The influence of environmental variability on baleen whale sustainable yield curves

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ABSTRACT
Variability is the norm rather than the exception in marine ecosystems, and a realistic characterisation of density-dependence and sustainable yield curves in baleen whale populations should allow for such variability. A theoretical model is developed for incorporating environmental variability into models of density dependence and sustainable yields. A distinction is made between r_{max}, the maximum growth rate that a species can achieve in ideal habitat, and r_0, the average growth rate that a population at a low level will achieve in a given habitat. For given r_{max}, the parameters r_0 and K (carrying capacity) are predicted to be related to each other. Environmental variability is predicted to influence net recruitment rates at all population levels, but to have larger effects on populations which occupy suboptimal habitats or which are close to their carrying capacity. Examples from right and gray whale populations are consistent with this, but precise quantification of environmentally-driven fluctuation is possible only in the best-studied populations. The consequence of environmental variability for the estimation of *MSYR* (the *per capita* net recruitment rate at optimal population size) and *MSYL* (the relative population level at which the maximum net annual increment is achieved) at is investigated through the use of simulated data sets.

Introduction

The level of catch that baleen whales can sustain has been one of the central questions since the first attempts to place the management of whaling on a scientific basis in the mid-20th century following the establishment of the International Whaling Commission (IWC) and its Scientific Committee (SC).

The question involves two related quantities: the population level at which the maximum sustainable yield is obtained (*MSYL*) and the fraction of this population that can be sustainably extracted on an annual basis (*MSYR*). The maximum sustainable yield rate and level played an explicit role in the so-called New Management Procedure which the IWC adopted in 1974, and which is still nominally in force in the IWC Schedule. In the absence of a means to determine these quantities directly for most baleen whale stocks, the practice of the Scientific Committee in the operation of the NMP was to assume that the MSYL occurred at 60% of carrying capacity, *K* (the notional population level in the absence of exploitation), and that, in the absence of evidence to the contrary, the MSY rate was 4% of the MSYL population level.

In the late 1980s and early 1990s the Scientific Committee developed the Revised Management Procedure (RMP). The procedure was aimed to be robust to assumptions, and in particular to provide for safe management over the entire plausible range of *MSYR* and *MSYL* values (Kirkwood 1992). At the time, the plausible range was initially taken to be 1%-4% for

MSYR (referred to the mature population); this was later revised to 1%-7%. The need to provide for safe management when *MSYR* is as low as 1% was a major constraining factor in the design of the RMP, and led to a relatively conservative management procedure with respect to the level of allowed catch. Because of this, there has been substantial interest in raising the lower end of the accepted plausible range of MSY rates, in order to provide a scientific basis for higher catches levels than the current version of the RMP allows.

The last time the Scientific Committee reviewed the *MSYR* issue in depth was in 1993 (IWC 1994). That review concluded that the available data did not permit a narrowing of the accepted range of 1%-7%. The *MSYR* issue was revisited again in 2003 in the context of RMP implementation for North Pacific minke whales, where arguments were raised both for and against raising the lower end of the plausible range of *MSYR* values (Butterworth and Punt 2003; Cooke 2004). It was agreed that the values 4% and 7% had high plausibility, while 1% had only medium plausibility. According to the Scientific Committee's agreed guidelines, the MSYR=1% would need to be assigned low plausibility in order for scenarios involving MSYR=1% to be discarded (IWC 2004).

The Scientific Committee agreed in 2006 that sufficient new in formation had been obtained since the last review of MSY rates in 1993, to merit a new review to be conducted during 2007-8 (IWC 2007).

A tabulation of the specific new information on observed net recruitments in baleen whale stocks is provided by Cooke *et al.* (2007). However, there remain some general questions regarding the interpretation of such information, which may merit discussion in the context of the current review, particularly in light of changed perceptions or understanding since the previous *MSYR* reviews were conducted.

An important shift in perception that has occurred in recent decades is an awareness of the ubiquity of environmental variability, and its influence on cetacean populations. Fisheries biologists have at least since the mid-20th century been aware of the significance of fluctuations in recruitment for the performance of fisheries and the management of fish stocks, but the tendency in the whaling management context has until recently been to continue to use largely deterministic population models. Quantities such as *MSYR*, and *K*, the carrying capacity, have usually been treated as constants. In specific cases it has been found necessary to invoke changes in *K* to fit observed trends in populations, e.g. for minke, gray and humpback whales (Butterworth and Punt 1999; Butterworth *et al.* 2002; Punt *et al.* 2006), but such hypothesised changes have mainly been of a retrospective, "one-time" nature, without consideration for what kind of variability in *K* and other parameters might "normally" be expected in whale populations now and in the future.

During the development of the RMP, some scenarios involving arbitrary changes in *K* and *MSYR* were developed for the purpose of robustness testing (Kirkwood 1992). Because the RMP was found to be robust to such changes, at least with respect to the risk of depleting stocks, no in-depth investigation was conducted of the level and nature of variability in population parameters that might ordinarily be expected. The specification of performance measures that are appropriate in cases of parameter variability has received only limited attention.

In this paper, a simple framework is developed for incorporating environmental variation into model of the net recruitment rate of baleen whales. Of particular interest is the interaction between environmental and density-dependent effects, and the extent to which populations at various levels of depletion (fractions of K) may be expected to be impacted by different levels of variability. The predictions of the model are discussed in qualitative terms in relation to three populations of gray and right whales, two of which are believed to be at low levels and one close to K.

Finally, the implications of environmental variability for the estimation of *MSYR* and *MSYL* are investigated using simulated data. It is important that methods used to estimate these quantities remain valid in the presence of substantial environmental variability.

Modelling the relationship between net recruitment rate and environmental resources
For the purpose of the relatively broad-brush analysis of this paper, we combine effects on mortality and reproduction and focus on the net recruitment rate, r, and its relationships with population size and environmental factors, principally food availability.

The reproduction of whales is limited by physiological constraints, such that even under "perfect" conditions the net recruitment rate will be constrained by some maximum, which varies between species. For example, for southern right whales *Eubalaena acutorostrata* the minimum calving interval, with rare exceptions, appears to be three years (Cooke *et al.* 2003) while for western gray whales *Eschrichtius robustus* the minimum is two years (Cooke *et al.* 2007). The actual calving interval fluctuates above this minimum according to environmental conditions.

We can expect the relationship between net recruitment rate and environmental resources to be of the general form shown in Fig. 1. When food resources are plentiful, the net recruitment rate is close to the biological maximum, $r_{\max}$, whereas lack of resources leads to enhanced mortality and negative r.

The simplest functional form which generates the right overall shape of the relationship (namely $r \to r_{\max}$ as $u \to \infty$, and $r \to -\infty$ as $u \to 0$) is given by:

$$r(u) = r_{\max}\left(1 - u^{-1}\right) \tag{1}$$

where u is expressed units such that $u = 1$ corresponds to the "break-even" point $r = 0$. However, it is hard to predict on purely theoretical grounds how strongly curved the true relationship might be. We can generalize this relationship to produce the family of curves shown in Fig. 1 by including an exponent z:

$$r(u) = r_{\max}\left(1 - u^{-z}\right) \tag{2}$$

where $z > 0$. The higher the value of the exponent z, the more rapidly r approaches $r_{\max}$ when the resources exceed the reference level $u = 1$.

Because baleen whales have the potential to store energy through fat reserves, their condition will be determined not by the instantaneous availability of resources, but by a moving average integrated over an appropriate time interval related to the storage capacity of the given species. One expects the integration time to be longer for species with multi-year breeding cycles such and right and gray, and shorter for annual breeders such as minke whales. As food availability integrated over the relevant time period tends to zero, the energy reserves of the animal will become exhausted, and it will die with probability tending to one, which corresponds to $r \to -\infty$.

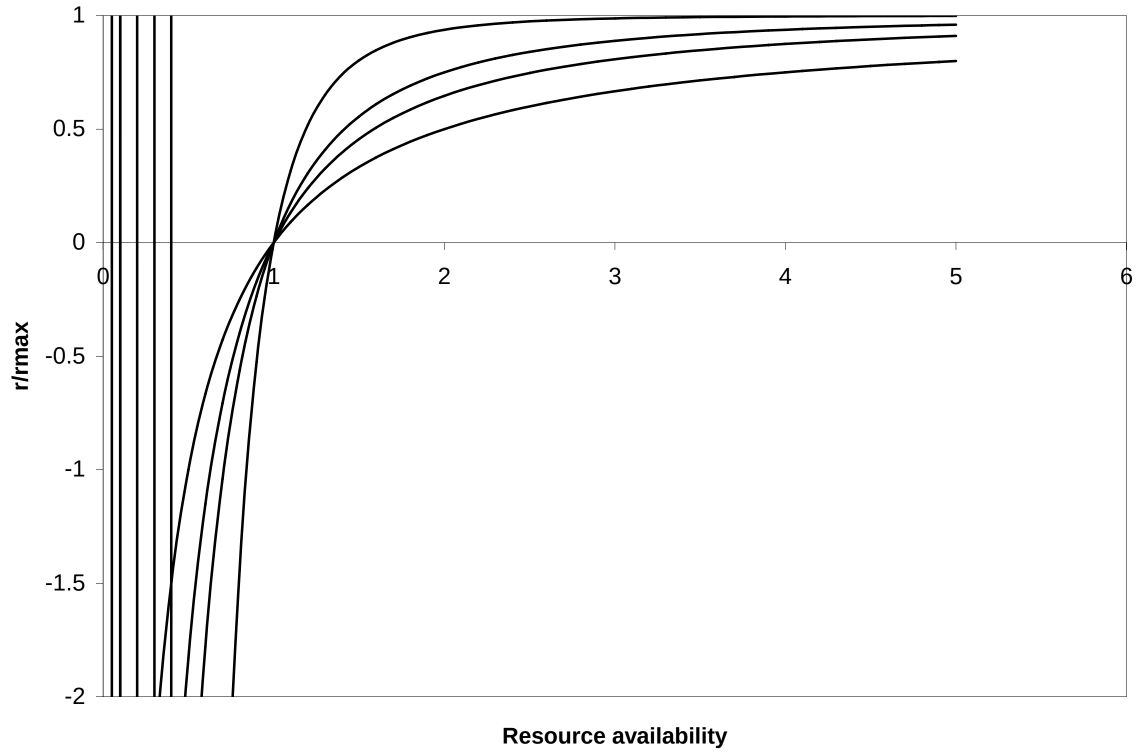


Fig.1. Expected shape of relationship between food availability and net recruitment rate.

In analyses to date, the maximum rate of increase, r_{max} has tended to be regarded as synonymous with r_0, the rate of increase at low population sizes in a traditional constant-environmental density-dependent model. In the model developed here, r_0 is related to habitat quality, and $r_0 \leq r_{max}$, with equality only in ideal habitats.

Influence of whale density
Dependence of the net recruitment rate on the density of whales can be introduced into the model by supposing that the whales deplete the resources. Such depletion can be at a small-scale, where it corresponds to the notion of predator interference, or can operate at a larger scale where it is associated with measurable reductions in the abundance of prey.

In tightly-coupled predator-prey systems, it is possible for the predator to hold the prey down at a low level (so-called top-down control). This can produce strongly non-linear dynamics, whereby harvesting of the predator, can, after an initial transient, lead paradoxically to an increase in abundance of both predator and prey, by relaxing the predation pressure on the prey (May *et al.* 1979). However, the balance of modern perception appears to be that extreme top-down control is not the norm in marine systems, and that observed trends in components of marine ecosystems are better fitted with models involving predominantly bottom-up control, where the prey limits the abundance of the predator, but the reverse link is less strong (refs). This is particularly the case when prey abundance is highly variable: even if a predator were to “succeed” in depressing prey abundance to a low level, a single strong prey year class would enable the prey to break out of this control, because the predator, with its slower dynamics, would not be able to fully utilise the increased resources in the short term.

If one supposes that whales deplete the prey during a feeding season, or at least make it less available for other whales, by consuming or dispersing it, but do not reduce prey production, then the consumption pressure on the prey can be assumed proportional to the density of whales, such that the relationship between the availability of prey and the density of whales will be of an exponential form, as illustrated in Fig. 2:

$$u(x) = e^{a-bx} \tag{3}$$

where x denotes whale density on the feeding grounds, and the parameter a is proportional to the production of prey per unit habitat area, and the parameter b is proportional to the *per capita* impact of whales on prey density.

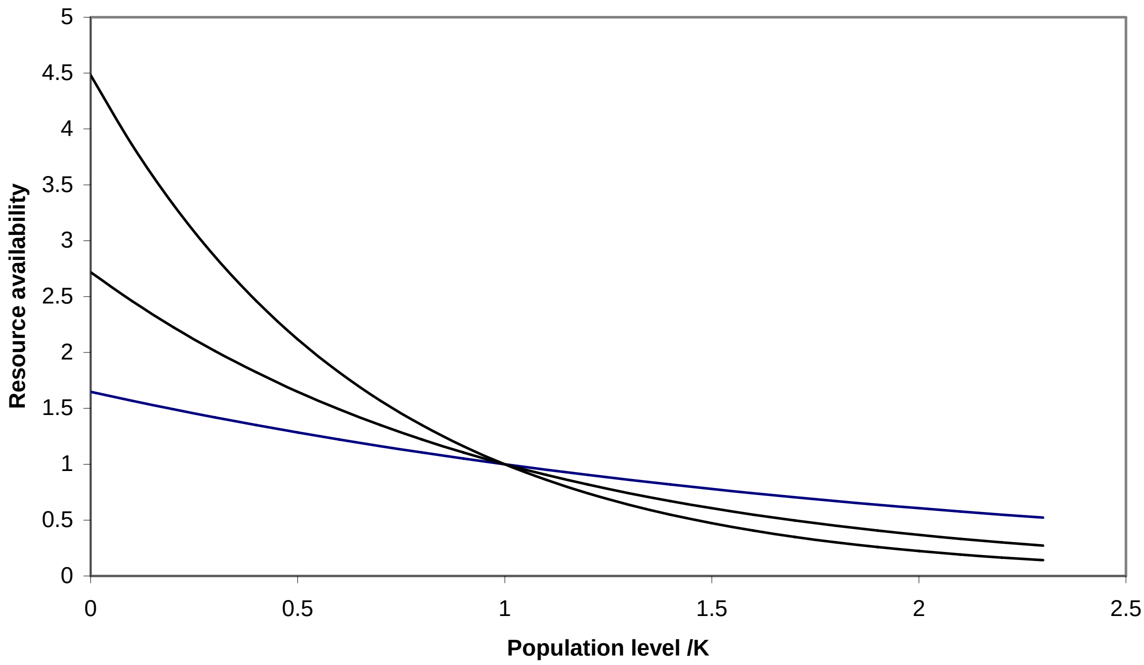


Fig. 2. Schematic relationship between population density and the level of resources avialble to individual whales

Incorporation of environmental variation
Environmental variability can be introduced by supposing that the availability of prey fluctuates randomly according to a log-normal distribution:

$$u(x,t) = \exp\left(a + \sigma v_t - bx\right) \tag{4}$$

where v_t are year-specific standard normal random variables (not necessarily uncorrelated), and σ is a parameter that reflects the extent of environmental variability. The whale may be able to buffer the variation in food availability to some extent, by storage of energy in fat reserves, particular in those species with multi-year breeding cycles. In this case, the effective value of the variance parameter σ from the whales' point of view will be reduced by a factor of approximately $T^{½}$ where T is the integration time of the whale. One would expect the value of T to correspond roughly to the length of the breeding cycle.

The net recruitment rate is given by:

$$r(x,t) = r_{\max}\left(1 - \exp\left(-z\left(a + \sigma v_t - bx\right)\right)\right) \tag{5}$$

The time-averaged mean net recruitment at a given population size is given by:

$$\bar{r}(x) = r_{\max}\left(1 - \exp\left(-z\left(a - \tfrac{1}{2}z\sigma^2 - bx\right)\right)\right) \tag{6}$$

It is convenient to define r_0 as the mean per capita net recruitment rate at low population size:

$$r_0 \equiv \bar{r}(0) = r_{\max}\left(1 - \exp\left(-az + \tfrac{1}{2}z^2\sigma^2\right)\right) \tag{7}$$

The "mean carrying capacity" $\bar{K}$ is defined as the population level at which the mean net recruitment rate is zero, and is given by:

$$\bar{K} = \left(a - \tfrac{1}{2}z\sigma^2\right)/b \tag{8}$$

This implies that r_0 and $\bar{K}$ are positively related:

$$r_0 = r_{\max}\left(1 - \exp\left(-zb\bar{K}\right)\right) \tag{9}$$

The relationship between r_0 and $\bar{K}$ is illustrated in Fig. 3.

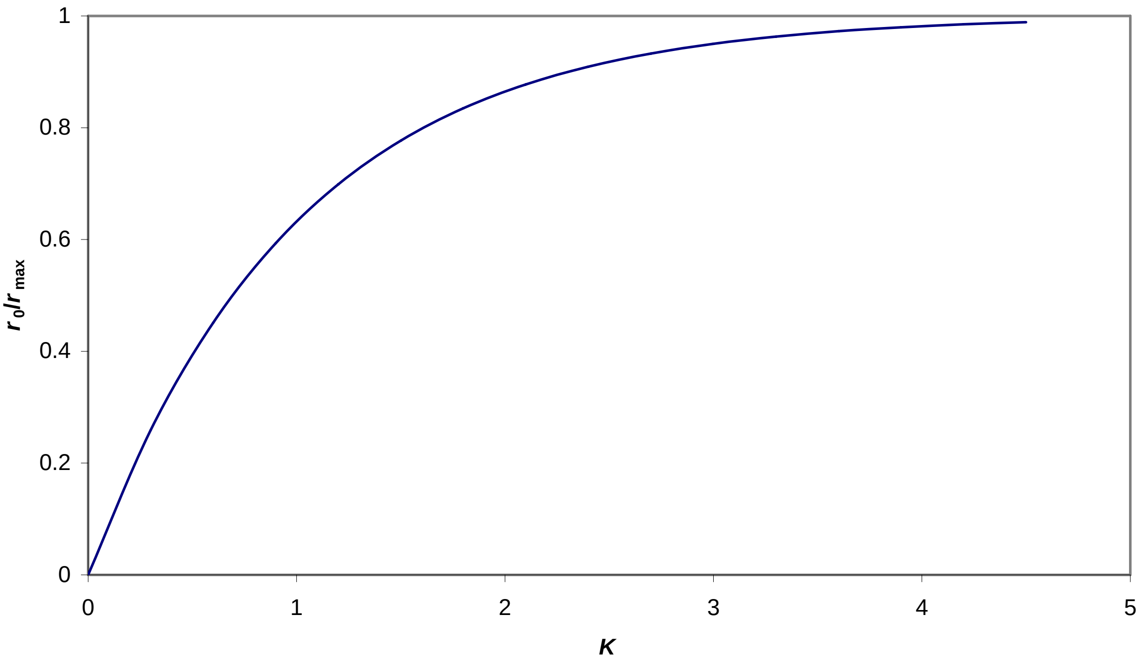


Fig. 3. Predicted relationship between r_0 and K, for fixed values of the remaining parameters.

The ratio $q = r_0 / r_{\max}$ can be regarded as an index of effective habitat quality for the whale species in question: $q = 1$ would correspond to ideal habitat such that $r_0 = r_{\max}$; $q = 0$ is the break-even point, where the population can just persist under median environmental conditions; $q < 0$ means the population will die out under median environmental conditions.

We assume that no real habitat is perfect, such that in all real cases, $q < 1$ and $r_0 < r_{\max}$.

A convenient reference point for habitat quality is the value $q = 1 - 1/e \approx 0.632$, which we shall call "medium quality" habitat. "Medium quality" is not necessarily synonymous with "average quality". A useful reference level for whale density is the density corresponding to the carrying capacity in medium quality habitat. If we express whale density in units of this reference level, then the net recruitment rate satisfies:

$$\frac{r}{r_{\max}} = 1 - e^{x-K} = 1 - \left(1 - q\right)e^{x} \tag{10}$$

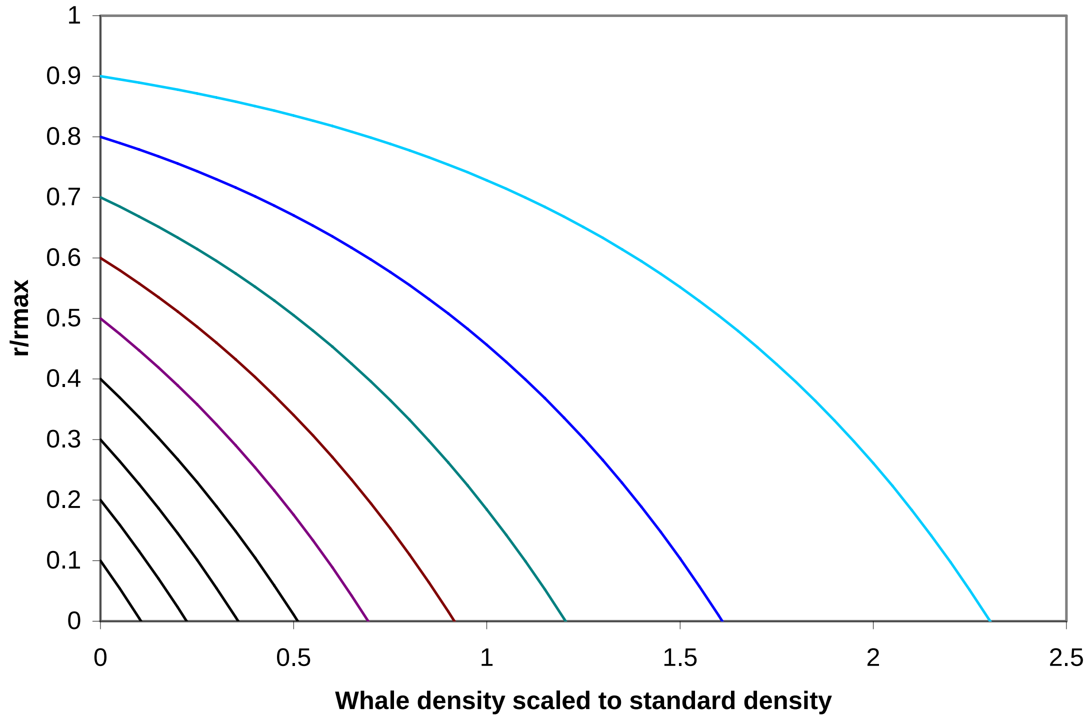


Fig. 4. Predicted family of net-recruitment as a function of population level.

Fig. 4 illustrates the resulting family of *per capita* net recruitment curves for different values of q ranging from 0.1 to 0.9. The y axis is in units of $r_{\max}$, so that the habitat quality for a given curve is given by the intercept on the y-axis. The carrying capacity, K, for a given curve, is given by the intercept on the x-axis. For poor quality habitat quality, both r_0 and K are low and the curves are nearly linear. For high quality habitats, both r_0 and K are larger, and the curves are noticeably, but not strongly, non-linear.

The corresponding sustainable yield curves are shown in Fig. 5, illustrating that both the height and width of the curve depends on habitat quality.

The mean net recruitment rate can be expressed in terms of $r_{\max}$, q and K as follows:

$$\bar{r}(x) = r_{\max}\left(1 - (1-q)^{1-x/K}\right) \tag{11}$$

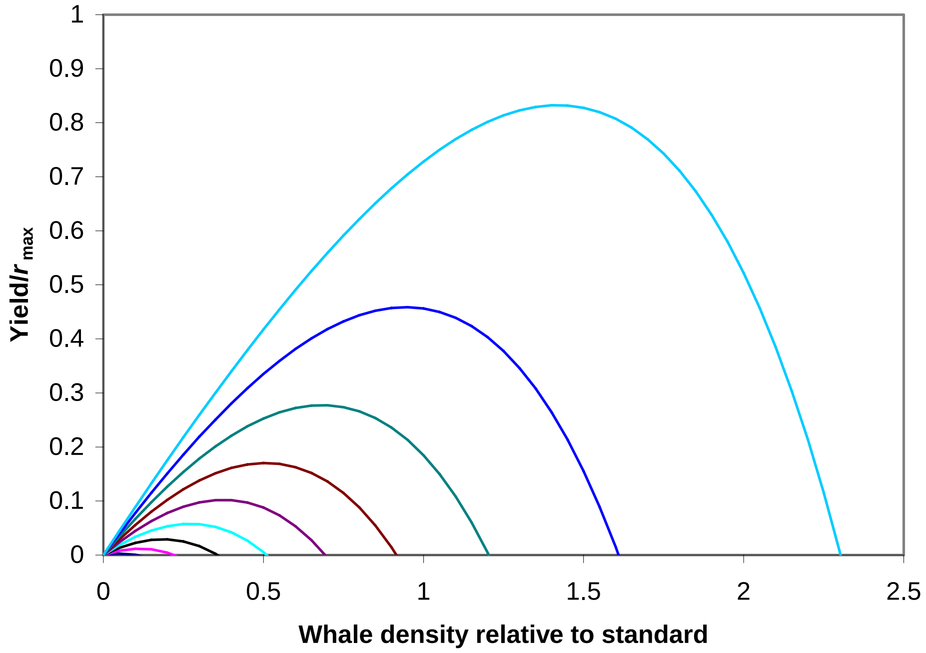


Fig. 5. Predicted family of sustainable yield curves as a function of absolute population level.

This formulation is in accordance with the conventional way of expressing families of net recruitment curves, but it is somewhat misleading in that it hides the fact that K itself depends on q. Fig. 6 shows the same curves as in Fig. 5, but parameterised in this more conventional way.

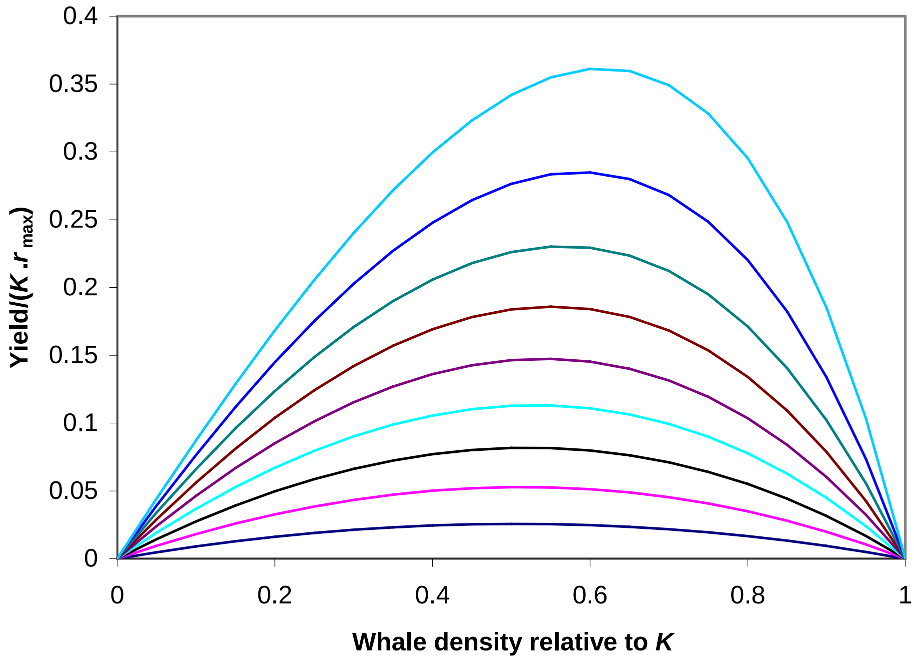
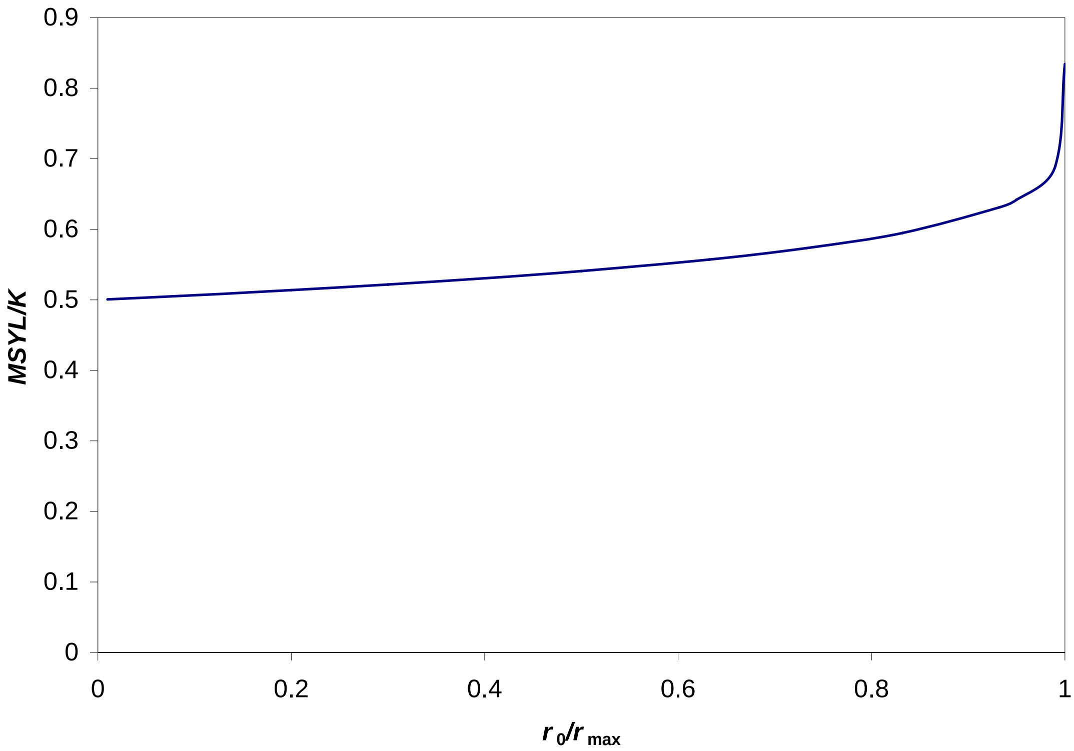


Fig. 6. Predicted family of sustainable yield curves, scaled to *K* on both axes.

The relationship between the MSY level (relative to *K*) is shown in Fig. 7. We see that *MSYL* lies in the range 0.5*K* to 0.65*K* except for very high-quality habitats. For medium quality habitat (as defined above), *MSYL* = 0.56*K*. From this admittedly rather theoretical perspective, the conventionally assumed value of *MSYL* = 0.6*K* for baleen whales, seems not to be unreasonable. There is no closed algebraic expression for the *MSYR* and the *MSYL* for this model.



The standard deviation of r is given by:

$$\begin{aligned} SE(r) &= r_{\max} e^{-z(a-bx)}\, e^{\frac{1}{2}z^2\sigma^2} \sqrt{e^{z^2\sigma^2} - 1} \\ &= \left(r_{\max} - \bar{r}\right)\sqrt{e^{z^2\sigma^2} - 1} \\ &\approx z\sigma\left(r_{\max} - \bar{r}\right) \end{aligned} \tag{12}$$

The variability of the net recruitment rate is thus expected to increase with increasing whale density, but even at low population sizes there will be some variability in net recruitment rate, except in ideal habitats.

Fig. 8 shows the expected distribution of net recruitment rate for three levels of population size or habitat quality . In good quality habitats, the distribution of r at low population sizes will be highly skewed, with r being close to $r_{\max}$ in most years, and with deviations only being seen in poor years (rightmost, strongly peaked curve). In medium-quality habitats, and/or at medium population levels, both positive and negative deviations relative to the median conditions can be manifest (middle curve) while at high population levels r will fluctuate around a zero long-term mean (leftmost, shallow curve).

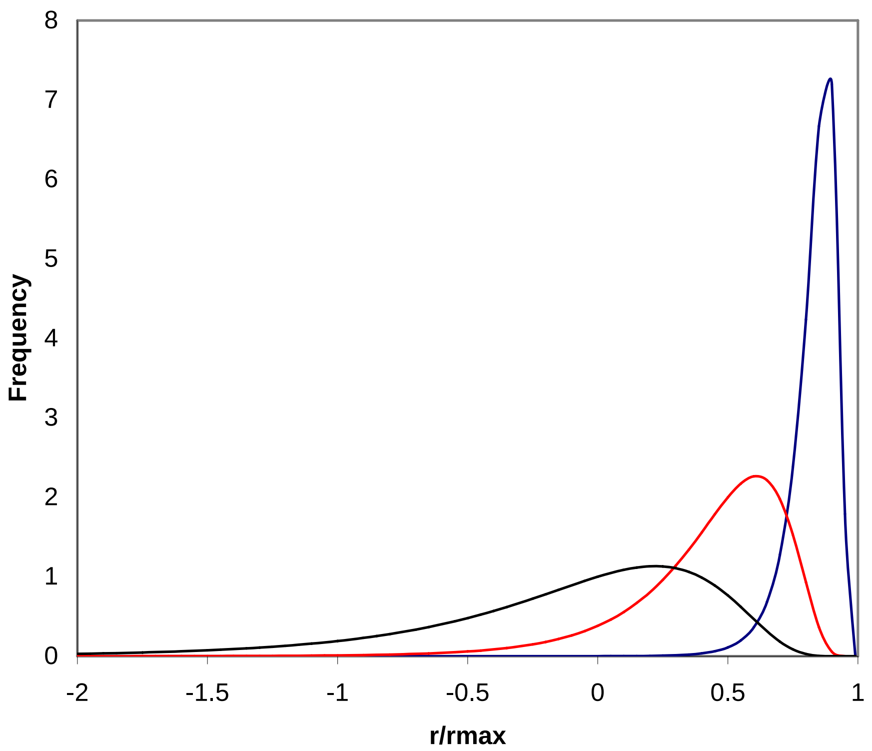


Fig. 8. Frequency distribution of net recruitment rate for three different levels of habitat quality and/or population relative to *K* (see text).

Serial correlation and variability in population size

The level of variability in population size that results from a given level of variance in the net recruitment rate will depend on the level of serial correlation in the environmental variability. If good and bad years occur independently, the population will buffer the variability in the net recruitment rate, but if longer runs of good and bad years occur, substantial variation in population size can result. Assuming that the population is subject to constant fishing mortality and in a dynamic equilibrium, then by applying first-order perturbation theoiry around the mean stock size, the approximate CV of the stock size is given by:

$$CV(x) \approx SE(r)\sqrt{\frac{1+\rho(1+r')}{-r'\left(2+r'\right)\left(1-\rho(1+r')\right)}} \tag{13}$$

where $r' = \partial r/\partial x = zb\left(\overline{r} - r_{\max}\right)$ and ρ is the correlation between the environmental conditions in successive years.

In practice on would estimate the variability in stock size through simulation modelling, and therefore it is not worthwhile to seek a more precise formula. Fig. 9 shows the relationship between stock size and its CV for different values of ρ. An important qualitative result is that the CV in stock size increases with the equilibrium stock size.

This is the reverse of the results of some previous studies (e.g. Beddington and May 1977), which predicted that stocks subject to harvesting would be less stable when held to lower levels, because density dependence leads to greater stabilising feedback at higher stock sizes. The previous studies treated the perturbations as exogenously given, and did not account for the possibility that environmentally driven perturbations that result in food shortage can cause larger proportional impacts on populations at higher stock levels.

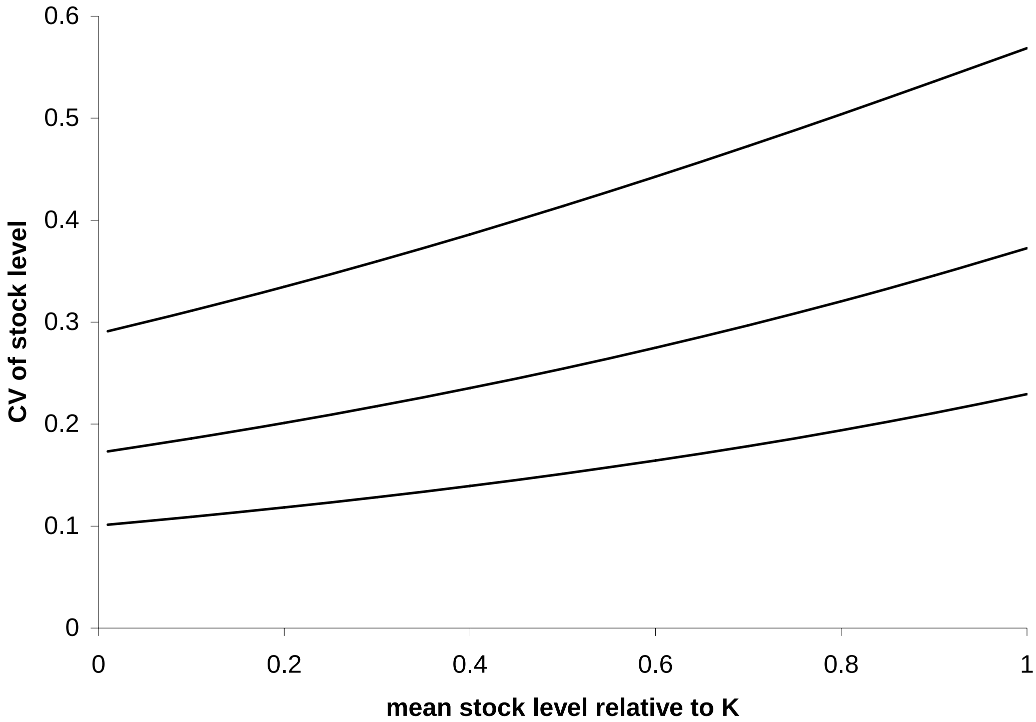


Fig. 9. CV of stock level as a function of mean stock level (under constant fishing mortality), for three different values of ρ. Lower curve: $\rho = 0$; middle curve $\rho = 0.5$; upper curve $\rho = 0.8$. Other parameters are: $r_{\text{max}} = 0.1$, $r_0 = 0.063$ (= medium habitat quality).

Examples

There are not many examples where the variance in net recruitment rate has been explicitly calculated, but there are several cases where the information exists in principle to do so.

SW Atlantic right whales

The mean calving interval exhibits statistically significant fluctuations (Cooke et al. 2003), which appear to be correlated with environmental conditions in the known feeding grounds in South Georgia, and with the breeding success of other krill predators feeding in that area (Leaper *et al.* 2006). Although the normal calving interval for a reproductive female is three years, in some years a proportion of the females due to calve postpone the calving for two further years, causing a five-year calving interval. No statistically significant variation was found in any other demographic parameters, although the power to detect changes in parameters other than calving interval was probably low. A conservative estimate of the variability in net recruitment rate can be obtained by supposing that at the current, still relatively low population level, all parameters other than the calving interval remain constant.

Although the analysis of Cooke *et al.* (2003) was not directed specifically at estimating the variance of the net recruitment rate, a rough indication can be gained from the results from the results presented. On the log-odds scale, the parameter representing the probability of whales postponing a calving had a median value of -1.8 with a standard deviation of 0.9. This implies that the proportion of mothers who are scheduled to calve (i.e. 3 years elapsed since previous calving) but who fail to do so, will range from about 5% in "good" years (environmental conditions 1 standard deviation above the mean), to about 15% in median years, to about 30% in poor years (environmental conditions 1 standard deviation below the mean). The population appears still to be low compared to its historical level (IWC 2001). Juvenile and adult survival rate estimates are high, and the median rate of increase may be close to r_{max}.

Western gray whales
This population is estimated at around 120 individuals (Cooke *et al.* 2007) is also considered to be low compared to historical levels (Weller *et al.* 2002). The calving cycle appears to fluctuate, with 2-year intervals predominating in good conditions, and 3-year intervals predominating in poor conditions. In addition to the influence on the calving interval, varying conditions also manifest themselves through the proportion of "skinny" animals (Weller *et al*. 2007), but has not yet been determined whether observed body condition is related to reproduction and/or survival. Adult survival rate is high (0.97-0.99), but that of yearlings less so (0.6-0.9), such that the median r is probably not as close to r_{max} as it is for SW Atlantic right whales. There are insufficient data for a quantitative estimate of the variance in r.

Eastern gray whales
This population may be in the neighbourhood of its mean K (Rugh *et al.* 2007). The population had been increasing until the late 1990s, but a period of low calf production and increased mortality was observed during 1999-2001 (LeBoeuf *et al*. 2000; Gulland *et al.* 2005), which appears to have reduced the population (Rugh *et al.* 2005). Based on stranding rates, mortality during 1999-2000 was eight times the previously prevailing rate (Gulland *et al.* 2005). Given the median natural mortality rate estimate of 0.018 for 1967-96 (Wade 2002), this means that quite a substantial mortality involving over 20% of the population may have occurred over these two years. This possibility is broadly consistent with decline in abundance estimates, but there is much uncertainty. The overall picture is consistent with the prediction of the model that population fluctuations can be quite large near K.

Estimation of MSYR and MSYL in the presence of environmental variability

From a scientific and management perspective, the effect of environmental variability on the estimation of yield curves is perhaps an important as the effect on the yield curves themselves. This was investigated using simulation studies. Time series of population size estimates were generated from an hypothetical population subject to environmental variability with dynamics in given by the model of this paper. These data were then used to estimate *MSYR* and *MSYL* by fitting: (i) the true model; and (ii) the standard deterministic Pella-Tomlinson model. The purpose of this analysis was to investigate the consequences of ignoring environmental variability when fitting population models or trends to estimate *MSYR* and *MSYL*.

The hypothetical population was perturbed to $0.25K$ and allowed to recover for a period of 10, 20 or 30 years. The dynamics of the simulated population were in accordance with the model of this paper, with parameters: $r_{max} = 0.10$; q (habitat quality) = 0.25 (poor), 0.632 (medium), and 0.9 (high). The values of r_0, *MSYR* and *MSYL* implied by these parameters are listed in Table 1. Three levels of variability in environmental conditions were tested: $\sigma = 0$ (no variability); $\sigma = 0.5$ (medium variability); and $\sigma = 1$ (high variability). The stock level was monitored annually through population estimates with CVs of zero, 0.2 or 0.5. The set of combinations for which data sets were generated are listed in Table 2. 1,000 simulated data sets were generated randomly for each set of parameter values.

The Pella-Tomlinson net recruitment model conventionally used for baleen whales is given by:

$$r(x) = r_0\left(1 - \left(x/K\right)^z\right) \tag{14}$$

The parameters of interest are $MSYR = r_0\, z\big/\left(1+z\right)$, $MSYL = \left(1+z\right)^{-1/z}$

Both the Pella-Tomlinson model and the model of this paper were fitted to each simulated data set by maximum likelihood. The 5th, 50th and 95th percentiles of the resulting parameter estimates are listed in Table 2.

[Table and discussion to be supplied as addendum.]

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