committee.

There thus appear to have been one hypothesis and five substantive independent data-based sources for views on *MSYR* in 1987, two suggesting "high" values (~4%) and four indicating "low" values (~1%). Of the two "high" values, the gray whale result (3.7%) was fairly well established at that time, although Cooke (1986) had questioned the reliability of the increasing trend indicated by census estimates upon which this net recruitment rate value was based; what was less clear then was how the gray whale population size at that time might relate to the MSY level for that population. The estimate for Southern Hemisphere minke whales of 2-4%, based on analysis of catch-at-age data, was then in dispute, given counter-arguments at that time that these data were equally consistent with, for example, a lower net recruitment rate together with an increasing natural mortality with age.

Three of the sources of "low" *MSYR* values were linked to specific stocks. The details of the inference for Southern Hemisphere fin whales from the analysis of catch-at-age data from that fishery are not entirely clear (see discussion in Butterworth and Punt, 1992a). In contrast, the inferences for North Atlantic and North Pacific minke whales were strongly argued by Holt *et al*. (1986) on the basis of assessments conducted by the Scientific Committee using CPUE data for these stocks. Holt (1990) subsequently based much of "An opinion about MSY%" on discussion of estimates for the Northeast Atlantic minke whale population; while acknowledging that the estimates of *MSYR* obtained earlier had subsequently been shown to be of low precision and therefore meriting less weight, he went on to state that: "Nevertheless, there appears to be no reason why estimates so obtained would be biased downward."

The "no supercompensation" hypothesis (Holt, 1985) placed a generic upper bound on *MSYR*, whose value in a particular case depends on the value of the natural mortality *M*. Holt and Chapman, on the basis of results in Holt (1985), expressed the view that net recruitment rates (and hence *MSYR*) are likely to be less than 2% (IWC, 1985, p.42). Holt (1985) had argued that the data for the Southern Hemisphere fin whale did not contradict the "no supercompensation" hypothesis.

SUBSEQUENT CHANGES IN PERCEPTION OF 1987 *MSYR* EVIDENCE

In relation to the two instances of “high” *MSYR* in 1987, the most recent assessment of the Eastern North Pacific gray whale population was conducted by the Scientific Committee in 2002 (IWC, 2003a). Two slightly different versions of a Bayesian application of the Baleen II population model (see Punt *et al*., 2002 and Wade and Perryman, 2002) were considered, yielding *MSYR*(1+) estimates of 4.4% [3.0; 5.5] and 5.1% [3.0; 6.7] respectively (these are 90% probability intervals). If calf data were taken into account, these estimates decreased slightly.

For Southern Hemisphere minke whales, long-standing controversy about the potential utility of catch-at-age data in the assessment of these populations was seemingly resolved when in 1999 the Scientific Committee agreed that analyses presented (e.g. Butterworth *et al*., 1999) “show that parameters important for management (natural mortality, trends in recruitment) can be estimated from age data obtained from the catch” (IWC, 2000, p.27). Butterworth and Punt (1999) use the estimates of recruitment for minke whales for Area IV provided by the ADAPT-VPA fit of the model of Butterworth *et al*. (1999) (to catch-at-age data from the commercial fishery and JARPA programme, and also IDCR and JARPA abundance estimates) as input to a Baleen II population model which allows for changes in carrying capacity. This yielded an estimate of *MSYR*(1+) of some 6% (*MSYR*(mat) ~ 13%), which is reasonably robust to changes in a number of the assumptions of the model. These results were noted by the Scientific Committee, but without comment (IWC, 1998, p.101).

Updates of the ADAPT-VPA analyses of Butterworth *et al.* (1999), extending the JARPA data input to include subsequent surveys, are provided in Butterworth *et al.* (2002). For the conventional 3-year-3-age grouping of catch-at-age data under this approach, the assessment yielded historic annual rates of increase in recruitment as follows:

Area IV (1947 to 1968) : 4.4% [2.2; 7.8]
Area V (1950 to 1968) : 11.7% [5.4; 17.7]

Associated concerns raised in discussion of these analyses related to the fit to the age-distribution of older animals and the apparent absence of recent changes in biological parameters corresponding to recent estimated drops in the recruitment rate, are recorded in IWC (2002b).

Further work on this topic has seen the ADAPT-VPA approach applied to data on a 1-year-1-age basis and extended to incorporate internal estimation of the parameters of a stock-recruitment relationship (e.g. Mori *et al.*, 2007), and the development of a parallel approach based on statistical catch-at-age methodology (e.g. Punt and Polacheck, 2007). For reference cases for the I-stock (Areas IIIE+IV+VW), both approaches yield *MSYR*(1+) of about 5.5%; estimation is less reliable for the P-stock (Areas VE+VIW) and yields reference case results of 3.6% for the ADAPT-VPA and 2.6% for statistical catch-at-age. However, the estimation of *MSYR* using these approaches is heavily reliant on the catch-at-age data from the period of commercial whaling, concerning which some problems have recently been identified and agreed to require resolution (IWC, 2007c).

The multi-species modeling of the Antarctic ecosystem by Mori and Butterworth (2006) suggests that per capita growth rates (equivalent to sustainable yield rates) for Antarctic minke whales reached 10% for the Atlantic-Indian sector of their model, and 2% for the Pacific.

Past estimates of *MSYR* for the Northeast Atlantic minke whale population have been based on input of a CPUE series for whaling in the Barents Sea. Two different analyses of the CPUE data (Schweder and Volden, 1994 and Cooke, 1993) yield different trends, and the Scientific Committee has not resolved which analysis is to be preferred. Butterworth and Punt (1995) carried out HITTER analyses based upon these two series and the then agreed 1+ population estimate from a 1989 survey of this stock of 86 736. This yielded *MSYR*(1+) estimates of 6.1% [2.1; 11.5] and 1.1% [0.0; 3.7] respectively, for the standard variant of HITTER which assumes density-dependent fecundity. Hence, even if the Cooke CPUE analysis is used, *MSYR*(1+) is not restricted to fall below an *MSYR*(rec) value of 2% as perceived in 1987. The Scientific Committee did not discuss these results.

These analyses are updated in the Appendix to this paper, which applies FITTER to a combination of estimates of absolute abundance from recent surveys and new standardizations of older and now also recent CPUE series, where these analyses cover an area greater than the Barents Sea alone.. The results suggest an *MSYR*(1+) estimate of 1.9% with approximate 95% confidence interval of [0.1; 3.8].

For the North Pacific minke whales, earlier estimates of *MSYR* for the Okhotsk-Sea – West Pacific (“O”) stock lapsed in 1991 when agreement was reached in the Scientific Committee that no suitable series of relative abundance data (from which *MSYR* might have been estimated) were available. For the Sea of Japan – Yellow Sea – East China Sea (“J”) stock, a CPUE series has been used previously to condition RMP *IST*s, and this could potentially have been used to provide an estimate of *MSYR*. In 2000, an extension of this CPUE data set to include more years yielded to an overall downward trend which was not as appreciable as indicated beforehand; the Scientific Committee decided not to use this series further, recalling “that the use of CPUE as an index of abundance for whales is seldom considered reliable and accepted as a basis for estimating abundance in the Committee", though Hatanaka and Kim recorded dissenting views (IWC, 2001a, p.94 and p.7 respectively).

A further "low" *MSYR* inference from 1987 is that by Chapman relating to Southern Hemisphere fin whales (IWC, 1984, p.84), which he developed from the catch-at-age analysis of Clark (1982). Subsequently Clark (see Butterworth and Punt, 1992a) advised that the method developed by Sampson (1990) for analyzing data from this fin whale population was superior. Sampson later commented that his results "were consistent with sustainable yield rates in the range of values from below zero to 5% per year" (IWC, 1994a, p.183).

The final basis for the "low" *MSYR* inference in 1987 was the "no supercompensation" hypothesis. While the current status of this hypothesis is formally "unclear" (Butterworth and Punt, 1992a, Table 1), it has not been re-raised in more than fifteen years in the Scientific Committee as a suggested basis upon which to draw inferences about *MSYR*

Thus none of four bases (in 1987) for inferring that *MSYR* definitely had a "low" value (at least for some populations) appear to have survived.

POST-1987 INFORMATION FOR OTHER SPECIES/STOCKS

MSYR estimates obtained for other species/stocks since 1987 fall into three categories:

(a) those based on population model fits to relative and absolute abundance data,

(b) inferences drawn from growth rates of depleted stocks using the *MSYR* > *r*(0)/2 relationship developed by Butterworth and Best (1990) [where *r*(0), the per capita growth rate in the zero population size limit, is estimated from a time series of resource abundance data at low population size], and

(c) information on population growth where the status of the population or of the information is unclear for one or other reason.

A difficulty that arises is the more recent use of Bayesian estimation methodology in population model fits. The purpose of this paper is (ideally) to document *independent* estimates of *MSYR* for specific populations; if priors based on results for other populations have been used, a false impression may be given. Even if a supposedly non-informative prior is used (e.g. U[0; 10%]), the result can be misleading as a posterior median estimate of some 5% would follow even if the data failed to meaningfully update the prior. This is not an issue for cases which are "rich" in data that inform on population trend, such as Eastern North Pacific gray whales (above) and Bering-Chukchi-Beaufort Seas bowheads (below). However it can be important for some of the recent assessments of Southern Hemisphere humpback breeding populations for which such data are limited. Thus summaries below will endeavour to draw attention to Bayesian estimates of *MSYR* heavily influenced by priors, and in these Southern Hemisphere humpback cases also show results for the *MSYR* > *r*(0)/2 relationship using only the available trend data (where this might refer to a population some way above minimal abundance and hence subject to some density dependence, this means that the resultant *MSYR* estimate is even further negatively biased).

The summaries below of analyses of individual stocks refer in the main only to the most recent analysis available, rather than to all analyses conducted since 1987, in the interests of brevity. All *MSYR* estimates quoted hereafter in this paper will refer to uniform selectivity harvesting on the total (1+) population, unless otherwise indicated.

Confidence/probability intervals shown (in square parenthesis) are 95% intervals unless otherwise stated.

Population Model Fits (see Table 2a)

(i) *East Greenland-Iceland fin whales*

Gunnlaugsson *et al.* (1989) first drew attention to the implications of the 1915 banning of catches of fin whales from land stations in Iceland for likely population trajectories, and hence *MSYR* values, for this population. The Special Meeting on North Atlantic fin whales in 1991 (IWC, 1992c) considered a variety of assessments of this resource, but could not reach agreement on inferences for *MSYR* values.

Butterworth and Punt (1992b), in a subsequent extension of an analysis, using the HITTER-FITTER formulation of the Baleen II population model (de la Mare, 1989; Punt, 1996) that was first presented to that Special Meeting, addressed a number of the issues which the Meeting left unresolved. They concluded that despite indications of model mis-specification (which rendered confidence interval estimation problematic) and other uncertainties, certain features of the assessment results nevertheless appeared to be robustly estimated, unless all the CPUE data and the history of the fishery in the early decades of the 20th century were to be completely disregarded. These features included an *MSYR* value unlikely to be less than 3%.

More recently, in a submission to the NAMMCO Scientific Committee, Butterworth and Cunningham (2000) show that the apparent incompatibility of the CPUE series and survey estimates of abundance for this population can be resolved by modeling it as two sub-stocks with identical *MSYR* values and diffusive mixing, where all the catches have been taken from the sub-stock nearer the coast of Iceland. Estimating mixing rates within the framework of an age-aggregated model leads to an estimated *MSYR*(1+) of 3.4% [1.0; 17.6]. If the mixing rate is set to zero, *MSYR*(1+) is estimated with much greater precision: 5.2% [5.1; 5.6].

This work was extended by Branch and Butterworth (2006) who applied an age-structured model comprised of four sub-populations with movement among them, which was fitted to mark-recapture as well as CPUE indices and sighting survey abundance estimates. The resultant maximum likelihood estimate of MSYR(1+) was 1.7% with approximate 95% confidence interval [1.0; 2.9]. While no firm conclusions have been drawn from this exercise by the Scientific Committee, it was noted that such compartmentalized models did fit the data better than those for a single homogeneous stock (IWC, 2007b).

(ii) *Bering-Chukchi-Beaufort Seas bowhead whales*

Considerable debate took place during the 1990s concerning the best method to assess this population, with a number of variants of a Bayesian approach which takes account of biological as well as abundance and past catch data being pursued. The Scientific Committee in 1999 agreed an assessment using a “backwards” Bayesian approach which yielded an *MSYR* estimate of 2.5% [1.4; 4.1] (IWC, 1999). Equal weight was given at that time to the results from a “full pooling” Bayesian approach. Unfortunately it is not possible to quote the *MSYR* estimate for this approach because the pertinent Appendix 5 of IWC

(1999) was omitted from the final printed version. However, the close similarity between corresponding results quoted in IWC (1999) for the "backwards" and "full pooling" approaches suggests that the estimates of *MSYR* they provide would hardly differ. Subsequent work to develop a *Strike Limit Algorith*m for this population has been based on the "backwards" approach.

Punt and Butterworth (2000) put forward a "bounded maximum likelihood" method for assessment of this population, which results in a higher estimate of *MSYR*(1+) of 4.0% [1.9; 5.5]. The most recent assessment presented to the Scientific Committee is that by Brandon and Wade (2006), which uses a Bayesian approach. Their reference case for the "backwards" method for the entire population trajectory since 1848 yields an MSYR(1+) of 3.3% with 90% credibility interval of [1.9; 4.8].

(iii) *Southern Hemisphere humpback whales*

In the first version of this paper, the survey-based estimates of growth for the West and East Australian populations of humpbacks (breeding stocks BSD and BSE respectively) were treated as estimates of this rate at very low abundance ($r(0)$). However, modeling studies by Johnston and Butterworth (2002) suggested that BSD in particular might currently be approaching intermediate levels relative to pristine, so that these two stocks are now more appropriately listed under the "population model fit" category.

Johnston and Butterworth (2002) apply a two (coastal) breeding stock model with mixing on the Antarctic feeding grounds, within an age-aggregated population modeling framework. They fit to coastal survey and JARPA estimates of abundance and CPUE data, together with recent target population sizes derived from the coastal surveys. Variant 1 of the approach yields *MSYR*(1+) estimates of 8.3% and 8.9% for BSD and BSE respectively

More recently, this framework has been extended to a Bayesian form. Recent applications for BSA, BSC1, BSD, BSE and BSG are reported in Table 2a and yield point estimates of *MSYR*(1+) ranging from 4.3 to 8.6%. However the results for BSG, and to lesser extents BSA and BSD are influenced by the choice of prior, and furthermore assessments of BSE are currently on hold pending clarification of sub-stock structure within this complex,

$\underline{MSYR > r(0)/2}$ (see Table 2b)

MSYR estimates obtained from the application of this relationship to increase rate estimates from survey series for nine highly depleted stocks of right, blue and gray whales, are given in Table 2b. These estimates are negatively biased because the relationship involves an inequality. The $r(0)$ estimates used for these computations are taken directly from observed population growth rates for the three right whales cases. For four of the five blue and pygmy blue populations considered, the growth rate estimates for each stock separately have been updated by the use of Bayesian meta-analysis (Branch *et al*., 2004). For the fifth (Southern Hemisphere blue whales), the result of Branch *et al*. (2004) from an exponential model fitted to abundance time series with a uniform prior on the rate of increase is quoted. It should however be noted that Holt (1992) has questioned the reliability of the estimate of the growth rate of the West Iceland blue whales by Sigurjonsson and Gunnlaugson (1990) used to obtain the estimate for that population in Table 1, on the grounds of confounding through changes in the location of the whaling grounds. The gray whale trend list is based on photo-id studies.

Table 2b includes results for four Southern Hemisphere humpback whale breeding stocks using increase rates derived from data for those populations alone so as not to be influenced by the *MSYR* prior chosen. The resultant estimates are generally only slightly less than the comparative values from the model fits in Table 2a.

When this approach for drawing inferences about *MSYR* was discussed by the Sub-Committee on Biological Parameters and MSY Rates at the 1989 Annual Meeting of the Scientific Committee (IWC, 1990), two objections were raised. The first involved the assumption of "convexity" of the net recruitment function $r(N)$ with population size N, upon which the $MSYR > r(0)/2$ bound is based. The bound requires only that $r''(N) < 0$ for $N < MSYL$, and holds for any functional form for $r(N)$ that satisfies this constraint, which Butterworth and Best (1990) argued from the empirical study by Fowler (1981). The counter argument to this was that populations could exhibit "hypercompensation" at low population levels - i.e. rates of increase at these levels which are substantially higher than would be suggested by extrapolation from rates at intermediate population levels (the definition provided by Fowler and Baker, 1991)[3]. It was further suggested that spatial variation in the environment could produce such an effect. De la Mare and Cooke (1992) developed a specific model incorporating this effect. They showed that this model exhibits hypercompensation, and that there are some quantitative differences between the growth rate of a protected resource and its sustainable yield rate, as functions of population size. MacCall and Tatsukawa (1994) addressed this question in the context of a “basin” model (McCall, 1990), and showed that even if the habitat is such that $r(N)$ is convex everywhere for the local habitat, $r(N)$ for the population as a whole need not be convex. However, these authors and others noted that if habitat selection is weakened by diffusive behaviour, the overall $r(N)$ would move towards its local form, and the Scientific Committee agreed that such theoretical modeling is insufficient to determine whether the overall $r(N)$ is concave or convex (IWC, 1994a, p.186).

It thus seems that the counter-argument of hyper-compensation remains essentially speculative in nature, and this raises a fundamental question of principle: to what extent can speculative arguments be entertained as bases for conclusions to be drawn by (or to be contested in) the Scientific Committee? If no bounds are placed on speculation, the drawing of agreed inferences by the Scientific Committee self-evidently becomes an impossibility. This point is of particular import in regard to the RMP and associated *IST*s. If no bounds are placed on speculation in the exercise of specifying the scenarios to which RMP *Implementations* are required to be robust, finding a generally acceptable *Implementation* necessarily becomes an impossibility. Clearly the question of assigning relative plausibilities when speculative arguments are advanced must arise. Indeed the Scientific Committee has in recent years moved in this direction for RMP *Implementations* (e.g. IWC, 2004)

The authors assert that the counter-argument of hypercompensation must have some basis in data before it can be considered acceptable/plausible. Fowler and Baker (1991) conducted an extensive literature review of animal population dynamics at extremely reduced population levels. While they found considerable evidence for the

[3] Further discussion on these empirical results in IWC (1994a), pp.184-5, should be noted. Further analyses by Fowler (1994) and by de la Mare (1994) yielded differing results concerning the sign of the second derivative with respect to N of factors contributing to $r(N)$. However, no agreement was reached in the Scientific Committee as to which analysis was more appropriate, and consequently on whether $r(N)$ tended to be convex.

reverse effect of depensation (the "Allee effect" of *reduced* growth rates at low population sizes), they uncovered not one single reported instance of hypercompensation. They add further that: "both theory and empirical information indicate that rates of increase for large mammals approach their maxima as populations are reduced only moderately below natural or pre-exploitation equilibrium."

Not all members of the Scientific Committee were persuaded by their arguments 14 years ago[3]. What further empirical evidence for whales has become available in the intervening period to address this question? Although populations of southern right whales have maintained their relatively high rates of increase (Bannister 2001, Best *et al*. 2005, Cooke *et al.* 2003), these populations likely remain well below their *MSYL*'s so that the possibility that they could still be in a hyper-compensation mode is not excluded. However, Johnston and Butterworth's (2005, 2007a) assessments of Southern Hemisphere humpback BSC1, BSD and BSE indicate that these are now recovered to intermediate levels without any evidence of hyper-compensation forthcoming in the form of a large recent reduction in growth rate.

The second objection expressed in IWC (1990) to estimates provided by the *MSYR* > *r*(0)/2 relationship, related to the validity of the practice of using estimates for other species or stocks on the basis of inter-stock and inter-specific analogy. Specifically, Cooke noted that the list of recovery rates then available could be self-selecting, arguing essentially that only stocks which were recovering rapidly would be large enough to have been monitored. Butterworth responded at that time that Cooke's self-selection hypothesis was more or less plausible depending on whether the number of such stocks whose increase rates had been estimated, was high or low compared to the number which were either being monitored but for which trends had not yet been estimated, or could potentially be monitored but had not been. He suggested that advice in this regard would be of assistance in assessing the pertinence or otherwise of Cooke's argument.

The review by Best (1992, 1993) sought specifically to resolve this point, which was left open by the Sub-Committee's discussions in 1989. Best (1993) listed a total of 26 stocks of baleen whales which were severely depleted and were also feasible to monitor. Of these, twelve had been or were being monitored and statistically significant rates of increase had been demonstrated for ten of these. At least 10 of the 16 stocks which could be monitored for which a significant rate of increase had not been demonstrated, were nevertheless believed to be increasing. Thus, in total: "at least 77% of monitorable stocks are either believed or demonstrated to be increasing" (Best, 1993).

Cooke's self-selection hypothesis seems inconsistent with Best's results. However, in further discussion of this matter in the Scientific Committee (IWC, 1994a, p.183) no consensus was reached. Concern was expressed that monitorable stocks included primarily coastal species, thus not including highly pelagic species such as minke whales. Interestingly the "continued rarity" of Southern Hemisphere blue whales was one of two examples cited at that time to support this counter-argument; subsequent data (Branch *et al*., 2004; Rademeyer *et al*., 2003) now show this population to be increasing relatively rapidly.

Other information on population growth (see Table 2c)

Under this heading first two population (complexes) are listed which do not fit readily under the headings above for the reasons indicated below.

(i) *North Atlantic humpbacks*

Efforts to link abundance and catch data from breeding and feeding aggregations in the North Atlantic under a single model incorporating mixing of breeding populations on the feeding grounds (in a similar manner to the approach of Johnston and Butterworth (2002) discussed above for the Southern Hemisphere humpback BSD and BSE populations) have unfortunately not yet proved particularly successful (IWC, 2003c). For this reason, all that has been done in Table 1 is to list estimates of growth rates for certain components of this complex that have effectively served as inputs to these modeling attempts. It is difficult to relate these rates to *MSYR* estimates as the levels of these populations relative to pristine are unclear, given the current failure of the modeling exercise. The three estimates are of 11.4% from aerial surveys in Icelandic coastal waters over 1986 to 2001 (Gunnlaugsson and Vikingsson, 2002), 3.1% from the West Indies over 1979-92 (Stevick *et al*., 2001) and 6.3% from the Gulf of Maine over 1979-1991 (Friday *et al*., 2002). The first mentioned rate is similar to an estimate of 11.6% from sightings recorded by whalers in Icelandic waters over 1970-1988, but some have suggested that this trend includes a contribution from immigration (IWC, 2003c).

(ii) *Northwest Atlantic right whales*

IWC (2001b) p.69 reports that an estimated growth rate for this heavily monitored population declined from +3% to –2% over the period from 1980 to 1995. This is linked to a decrease in survival rate and increase in calving interval from the 1980s to the 1990s: presumably as a result of a combination of anthropogenic factors (e.g. ship strikes) and habitat degradation. This information is difficult to interpret in the context of *MSYR*, a concept linked to the assumption of a per-capita growth rate r which is a function of population size N only, and generally declines with N. Clearly this population is at a low level, but the increase in calving interval shows that more than simple density dependent mechanisms must be playing a role in impacting growth rate in this case. This calving interval has however recently increased again to 3.2 years (North Atlantic Right Whale Consortium, 2006).

In addition to the estimates of past population growth rate for minke whales mentioned above, the Mori and Butterworth (2006) multi-species model of the Antarctic ecosystem indicates growth rates for all of blue, fin and humpback whales reaching some 10%.

Population growth rates for a number of species can be developed from the survey estimates of abundance from the JARPA and JARPN research programmes, but the abundance estimates for JARPA await refinement before they might be accepted by the Scientific Committee (IWC, 2007c).

OTHER COMMENTS

Two general arguments referenced above that have been advanced to rebut inferences made concerning *MSYR* are that r''(N) may not be negative for all $N < MSYL$ (hence invalidating the bound $MSYR > r(0)/2$), and that interspecies comparisons have questionable utility (IWC, 1994a, p.185).

Regarding the first of these arguments, it is important to note that the assumption that $r(N)$ is convex underlies the conventional assumption for baleen whale stocks that $MSYL = 0.6\ K$, and from that the choice of 0.54 as the “protection” level (Butterworth and Best, 1994). If indeed $r(N)$ was not convex, then the choice of 0.54 K needs to be revised downwards.

Furthermore, attitudes to the acceptability of inter-species comparisons as a basis to aid demographic parameter estimation seem to be changing of late in the marine population dynamics field, with increasing use of techniques such as hierarchical Bayes meta-analysis in fisheries (e.g. Hilborn and Lierman, 1998; Myers *et al*., 2002). The use of Bayesian approaches has gained acceptability in the Scientific Committee over the last decade, with assessments based on this approach being accepted for both bowhead and gray whales (e.g. IWC, 1999, 2003a). Prior distributions for biological parameters in such Bayesian analyses are developed essentially under the assumption that inter-species comparisons are acceptable and do have utility.

Cooke (2004) raises the question of the reliability of (essentially indirect, as in many cases above) estimates of *MSYR* in circumstances where K may be changing over time, and how indicative such estimates might be of genuinely sustainable levels of harvest. This matter merits further discussion, including consideration of the different ways in which K and *MSYR* might inter-relate in this situation, but it should be noted that the RMP has been shown to demonstrate robust performance in such circumstances.

CONCLUSIONS

In 1987, when the *MSYR* range for the RMP trials was first specified, there were four independent sources of information which pointed to "low" *MSYR* values (~1%), and only two (one of which was disputed) pointing to "high" values (~4%). Subsequent to that time, it seems that none of the four indications of definite low values have survived (having been either agreed to be rejected, updated or lapsed).

Since 1987, new evidence on *MSYR* has been forthcoming from population model fits for eleven stocks, and from application of the $MSYR(1+) > r(0)/2$ relationship to nine depleted stocks for which estimates of increase rates are now available. The resultant point estimates for *MSYR*(1+) are mainly in the 2%-6% range in the fourteen cases[4] for which these estimates are now available with relatively small confidence intervals, the lowest of these point estimates being 1.5% and the highest 8.6%. Only in one of these cases does the lower 90 or 95% confidence limit fall below 1%. Cases of low point estimates for *MSYR* have wide confidence intervals not incompatible with the 2-6% central range indicated above. As would be expected with the acquisition of further data over the past decade, the precision of specific estimates has improved. Of the two arguments against use of the $MSYR > r(0)/2$ relationship as a basis for inference, one is based on speculation with no supporting empirical evidence, while the other seems difficult to reconcile with the results of Best (1993).

Accordingly, it seems that considerable evidence has been forthcoming since 1987 (much of it subsequent to the Scientific Committee's last substantial discussion of this issue in 1993 (IWC, 1994a)) which would support a change in the Scientific Committee's perception of the plausible range of values for *MSYR* for baleen whale stocks, and relative plausibilities within this range.

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[4] ENP gray; two SH minke; NE Atlantic minke; EGI fin; B-C-B bowhead; Southern Hemisphere humpback BSC1, BSD and BSE; SA, Argentine and West Australian right; West Iceland blue; and WN Pacific gray.

REFERENCES

Bannister, J.L. 2001. Status of southern right whales (*Eubaleana australis*) off Australia. *J. Cetacean Res. Manage* (Special Issue) 2: 103-110.

Best, P.B. 1992. Increase rates in severely depleted stocks of baleen whales. Document SC/F92/Mg3 presented to the Special Meeting of the Scientific Committee on the Revised Management Procedure, Copenhagen, 2-6 March 1992 (9pp).

Best, P.B. 1993. Increase rates in severely depleted stocks of baleen whales. *ICES J. Mar. Sci*. 50: 169-86.

Best, P.B., Brandão, A. and Butterworth, D.S. 2005. Updated estimates of demographic parameters for southern right whales off South Africa. Document SC/57/BRG2 presented to the IWC Scientific Committee.

Branch, T.A., Matsuoka, K. and Miyashita, T. 2003. Evidence for increases in Antarctic blue whales based on Bayesian modeling. *Marine Mammal Science* 20(4): 726-54.

Branch, T.A. and Butterworth, D.S. 2006. Assessment of the East Greenland-Iceland fin whale population using a four-area model. Unpublished document presented to the Joint North Atlantic Marine Mammal Commission (NAMMCO)/International Whaling Commission (IWC) Scientific workshop on the catch history, stock structure and abundance of North Atlantic fin whales, Reykjavik, Iceland, 23-26 March 2006. SC/14/FW/23 and SC/M06/FW23. (33pp)

Brandon, J.R. and Wade, P.R. 2006. Assessment of the Bering-Chukchi-Beaufort seas stock of bowhead whales using Bayesian model averaging. *J. Cetacean Res. Manage*. 8(3): 225-39

Brown, M.R. Field, M.S., Clarke, E.D., Butterworth, D.S. and Bryden, M.M. 1997. Estimates of abundance and rate of increase for East Australian humpback whales from the 1996 land-based survey at Point Lookout, North Stradbroke Island, Queensland. Document SC/49/SH35 presented to the IWC Scientific Committee. (15pp.)

Butterworth, D.S. and Best, P.B. 1990. Implications of the recovery rate of the South African right whale population for baleen whale population dynamics. *Rep. int. Whal. Commn* 40: 433-47.

Butterworth, D.S. and Cunningham, C.L. 2000. Assessment of the East-Greenland-Iceland fin whale population based upon a two sub-stock model with mixing. NAMMCO document SC/8/FW/6 (15pp).

Butterworth, D.S. and Punt, A.E. 1990. The effects of different tunings of control parameters and of an independent estimate of *MSYR* on the performance of the Punt-Butterworth whale stock management procedure. Revised IWC document SC/J90/Mg1+Mg3, in press.

Butterworth, D.S. and Punt, A.E. 1992a. The Scientific Committee ... 'agreed that the MSY rate would most likely lie between 1 and 4%' - but which MSY rate? *Rep. int. Whal Commn* 42: 583-91.

Butterworth, D.S. and Punt, A.E. 1992b. Assessments of the East Greenland-Iceland fin whale stock. *Rep. int. Whal. Commn* 42: 671-96.

Butterworth, D.S. and Best, P.B. 1994. The origins of the choice of 54% of carrying capacity as the protection level for baleen whale stocks, and the implications thereof for management procedures. *Rep. int. Whal. Commn* 44: 491-7.

Butterworth, D.S. and Punt, A.E. 1995. Implications of different values of g(0) for the dynamics of the Northeast Atlantic minke whales. Document SC/47/NA13 submitted to the 1995 Annual Meeting of the IWC Scientific Committee (10pp).

Butterworth, D.S. and Punt, A.E. 1999. An initial examination of possible inferences concerning MSYR for Southern Hemisphere minke whales from recruitment trends estimated in catch-at-age analyses. *J. Cetacean Res. Manage*. 1(1): 33-39.

Butterworth, D.S., Punt, A.E., Geromont, H.F., Kato, H. and Fujise, Y. 1999. Inferences on the dynamics of Southern Hemisphere minke whales from ADAPT analyses of catch-at-age information. *J. Cetacean Res. Manage*. 1(1): 11-32.

Butterworth, D.S., Punt, A.E., Branch, T.A., Fujise, Y., Zenitani, R. and Kato, H. 2002. Updated ADAPT VPA recruitment and abundance trend estimates for Southern Hemisphere minke whales in Areas IV and V. Document SC/54/IA25 submitted to the 2002 Annual Meeting of the IWC Scientific Committee (20pp).

Clark, W.G. 1982. Historical rates of recruitment to Southern Hemisphere fin whale stocks. *Rep. int. Whal. Commn* 32: 305-24.

Cooke, J.G. 1986. On the net recruitment rate of gray whales with reference to inter-specific comparisons. *Rep. int. Whal. Commn* 36: 363-6.

Cooke, J.G. 1993. Further analysis of minke whale CPUE in the Northeast Atlantic with estimates of yield rates. Document SC/45/NA7 presented to the April 1993 meeting of the IWC Scientific Committee (18pp).

Cooke, J.G. 2004. Inferences on maximum sustainable yield rates of baleen whale populations. Appendix 6 of the Report of the sub-committee on the Revised Management Procedure. J. Cetacean Res. Manage. 6(Suppl.): 98-9.

Cooke, J.G., Rowntree, V.J. and Payne, R. 2003. Analysis of intra-annual variation in reproductive success of South Atlantic right whales (*Eubalaena australis*) from photo-identification of calving females observed off Peninsula Valdéz, Argentina. Document SC/55/O23 presented to the IWC Scientific Committee.

Cooke, J.G., Weller, D.W., Bradford, A.L., Burdin, A.M. and Brownell, R.L. 2006. Population assessment of the western gray whales in 2006. Document SC/58/BRG30 presented to the IWC Scientific Committee.

de la Mare, W.K. 1989. Report of the Scientific Committee, Annex L. The model used in the Hitter and Fitter programs. *Rep. int. Whal. Commn* 39: 150-1.

de la Mare, W.K. and Cooke, J.G. 1992. Some implications of biogeographical factors for the management of whale stocks. Document SC/F92/Mg13 presented to the Special Meeting of the Scientific Committee on the Revised Management Procedure, Copenhagen, 2-6 March 1992 (8pp).

de la Mare, W.K. 1994. Some analyses of the dynamics of reduced mammal populations. *Rep. int. Whal. Commn* 44: 459-466.

Donovan, G.P. 1984. Blue whales off Peru, December 1982, with special reference to pygmy blue whales. *Rep. int. Whal. Commn* 34: 473-6.

Findlay, K. and P. Best. 2006. The migration of humpback whales past Cape Vidal, South Africa, and a preliminary estimate of the population increase rate. Document SC/A06/HW16 submitted to the IWC southern hemisphere humpback workshop, Hobart, April 2006.

Fowler, C.W. 1981. Density dependence as related to life history strategy. *Ecology* 62(3): 602-10.

Fowler, C.W. and Baker, J.D. 1991. A review of animal population dynamics at extremely reduced population levels. *Rep. int. Whal. Commn* 41: 545-54.

Fowler, C.W. 1994. Further consideration of nonlinearity in density dependence among large mammals. *Rep. int. Whal. Commn* 44: 385-91.

Friday, N.A., Punt, A.E. and Smith, T.D. 2002. An expanded framework for the assessment of North Atlantic humpback whales, with illustrative examples. Document SC/54/H1 submitted to the 2002 Annual Meeting of the IWC Scientific Committee (?pp).

Gunlaugsson, T., Magnusson, K.G. and Sigurjonsson, J. 1989. Stock trajectories for the East Greenland/Iceland fin whale stock based on revised catch statistics, 1883-1987. *Rep. int. Whal. Commn* 39: 267-75.

Gunnlaugsson, T. and Vikingsson, G.A. 2002. Trends in humpback whale (*Megaptera novaeangliae*) sighting rates from aerial surveys in Icelandic waters during 1996-2001. Document SC/54/H6 submitted to the 2002 Annual Meeting of the IWC Scientific Committee (?pp).

Hilborn, R. and Liermann, M. 1998. Standing on the shoulders of giants: learning from experience in fisheries. *Rev. Fish. Biol. and Fisheries* 8: 273-83.

Holt, S.J. 1985. The classification of whale stocks and the determination of catch limits, under the current IWC management procedure, with limited information. *Rep. int. Whal. Commn* 35: 487-94.

Holt, S.J. 1990. Are measurements of increase rates of depleted stocks useful in estimating MSY rate? *Rep. int. Whal. Commn* 40: 517-24.

Holt, S.J. 1992. Comments on SC/F92/Mg2, SC/43/O15+O8 and SC/F92/Mg3. Document SC/F92/Mg11 presented to the Special Meeting of the Scientific Committee on the Revised Management Procedure, Copenhagen, 2-6 March 1992 (9pp).

Holt, S.J., Chapman, D.G., Lankester, K., de la Mare, W.K. and Cooke, J.G. 1986. Minority statement concerning Item 11.2.6. *Rep. int. Whal Commn* 36: 138.

Holt, S.J. 1992. Increase in blue whales in the Denmark strait. Document SC/44/O28 submitted to the 1992 Annual Meeting of the IWC Scientific Committee (8pp).

International Whaling Commission. 1984. Report of the Scientific Committee. *Rep. int. Whal. Commn* 34: 32-181.

International Whaling Commission. 1985. Report of the Scientific Committee. *Rep. int. Whal. Commn* 35: 31-152.

International Whaling Commission. 1986. Report of the Scientific Committee. *Rep. int. Whal. Commn* 36: 30-140.

International Whaling Commission. 1989. [Report of the] Comprehensive Assessment Workshop on Management. *Rep. int. Whal. Commn* (special issue 11): 21-8.

International Whaling Commission. 1990. Report of the sub-committee on North Atlantic minke whales. *Rep. int. Whal. Commn* 41: 132-71.

International Whaling Commission. 1991. Report of the sub-committee on biological parameters and MSY rates. *Rep. int. Whal. Commn* 40: 119-30.

International Whaling Commission. 1992a. Report of the Fourth Comprehensive Assessment Workshop on Management Procedures. *Rep. int. Whal. Commn* 42: 305-34.

International Whaling Commission. 1992b. Report of the Sub-Committee on Management Procedures. *Rep. int. Whal. Commn* 42: 87-136.

International Whaling Commission. 1992c. Report of the Comprehensive Assessment Special Meeting on North Atlantic Fin Whales. *Rep. int. Whal. Commn* 42: 595-644.

International Whaling Commission. 1994a. Report of the Working Group on MSY Rates. *Rep. Int. Whal. Commn* 44:181-9.

International Whaling Commission. 1994b. The Revised Management Procedure for baleen whales. *Rep. int. Whal. Commn* 44: 145-52.

International Whaling Commission. 1996a. Report of the Scientific Committee. *Rep. int. Whal. Commn* 46: 51-97.

International Whaling Commission. 1996b. Report of the sub-committee on Southern Hemisphere baleen whales. *Rep. int. Whal. Commn* 46: .117-38.

International Whaling Commission. 1997. Report of the Scientific Committee. *Rep. int. Whal. Commn* 47: 59-112.

International Whaling Commission. 1998. Report of the Scientific Committee. *Rep. int. Whal. Commn* 48: 55-118.

International Whaling Commission. 1999. Report of the Sub-Committee on Aboriginal Subsistence Whaling. *J. Cetacean Res. Manage.* 1(Suppl.): 179-94.

International Whaling Commission. 2000. Report of the Scientific Committee. *J. Cetacean Res. Manage*. 2(Suppl.): 1-65.

International Whaling Commission. 2001a. Report of the Scientific Committee. *J. Cetacean Res. Manage.* 3(Suppl.): 1-374.

International Whaling Commission. 2001b. Report of the Workshop on Status and Trends of Western North Atlantic Right Whales. *J. Cetacean Res. Manage*. (Special Issue) 2: 61-87.

International Whaling Commission. 2001c. Report of the Workshop on the Comprehensive Assessment of Right Whales. *J. Cetacean Res. Manage*. (Special Issue) 2: 1-60.

International Whaling Commission. 2003a. Report of the Sub-Committee on Bowhead, Right and Gray Whales. *J. Cetacean Res. Manage*. (Suppl.) 5: 226-47.

International Whaling Commission 2003b. Report of the Sub-Committee on Stock Assessment – In Depth Assessments. *J. Cetacean Res. Manage*. (Suppl.) 5: 248-92.

International Whaling Commission 2003c. Report of the Sub-Committee on the Comprehensive Assessment of Humpback Whales. *J. Cetacean Res. Manage*. (Suppl.) 5: 293-323.

International Whaling Commission 2004. Report of the Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage*. (Suppl.) 6: 75-184.

International Whaling Commission. 2007a. Report of the subgroup on review of MSY rates. Appendix 4 of the Report of the Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage*. (Suppl.) 9: xx-xx

International Whaling Commission 2007b. Report of the Sub-Committee on the Revised Management Procedure. *J. Cetacean Res. Manage*. (Suppl.) 9: xx-xx.

International Whaling Commission. 2007c. Report of the intersessional workshop to review data and results from special permit research on minke whales in the Antarctic, Tokyo 4-8 December 2006. Document SC/59/REP 1.

International Whaling Commission 2007d. Report of the Sub-Committee on other Southern Hemisphere whale stocks. *J. Cetacean Res. Manage*. (Suppl.) 9: xx-xx

Johnston, S.J. and Butterworth, D.S. 2002. An assessment of the west and east Australian breeding stocks of Southern Hemisphere humpback whales using a model that allows for mixing in the feeding grounds. Document SC/54/H17 presented to the IWC Scientific Committee (27pp).

Johnston, S.J. and Butterworth, D.S. 2005. A Bayesian assessment of the west and east Australian breeding populations (stocks D and E) of Southern Hemisphere humpback whales. Document SC/57/SH15 presented to the IWC Scientific Committee (25pp).

Johnston, S.J. and Butterworth, D.S. 2007a. Further assessments of the Southern Hemisphere humpback whale breeding stock C and its component sub-stocks. Document SC/59/SH4.

Johnston, S.J. and Butterworth, D.S. 2007b. Corrected assessment results for Southern Hemisphere humpback whales from breeding stocks D and G. Document SC/59/SH2.

MacCall, A.D. 1990. *Dynamic Geography of Marine Fish Populations*. University of Washington Press, Seattle, USA. 153pp.

MacCall, A.D. and Tatsukawa, K. 1994. Theoretical effects of habitat selection on distribution andproductivity of whales. *Rep. int. Whal. Commn* 44: 407-11.

Mori, M. and Butterworth, D.S. 2006 A first step towards modeling the krill-predator dynamics of the Antarctic ecosystem. *CCAMLR Science* 13: 217–277

Mori, M., Butterworth, D.S. and Kitakado, T. 2007 Further progress on application of ADAPT-VPA to Antarctic minke whales. Doucument SC/59/IA13.

Myers, R.A., Barrowman, N.J., Hilborn, R. and Kehler, D.G. 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. *N. Amer. J. Fisheries Manage*. 22: 351-64.

North Atlantic Right Whale Consortium. 2006. North Atlantic right whale report card November 2005 – October 2006. 5pp.

Punt, A.E. 1996. The effects of assuming that density dependence in the HITTER-FITTER model acts on natural mortality rather than fecundity. *Rep. int. Whal. Commn* 46: 629-36.

Punt, A.E. and Butterworth, D.S. 2000. Why do Bayesian and maximum likelihood assessments of the Bering-Chukchi-Beaufort Seas stock of bowhead whales differ? *J. Cetacean Res. Manage*. 2(2): 125-33.

Punt, A.E., Allison, C. and Fay, G. 2002. An examination of assessment models for the eastern North Pacific gray whale based on inertial dynamics. Document SC/54/BRG10. submitted to the 2002 Annual Meeting of the Scientific Committee (?pp).

Punt, A.E., Allison, C. and Fay, G. 2004. An examination of assessment models for the eastern North Pacific gray whale based on inertial dynamics. *J. Cetacean Res. Manage*. 6: 121-32.

Punt, A.E., and Polacheck, T. 2007. Further development of statistical catch-at-age models for Southern Hemisphere minke whales. Document SC/59/IA4.

Rademeyer, R.A., Brandão, A., Mori, M. and Butterworth, D.S. 2003. Trends in Antarctic blue whale populations taking account of Area effects (Subtitle: A response to Joe Horwood, 1990, RIWC 40: 47, footnote 2). Document SC/55/SH20 Submitted to this meeting (??pp).

Reilly, S.B. 1984. Observed and maximum rates of increase in gray whales, *Eschrichtius robustus*. *Rep. int. Whal. Commn* (special issue 6): 389-99.

Sampson, D.B. 1994. Estimates of sustainable yield rates from a length structured model for southern fin whales. *Rep. int. Whal. Commn* 44: 255-9.

Schweder, T. and Volden, R. 1994. Relative abundance series for minke whales in the Barents Sea, 1952 to 1983. *Rep. int. Whal. Commn* 45: 323-32.

Sears, R., Williamson, J.M., Wenzel, F.W., Berube, M., Gendron, D. and Jones, P. 1990. Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. *Rep. int. Whal. Commn* (Special Issue) 12: 335-42.

Sigurjonsson, J. and Gunnlaugson, T. 1990. Recent trends in the abundance of blue (*Balaenoptera musculus*) and humpback whales (*Megaptera novaeangliae*) off west and southwest Iceland, with a note on the occurrence of other cetacean species. *Rep. int. Whal. Commn* 40: 537-551.

Stevick, P.T., Allen, J., Clapham, P.J., Friday, N., Katona, S.K., Larsen, F., Lien, J., Mattila, D.K., Palsboll, P.J., Sigurjonsson, J., Smith T.D., Oien, N. and Hammond, P.S. 2001. Trends in abundance of North Atlantic humpback whales, 1979-1993. Document SC/53/NAH2 submitted to the 2001 Annual Meeting of the IWC Scientific Committee (?pp).

Wada, S. 1981. Japanese whaling and whale sighting in the North Pacific 1979 season. *Rep. int. Whal. Commn* 31: 783-92.

Wade, P.R. and Perryman, W. 2002. An assessment of the eastern gray whale population in 2002. Document SC/54/BRG7 submitted to the 2002 Annual Meeting of the Scientific Committee (?pp).

Ward, E., Zerbini, A.N., Kinas, P.G., Engel, M.H. and Andriolo, A. 2006. Estimates of population growth rates of humpback whales (*Megapetera novaengliae*) in the wintering grounds off the coast of Brazil (breeding stock A): Document SC/58/14 presented to the IWC Scientific Committee.

Zerbini, A.N., Ward, E., Engel, M.H., Androla, A. and P.G. Kinas. 2006. A Bayesian assessment of the conservation status of humpback whales (*Megapetera novaengliae*) in the western South Atlantic Ocean (Breeding stock A). Document SC/58/SH2 submitted to the IWC Scientific Committee. (25 pp.)

TABLE 1: Estimates (or inferences regarding) *MSYR* for baleen whales current in 1987, and changes in the status of these estimates since that time. Values in square parentheses are 95% confidence/probability intervals (90% if marked++). Cases where the estimate refers to the net recruitment rate are marked *. The 1987 estimates of *MSYR* relate to the recruited component of the stock, while those post-1987 refer to *MSYR*(1+), i.e. uniform selectivity harvesting on the total (1+) population.

Population or Rule	Perception in 1987		Updates/Perceptions post 1987	
	Estimate - *MSYR*(rec)	Status	Estimate – *MSYR*(1+)	Status
Eastern North Pacific gray	3.7%* Reilly (1984)	Agreed	4.4% [3.0;5.5]++ Punt *et al.* (2002)[1] 5.1% [3.0; 6.7]++ Wade and Perryman (2002)	Accepted (in the sense that management advice was agreed based on these results). IWC (2003a)
Southern Hemisphere minke	2-4%* IWC (1986) p.139	In dispute	5.7% [5.0; 6.5][2] Butterworth and Punt (1999) 5.5% I – stock, 3.6% P – stock: Mori *et al.* (2007) (Reference cases) 5.4% (SE = 0.5) I – stock, 2.6% (SE = 0.7) P – stock: Punt and Polacheck (2007)	Noted without comment IWC (1998) p.101 Results depend heavily on age readings from commercial whaling data, some problems with which are agreed to require resolution IWC (2007c)
North Atlantic minke	<2% Holt *et al.* (1986)	CPUE trend implication	6.1%[2.1;11.5][3], 1.1%[0.0;3.7][4]: Butterworth and Punt (1995) 1.9% [0.1; 3.8][5] This paper (Appendix)	Assessments on which 1987 perceptions were argued had lapsed – implicitly evident from IWC (1991) p. 139. Not discussed. IWC (1996a) Yet to be discussed
North Pacific minke ("O stock")	<2% Holt *et al.* (1986)	CPUE trend implication	-	CPUE based estimate agreed rejected. IWC (1992d)
Southern Hemisphere fin	<1% IWC (1984) p.84 based on Clark (1982)	Unclear	Range [<0; 5%] Sampson (1994) as Summarised by author in IWC (1994a) p.183	In dispute IWC (1994a) p.183
No super-compensation	(<2% IWC (1985) p.42 based upon generic arguments in Holt (1985)	In dispute	-	Unclear – lapsed?

Notes:
1) The subsequent published paper, Punt *et al.* (2004), quotes a baseline *MSYR*(mat) estimate of 7.0% with 90% probability interval [4.8; 9.2].
2) For Area IV for the second case shown in Table 4, CI's are inferred proportionally to those quoted for *MSYR*(mat) of 12.3% [10.8; 14.0].
3) Based upon Schweder and Volden (1994) CPUE analyses.
4) Based upon Cooke (1993) CPUE analysis.
5) Lower limit is 4% rather than 2.5%-ile.

TABLE 2: Estimates (or inferences regarding) *MSYR*(1+) for baleen whales at present. Values in square parentheses are 95% confidence/probability intervals (90% if marked [++]). Populations already covered in Table 1 are summarised more briefly. The estimates given are understood to be the most recent and likely most reliable.

a) Population model fits

Population	Estimate *MSYR*(1+)	Status/Comments
EN Pacific gray	4.4% [3.0;5.5][++] Punt *et al.* (2002) 5.1% [3.0;6.7][++] Wade and Perryman (2002)	Accepted. IWC (2003a)
Southern Hemisphere minke	~ 5% (I – stock) Mori *et al.* (2007) ~ 3% (P – stock) Punt and Polacheck (2007)	Problems with commercial catch ageing need checking. IWC (2007c)
NE Atlantic minke	1.9% [0.1;3.8] This paper	Awaits discussion.
EGI fin	1.7% [1.0;2.9][1] Branch and Butterworth (2006)	Not discussed specifically. IWC (2007)
BCB bowhead	3.3% [1.9;4.8][++2] Brandon and Wade (2006)	Discussed, but without comment. IWC (2006)
Southern Hemisphere humpback		
BSA	4.6% [1.3;6.5][++] Zerbini *et al.* (2006) IWC (2007d)	Appears agreed; relatively strong prior dependence
BSC1	6.3% [4.9;7.2][++] Johnston and Butterworth (2007a)	Awaits discussion.
BSD	7.7% [5.5;8.7][++3] Johnston and Butterworth (2005)	Awaits updating given agreement on E sub-structure; some prior dependence for D.
BSE	8.6% [7.6;8.9][++] Johnston and Butterworth (2005)	
BSG	4.3% [1.7;6.4][++] Johnston and Butterworth (2007b)	Correction of error in 2006 result awaits discussion; strong prior dependence.

Notes:
1) CI's inferred by proportionality to CI's for growth rate parameter *r*.
2) 1848 density dependent reference case.
3) Preferred here to the result for BSD in isolation in IWC (2007d) as Johnston and Butterworth (2005) takes account of D and E mixing on the feeding grounds.

b) *MSYR*(1+) > *r*(0)/2

Population	Estimate *MSYR*(1+)	Status/Comments
Right whales		
South African	3.6% [3.3;4.0] Best *et al*. (2005)	*r*(0) estimates accepted. IWC (2001c) p.20.
Argentine	3.5% [2.8;4.2] Cooke *et al*. (2001)	(South African estimate marginally updated
West Australia	4.4% [3.0;5.8] Bannister (2001)	thereafter.)
Blue whales		
West Iceland	2.6% [-0.9;4.4] Sigurjonsson and Gunlaugsson (1990)	All but Southern Hemisphere include Bayesian
North Pacific	-2.3% [-7.8;3.8] Wada (1991)	meta-analysis update to estimate for population
East Canadian	-0.6% [-6.3;5.2] Sears *et al*. (1990)	itself. Branch *et al*. (2004).
Southern Hemisphere	+4.1% [0.9;7.7] Branch *et al*. (2004)	
Peruvian pygmy	-3.4% [-8.5;2.5] Donovan (1984)	
Gray whales		
WN Pacific	1.5% [1.1;2.1] Cooke *et al*. (2006)	1994-2005
SH Humpback whales		
BSA	3.6% [0.2;6.9] Ward *et al*. (2006)	1995-1998
BSC1	6.2% [2.4;10.0][1] Findlay and Best (2006)	1988-2002
BSD	5.1% [1.4;8.8][1] IWC (1996b)	1982-1994
BSE	6.4% [5.2;7.5][1] Brown *et al*. (1997)	1981-1996

Notes: 1) From log-linear regressions on time series of relative abundance estimates.

c) Other

Population	Estimate *SYR*(1+) (i.e. growth rate)	Status/Comments
N Atlantic Humpback Iceland West Indies Gulf of Maine	 11.4% (se=2.1) Gunlaugsson and Vikingsson (2001) 3.1% (se=0.5) Stevick *et al.* (2001) 6.3% (se=1.1) Friday *et al.* (2002)	
NW Atlantic Right	$\left.\begin{array}{l}+3\%\\-2\%\end{array}\right\}$ IWC (2001b) p.69	1980s 1990s

Appendix

Application of FITTER to North East Atlantic Minke Whales

The assessment tool used for this purpose is the HITTER-FITTER package (de la Mare 1989, Punt 1996). This package is based upon a sex- and age-structured production model which assumes a constant pattern of age-specific selectivity of catches. FITTER analyses, which utilise all available abundance estimates to attempt to estimate *MSYR*(1+), are pursued.

Data

The sex-disaggregated catch data from 1930 to 2004 and three survey sighting estimates of abundance of the total (1+) population (with CVs) were provided by Nils Øien (Tables A.1 and A.2).

Relative abundance data consisting of two CPUE-based indices are taken from an analysis of a variant of the net catcher day method of Cooke (1984), adjusted for vessel efficiency and spatial effects Aldrin *et al*., 2006) (Table A.3). The log estimates were quadratically detrended to obtain standard deviations which were used as CV inputs for the two series (0.16 for the CPUE series from 1953-1983 and 0.35 for the series from 1994-2004).

Model Assumptions and Parameter Values

The parameter values assumed for the HITTER-FITTER runs are given in Table A.4. In all cases the maximum sustainable yield level ($MSYL^{exp}$) is expressed in terms of the exploitable component of the stock and taken to be $0.6K^{exp}$ (the exploitable component of carrying capacity). Density dependence is assumed to act upon the exploitable component of the stock. The maximum sustainable yield rate (*MSYR*(1+)) is expressed in terms of the total (1+) population and the model is to fit abundance estimates taken to represent the total (1+) population size. In addition, carrying capacity (*K*) is assumed to remain unchanged over the period considered. These choices were made for consistency with previous HITTER-FITTER assessments of the Central Stock minke whales considered by the NAMMCO Scientific Committee (NAMMCO 1999).

As a robustness test, some of these parameter values were modified to correspond to those used for the RMP *Implementation Simulation Trials* for this resource (Table A.4).

The minimum age at maturity is set at 3 and the minimum age at recruitment is set at 1.

The step size for the initial population (*K*) and *MSYR*(1+) are taken to be relatively small for FITTER, *viz* 10 and 0.1/100 respectively. This ensures an effective prior grid search of the parameter space before the automated minimisation procedure comes into play. The absolute estimates of abundance used for FITTER are treated as being unbiased. The relative (CPUE) estimates of abundance are all assigned nonlinearity factors of 1 (i.e. CPUE is assumed to be linearly proportional to the exploitable component of abundance).

Results

FITTER was run for cases in which data were sequentially added, i.e. i) with only the survey estimates of abundance, ii) with only one of the early or later CPUE series included and iii) with both CPUE series included. The robustness test was performed for case iii) only.

Some key parameter estimates are given in Table A.5. Figure A.1 shows the 1+ population trajectory fit to the survey abundance data and Figure A.2 shows the exploitable population trajectory fit to the CPUE data.

It is clear from Figure A.3 that the confidence intervals estimates from bootstrapping (reported in Table A.5) are narrower than the confidence intervals indicated on the likelihood profile, which is of concern. This suggests that not all of the bootstrap replicates were able to find the likelihood maximum, and hence the bootstrap CIs are likely too small.

The effect of the alternative biological parameters input in the robustness test is minimal (Table A.5, Figure A.1).

As a representative estimate for *MSYR*(1+), results from Table A.5 which take both CPUE series into account and use a likelihood profile based estimate of the associated confidence interval are quoted in the main text of the paper.

References

Aldrin, M., Storvik, B. and Schweder, T. 2006. Standardised catch per unit effort in minke whaling in Norwegian waters, 1952-83 and 1993-2004. Norwegian Computing Center report SAMBA/03/05. 23 pp.

Cooke, J.G. 1984. The relationship between the net catcher day and the gross catcher day as a unit of effort, with reference to the Norwegian minke whale fishery. *Rep. int. Whal. Commn* 34: 288-90.

de la Mare, W.K. 1989. Report of the Scientific Committee, Annex L. The model used in the HITTER and FITTER programs (Program: Fitter.SC40). *Rep. int. Whal. Commn* 39:150-157.

NAMMCO (North Atlantic Marine Mammal Commission). 1999. Report of the Working Group on Management Procedures, Annex 2 of Report of the Sixth Meeting of the NAMMCO Scientific Committee. In: NAMMCO Annual Report 1998, pp. 117-31.

Punt, A.E. 1996. The effects of assuming that density dependence in the HITTER-FITTER model acts on natural mortality rather than fecundity. *Rep. int. Whal. Commn*. 46:629-36.

Table A.1: Historic sex-disaggregated catch series for North East Atlantic minke whales (Nils Øien *pers. commn*).

Year	Male	Female	Year	Male	Female
1930	6	4	1968	1244	864
1931	105	70	1969	1019	1013
1932	205	145	1970	894	1018
1933	305	220	1971	866	936
1934	400	300	1972	797	1378
1935	500	375	1973	648	914
1936	580	470	1974	536	884
1937	660	565	1975	601	829
1938	752	594	1976	620	1269
1939	489	427	1977	713	986
1940	298	254	1978	471	912
1941	1140	970	1979	768	1018
1942	1212	921	1980	788	1019
1943	943	670	1981	764	1007
1944	707	642	1982	636	1146
1945	1012	771	1983	615	1073
1946	1059	824	1984	336	294
1947	1438	1118	1985	323	311
1948	1889	1598	1986	227	102
1949	1905	1936	1987	154	169
1950	962	1028	1988	21	8
1951	1418	1334	1989	2	15
1952	1481	1844	1990	4	1
1953	1234	1201	1991	0	0
1954	1753	1746	1992	51	44
1955	2053	2256	1993	90	123
1956	1817	1839	1994	128	111
1957	1661	1973	1995	30	146
1958	1999	2342	1996	52	296
1959	1633	1443	1997	113	370
1960	1533	1718	1998	120	448
1961	1453	1654	1999	153	380
1962	1389	1673	2000	151	279
1963	1442	1624	2001	192	329
1964	1191	1278	2002	220	379
1965	1027	1095	2003	215	411
1966	863	1060	2004	155	372
1967	931	896	2005	150	484

Table A. 2: Abundance estimates for North East Atlantic minke whales from surveys (Nils Øien *pers. commn*), for use in FITTER analyses.

Year (mid-year for the survey period 1996-2001)	Abundance Estimate	CV
1989	64 730	0.192
1995	112 125	0.104
1999	80 487	0.154

Table A.3: CPUE-based relative abundance series for North East Atlantic minke whales (from Aldrin *et al* 2006, Table 1)

Year	Early CPUE Series	Year	Later CPUE Series
1953	0.966	1994	1.217
1954	0.855	1995	1.108
1955	0.992	1996	2.030
1956	0.814	1997	2.664
1957	0.799	1998	2.846
1958	0.943	1999	1.929
1959	0.618	2000	2.034
1960	0.598	2001	1.361
1961	0.605	2002	2.930
1962	0.656	2003	2.370
1963	0.844	2004	1.861
1964	0.737		
1965	0.776		
1966	0.686		
1967	0.662		
1968	0.708		
1969	1.024		
1970	0.657		
1971	0.834		
1972	0.920		
1973	0.662		
1974	0.670		
1975	0.744		
1976	0.757		
1977	0.550		
1978	0.694		
1979	0.766		
1980	0.520		
1981	0.498		
1982	0.507		
1983	0.624		

Table A.4: Biological and operational parameter values assumed for FITTER runs.

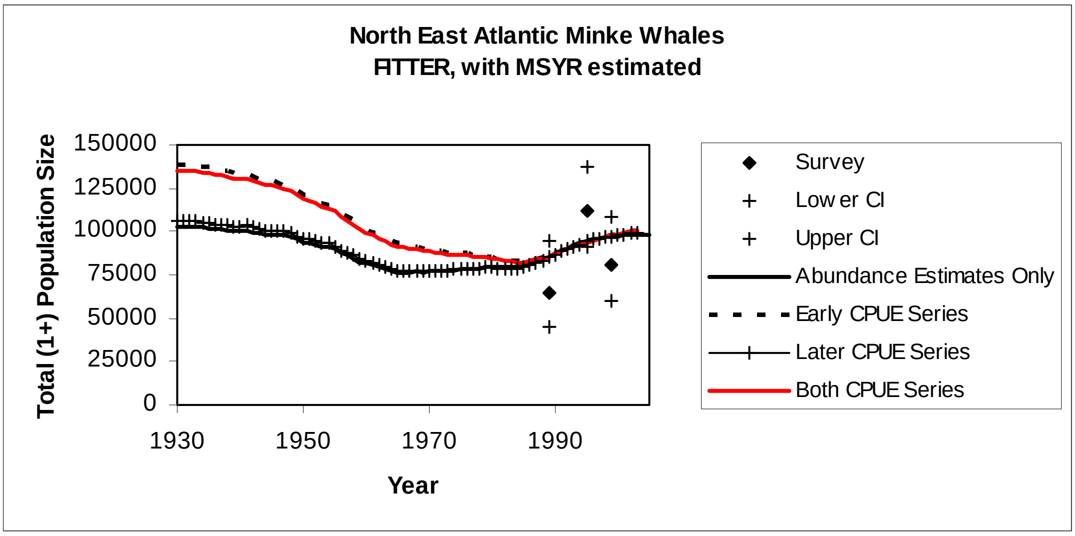
	Minke Whales	Robustness Test
Maximum age class	20	20
Natural mortality rate (taken here to be age-independent)	0.09 [Most recent estimate from Table 5.2.2 NAMMCO (1999)]	Increasing with age from M(0)=0.085 to M(20)=0.115
Female age at 50% maturity[5]	7	7
Female age at 95% maturity	12 [Most recent estimate from Table 5.2.2 NAMMCO (1999)]	13.7
Female age at 50% recruitment	5.5	4.0
Female age at 95% recruitment	11.5	7.8
Male age at 50% recruitment	5.5	4.0
Male age at 95% recruitment	11.5 [Table 5.2.1 / Central value from Table 5.2.2 NAMMCO (1999)]	7.8
Minimum age at maturity	3	3
Minimum age at recruitment	1	1
Minimum possible *MSYR*	0.00	0.00
Maximum possible *MSYR*	0.10	0.10
First year of simulation	1930	1930
Last year of catches in simulation	2005	2005

[5] Corresponds to age at first parturition – 1 year

Table A.5: Statistics of population trajectories which fit the survey estimates of total (1+) population size for the North East Atlantic minke whale population. Results are shown for $MSYR^{1+}$, MSY, the pristine (pre-exploitation) total population size (K^{1+}, in thousands), the current status of the mature female component of the population relative to pristine (N^{mat}_{2005}/K^{mat}) and that of the 1+ component (N^{1+}_{2005}/K^{1+}). The 95% confidence interval from 1000 bootstraps is given in parenthesis. For $MSYR^{1+}$ the 95% confidence interval obtained from the likelihood profile is also given (see Figure A.3) below that obtained from bootstrapping.

	Abundance Estimates Only	Including Early CPUE	Including Later CPUE	Including Both CPUE Series	Robustness Test (Both CPUE Series)
$MSYR^{1+}$	3.40[0.60; 10.00] [0.10[6]; 6.24]	1.80[0.12; 2.39] [0.10[2]; 3.82]	3.20[0.24; 10.00] [0.10[7]; 5.63]	1.90[0.16; 2.45] [0.10[3]; 3.84]	2.00[0.16; 2.57] [0.10[3]; 4.11]
MSY (exploitable)	2172 [177; 8163]	1449 [130; 1782]	2089 [275; 8163]	1502 [179; 1800]	1500 [181; 1862]
K^{1+}	103.1 [92.9; 208.6]	138.2 [117.2; 209.3]	106.1 [92.8; 208.7]	135.1 [117.1; 209.3]	133.8 [115.8; 206.6]
N^{mat}_{2005}/K^{mat}	0.86 [0.43; 0.94]	0.65 [0.41; 0.75]	0.84 [0.45; 0.94]	0.66 [0.42; 0.76]	0.68 [0.42; 0.78]
N^{1+}_{2005}/K^{1+}	0.96 [0.44; 1.04]	0.74 [0.42; 0.85]	0.94 [0.47; 1.04]	0.76 [0.44; 0.86]	0.76 [0.44; 0.86]

[6] This lower limit corresponds to the lower 6 percentile, rather than lower 2.5 percentile.
[7] This lower limit corresponds to the lower 4 percentile, rather than the lower 2.5 percentile.



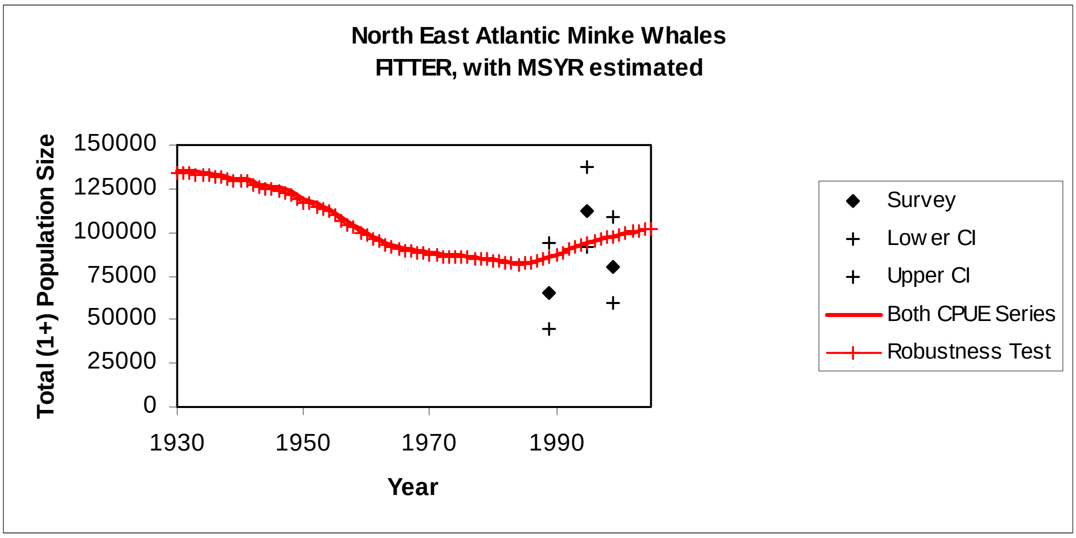


Figure A.1: Total (1+) population trajectories from 1930 to 2005 of the North East Atlantic minke whales using FITTER. The survey sighting estimates of abundance are shown with 95% confidence intervals. The lower panel shows the trajectories for fits to both CPUE series for both the base case and the robustness test (which the plot is scarcely able to distinguish).

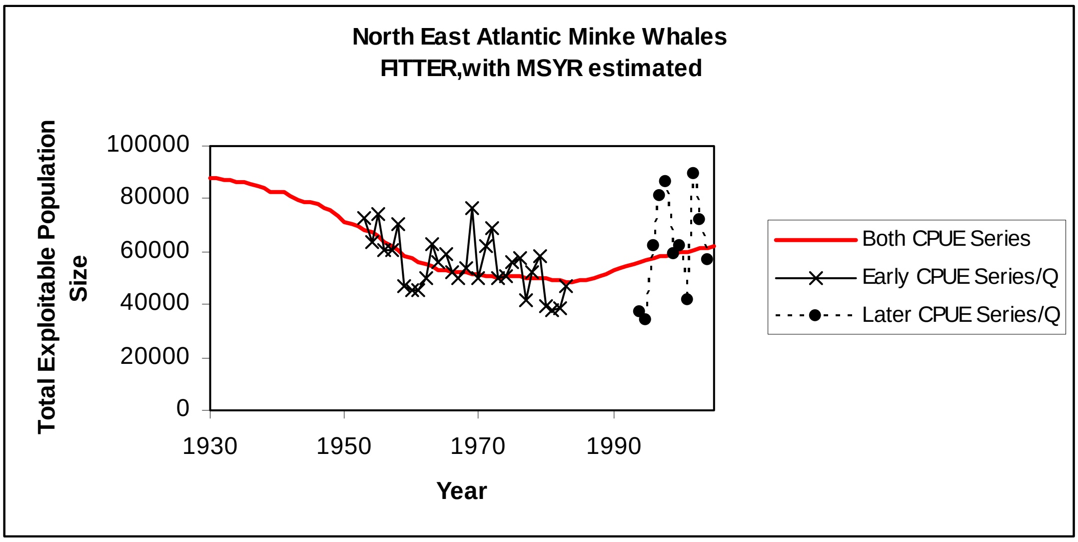
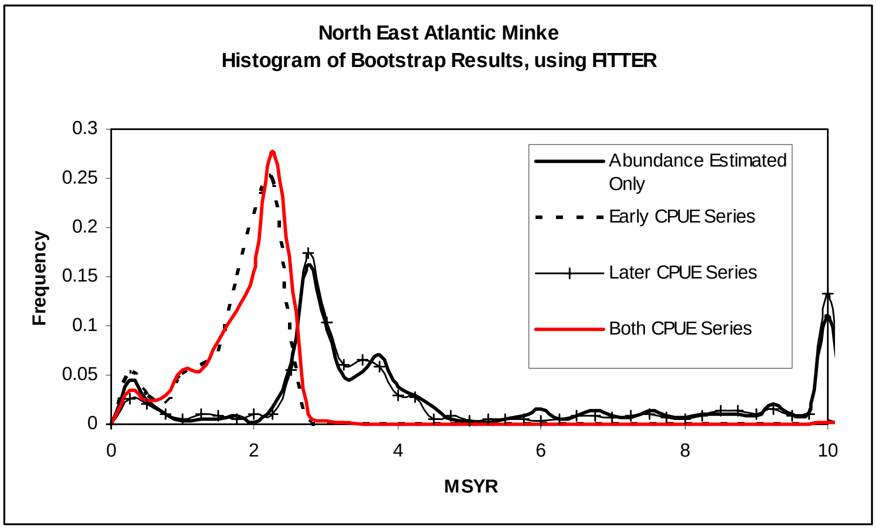


Figure A.2: The fit of the exploitable population to both CPUE series. These CPUE series values are divided by the associated catchability (*q*) estimates for the purposes of this comparison.



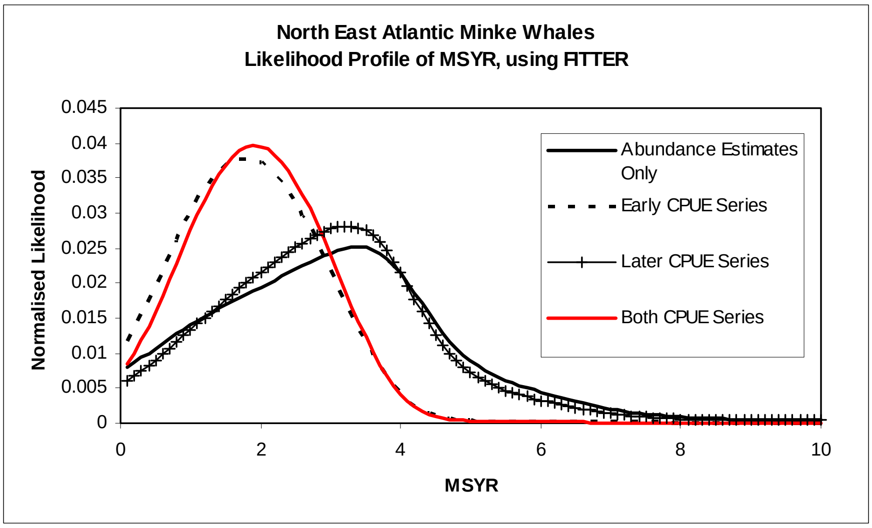


Figure A.3: Histogram of $MSYR^{1+}$ from 1000 bootstrap replicates using FITTER (upper figure) and the likelihood profile of $MSYR^{1+}$ using FITTER (lower panel); the narrower bootstrap confidence intervals are evident.