# Modelling the past and future of whales and whaling

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Historical reconstruction of the population dynamics of whales before, during and after exploitation is crucial to marine ecological restoration and for the consideration of future commercial whaling. Population dynamic models used by the International Whaling Commission require historical catch records, estimates of intrinsic rates of increase and current abundance, all of which are subject to considerable uncertainty. Population genetic parameters can be used for independent estimates of historical demography, but also have large uncertainty, particularly for rates of mutational substitution and gene flow. At present, demographic and genetic estimates of pre-exploitation abundance differ by an order of magnitude and, consequently, suggest vastly different baselines for judging recovery. Here, we review these two approaches and suggest the need for a synthetic analytical framework to evaluate uncertainty in key parameters. Such a framework could have broad application to modelling both historical and contemporary population dynamics in other exploited species.

The legacy of commercial whaling has provided an experiment in conservation biology on a grand, if tragic, scale. Populations of baleen whales (suborder: Mysticeti) and the sperm whale *Physeter macrocephalus* (suborder: Odonotoceti) have been systematically hunted to near extinction during the past two hundred years. This exploitation almost eliminated an entire trophic level of the marine ecosystem, particularly in the southern hemisphere. In spite of decades of protection, some populations, including those of the North Atlantic right whales *Eubalaena glacialis*, the North Pacific right whales *Eubalaena japonica*, the western Pacific gray whale *Eschrichtius robustus* and the southern hemisphere blue whales *Balaenoptera musculus*, have yet to show signs of recovery [1].

Here, we review recent efforts to model the dynamics of exploited whale populations in the context of both ecological restoration and potential future commercial whaling. Estimating the former abundance of whale populations or 'stocks' and reconstructing the historical trajectory of their decline are essential to make an accurate assessment of the true impact of whaling on the marine ecosystem, and to establish a baseline for judging the recovery of whale stocks. A baseline of pre-exploitation abundance is not simply of historical interest: it has important consequences for the future management of whales. If the pre-exploitation abundance of a population is underestimated, the level of current recovery will be overestimated and could increase pressure to resume hunting of depleted populations prematurely. It could also mask future responses of whale populations to environmental and ecological changes, such as global warming, ozone depletion and overfishing by humans [2–5]. These so-called 'regime shifts', in effect, change the carrying capacity of the marine ecosystem and could alter the dynamic response of recovering whale populations.

## Models of whale population dynamics and historical reconstruction

The conventional approach to estimating pre-exploitation abundance of whales has been to summarize catch records from logbooks and add the total number of whales killed to estimates of current abundance from sighting surveys or capture−recapture analyses of naturally marked individuals [6]. If accurately reported, total past catches (Box 1), added to current abundance (if accurately estimated) should give an upper limit to the pre-exploitation population size. These are corrected downward to account for the difference between reproduction and natural mortality (i.e. net reproduction, $r$) during the period of exploitation and recovery following protection. The process of correction usually involves applying a generalized logistic model of population dynamics in which the difference between reproduction and natural mortality is assumed to be density dependent, with net annual reproduction declining continuously (although not necessarily linearly) from a maximum value ($r_{max}$) when the population is very depleted, to zero when the population is at its environmental carrying capacity, $K$. Given a time series of catches, an estimate of current abundance and a value of $r_{max}$, the model can extrapolate backwards to reconstruct historical trends in abundance, including pre-exploitation abundance, and forwards under various scenarios of protection or exploitation (Box 2).

This approach is illustrated in the recent comprehensive assessment of southern right whales *Eubalaena australis* (Figure 1) [7]. Summaries of available logbooks document catches of ~110 000 southern right whales throughout the southern hemisphere, most of which occurred during the first half of the 19th century.

## Box 1. How many whales were killed?

A time series of catch records is essential for modelling the dynamics of exploited whale populations. However, the accuracy of these records differs considerably across the long history of exploitation. The hunting of whales is ancient in some cultures and the numbers taken before European contact can only be approximated or guessed. Early commercial whaling along the coastal North Atlantic dates back to the 11th century [45] and along coastal Japan to the late 16th century [46]. The broad outline of these hunts is known but detailed records are not available. Records, in the form of ship logbooks, improved during the 18th and 19th centuries, but still include large gaps and are difficult to assemble for a particular stock (e.g. the North Atlantic humpback whale [26]).

The official catch records of modern whaling, held by the International Whaling Commission (IWC), were long considered to be accurate for the purposes of population modelling. It is now known that these records were subject to large-scale, systematic falsification. The pelagic whaling fleet of the Soviet Union, operating from 1948 to 1972, killed >260 000 whales in the southern hemisphere alone, but reported only 185 000 of these to the IWC [47]. The full extent of this illegal hunting was revealed only in 1994 [48], after the end of the Cold War and, consequently, these records were not used in previous models of population dynamics or the role of whales in the ecosystem (Box 3). A revised summary of catches, corrected for the illegal Soviet hunting, shows that the total number of whales killed in the southern hemisphere during the 20th century was >2 000 000 [49]. This total does not include catches of southern right, sperm and, to a lesser extent, humpback whales during the 18th and 19th centuries [50].

Comparable summaries of total whales killed are not available for the North Atlantic or North Pacific Oceans, where commercial and aboriginal hunts have a much longer history, and where falsification of modern whaling records is less well documented. However, recent revelations that Japanese coastal whaling stations falsified catch records during the 1960s and 1970s [51], and evidence of continued undocumented catches sold in commercial markets of Japan and Korea [52,53], inevitably raise questions about the certainty of data underlying current population models.

## Box 2. The basic model of population

Most historical reconstructions of exploited whale populations use some variant of a basic discrete time, generalized logistic model of population dynamics (Eqn I) [54,55],

$$P_{t+1} = P_t + r_{max}P_t(1 - (P_t/K)^z) - C_t, \qquad \text{(Eqn I)}$$

Where $P_t$ is total population size during year $t$; $r_{max}$ is the intrinsic rate of increase; that is, the maximum net rate of reproduction that the population can achieve; $K$ is the carrying capacity, which is assumed to be equal to abundance before exploitation; $z$ is the exponent setting the maximum sustainable yield level (MSYL); that is, the size of the population, relative to $K$, at which the maximum number of whales can be taken without changing the population size (e.g. 2.39 when MSYL is 60% of $K$, as conventionally assumed for whales); and $C_t$ is the total catch in terms of numbers of whales during year $t$.

Given an annual catch series, a value for $r_{max}$ and a value for MSYL, Equation I can be used to calculate population size for each year from the start of exploitation until the present ($t = 0$ to $t_{current}$). This assumes that the population at the start of the year of first catches was at the environmental carrying capacity ($P_0 = K$) and that catches were not age or sex biased. Given only one estimate of current abundance, as in the southern right whale example (Figure 1, main text) pre-exploitation abundance is found by successively substituting initial values for $P_0$ until the trajectory 'hits' the estimated current population size. The basic model can also project future trends under various scenarios of exploitation, as in the predicted decline of the 'J' stock of the North Pacific minke whales *Balaenoptera acutorostrata scammoni* based on estimates of unregulated catches sold in Japanese and Korean market [56,57].

As part of its comprehensive assessment of stocks, the International Whaling Commission has often used an age- and sex-structured variant of the basic model, referred to as BALEEN II [58,59]. BALEEN II has been used with both maximum likelihood and Bayesian estimators of population parameters, as well as with other approaches (e.g. [15,37]). The model is implemented in two programs: 'HITTER' and 'FITTER' [60]. HITTER implements the approach described above, finding a population trajectory that 'hits' a single abundance estimate by using fixed values of $r_{max}$ and MSYL. FITTER finds a trajectory that best 'fits' a time series or trend in abundance by estimating the required population parameters, such as $r_{max}$ and MSYL.

Documented catches were adjusted upwards by a factor of 1.35, to a total of ~ 150 000, to account for whales struck but lost during early whaling operations (i.e. whales killed but not recovered and thus not entered into logbooks). This total includes >3400 right whales killed illegally by the Soviet Union during the 1960s [8] but is known to be incomplete as a result of missing logbooks from 18th- and 19th-century whaling (Box 1). Current population size was based on a combined estimate of ~ 1600 adult females from 11 breeding stocks. This was adjusted upward to account for males and juveniles, giving a total population estimate of ~ 7600 animals for the year 1997. An upper value of 7.5% $y^{-1}$ for maximum net reproduction ($r_{max}$) was estimated from three of the recovering stocks [9]. Two lower values of $r_{max}$ were chosen to account for uncertainty in this parameter.

The historical trajectories of the different model runs showed a sharp decline during the mid 1800s, with a slow increase following international protection in 1931 and another decline resulting from illegal Soviet catches during the 1960s (Figure 1). The lowest point of population abundance ($N_{min}$) was in 1920, when as few as 60 adult females were estimated to have survived. The extrapolations of pre-exploitation abundance ranged from ~ 60 000 to 100 000 animals, with higher values of $r_{max}$ resulting in lower extrapolations of pre-exploitation abundance

(as expected from the generalized logistic model). The Soviet catches had the effect of delaying the current level of recovery by >20 years. With continued protection from hunting, full recovery to historical $K$ will require another 40–50 years if $r_{max}$ is 7.5% $y^{-1}$, and more than a century if $r_{max}$ is 4% $y^{-1}$.

### Accounting for uncertainty in the basic model

The trajectories derived by the basic model (and, consequently, the extrapolated pre-exploitation abundance) are very dependent on the input specifications, which often have considerable uncertainty. Uncertainty is usually accounted for by running the model with a 'base case' set of reasonable or estimated values and a limited range of fixed values for key parameters, such as $r_{max}$, (e.g. Figure 1). This limits the parameter space that can be explored using the basic model and often results in unjustified confidence in the base-case reconstruction.

To avoid the constraints of fixed values, Whitehead [10] used a randomized resampling scheme to account for uncertainty in reconstructing the historical trajectory of global sperm whale abundance (Figure 2). He applied the basic population dynamic model, modified for the lower
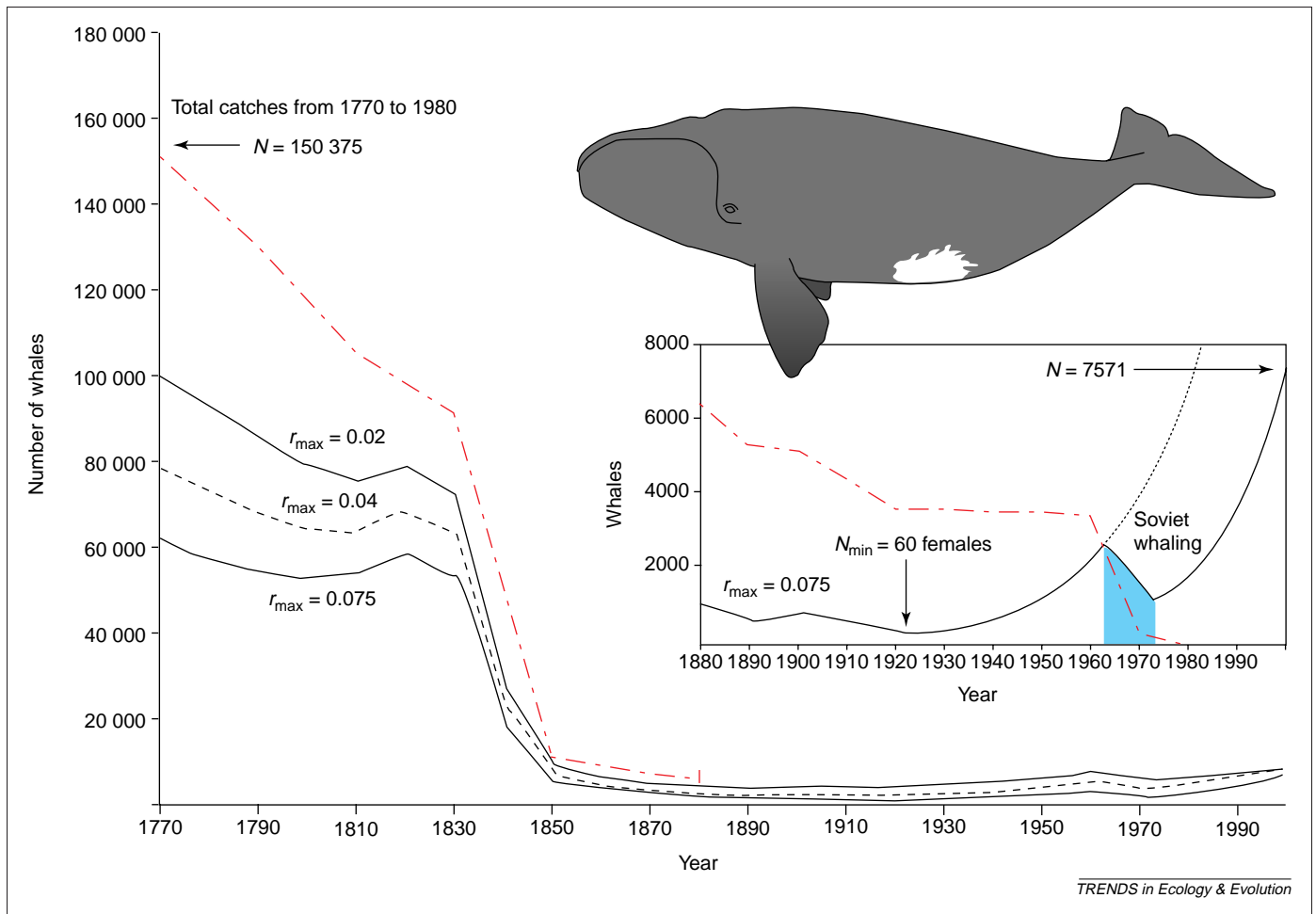
**Figure 1**. Historical reconstruction of the abundance of southern right whales from the start of whaling in 1770 to 1997. The reconstruction is based on the basic population dynamic model (Box 2), using the estimated current abundance ($N = 7571$), historical catch records and fixed input values for demographic parameters. Reconstructions for three values of maximum net reproduction ($r_{max}$) are shown: 0.02, 0.04 and 0.075. To better mirror population decline, total cumulative catches of 150 375 whales (red dashed-dot line) are plotted in reverse time, that is, from 1770 to present, from 1780 to present and so on. Inset shows an expanded scale for the period of 1880 to present (year 1997) with an arrow pointing to the year of minimum population size when as few as 60 mature females were estimated to have survived. The dotted line shows the predicted recovery if there had been no illegal hunting by the Soviet Union. Reproduced, with permission, from [7].

rate of reproduction of sperm whales, to a fixed set of 'best' parameter estimates, as well as other sets of values drawn at random for each run from the coefficient of variation or range of each parameter. For example, the best estimate of current global abundance ($N = 360\,000$ for the year 1999)
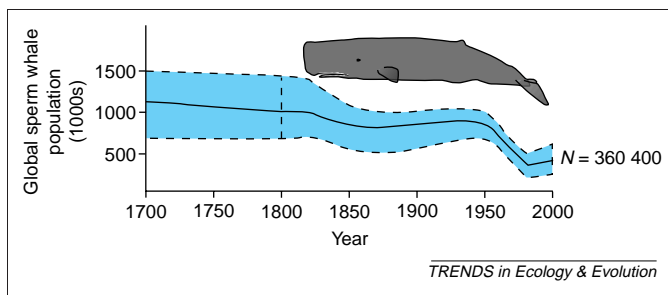


**Figure 2**. Estimated population trajectories for the global sperm whale population from 1700 to 1999. The solid line shows the trajectory based on the best estimate of current and historical abundance. The shading shows the range of 20 representative trajectories generated using randomized resampling from the estimated or reasonable range of values for several model parameters: current abundance, proportional distribution among oceans, depletion before logbook records, maximum rate of increase, maximum sustainable yield levels, correction for open-boat catches and correction for modern catches. The dashed vertical line marks the period before the year 1800, for which catch records are very limited. Reproduced, with permission, from [10].

was based on regional shipboard and aerial surveys covering $\sim 24\%$ of primary sperm whale habitat with an extrapolation to unsurveyed areas using several scaling factors (e.g. depth, productivity and the distribution of historical catches). For the randomized run of the model, values of current abundance were drawn from a normal distribution using the mean and coefficient of variation of the best estimate. Where empirical estimates of parameters were unavailable, such as the correction for whales struck but lost, values were drawn from a uniform distribution with a 'reasonable range' [10]. The model was run 1000 times and $\sim 95\%$ confidence intervals were obtained for the historical trajectory (and pre-exploitation abundance) by discarding the 25 lowest and highest values. If the run failed to reach the chosen value of current abundance, the combination of inputs was discarded and a new set chosen. From this, pre-exploitation abundance was estimated to be 1 110 000 (95% CI: 672 000–1 512 000), with the current population at $\sim 32\%$ of this former abundance. This is much lower than most previous estimates of current abundance or recovery, which did not account fully for uncertainty in many of the model parameters [10].

## Looking to the future to reconstruct the past

Although uncertainty in historical reconstructions is better represented by the randomization procedure used in the sperm whale model, the approach does not, by itself, reduce this uncertainty. In theory, uncertainty in the historical extrapolation of a density-dependent model can be reduced by fitting a trajectory to a time series of abundance estimates for a recovering population (e.g. 'FITTER', Box 2). This is because the net reproduction rate of a formerly depleted population is expected to decline towards zero as the abundance of the population recovers towards $K$. A trajectory fitted to this trend should provide a forward extrapolation of $K$ that is consistent with the backward extrapolation of $K$. In practice, however, this approach has revealed more, rather than less, uncertainty in the historical reconstruction of the eastern Pacific gray whale, the population with the longest documented time series of recovery.

Gray whales have been taken as part of aboriginal hunts since before European arrival and have been exploited commercially on both sides of the North Pacific for the last two centuries. The 'Asian' or western stock of gray whales survives as a remnant population of perhaps 100 animals [11]. By contrast, the eastern stock, considered to have been commercially extinct since the end of the 19th century, has now increased to > 26 000 whales (http://www.iwcoffice.org/conservation/estimate.htm). However, the basic density-dependent model and its variants (e.g. BALEEN II, Box 2) cannot reconcile the current abundance and continued increase of this population with the historical catch records [12,13]: the population seems to have overshot its historical $K$ by 200–300%. A consistent trajectory can be achieved only by assuming large historical 'adjustments', such as under-reporting historical catches by a half to a third [14], or by assuming density-dependent selection on life-history parameters resulting in long-period oscillations in abundance [15]).

As an alternative to backward extrapolation using uncertain historical records, Wade [16] considered only the 'known' catch data available since the start of shore-based surveys during 1966–1967 (ignoring all catches before this time), and the trend in the 21 years of abundance surveys. Using several modifications of the basic model and incorporating Bayesian statistical estimators, Wade [16] concluded that the variance of the time series of abundance estimates was greater than was estimated previously. As a consequence, previous models had derived estimates for $K$ and other population parameters (e.g. rates of increase) that were overly precise. Taking this additional variance into account, the 95% confidence intervals of predicted current carrying capacity ($K$) were much wider than calculated in previous models, extending from 19 980 to 66 720 (Figure 3). Consequently, there was a moderately large probability (> 0.20) that the current population is still below 50% of $K$ [16].

## Looking to the deep past to restore the future

Estimates of long-term effective population size based on the diversity of genetic markers offer an alternative to the demographic estimation of pre-exploitation abundance of
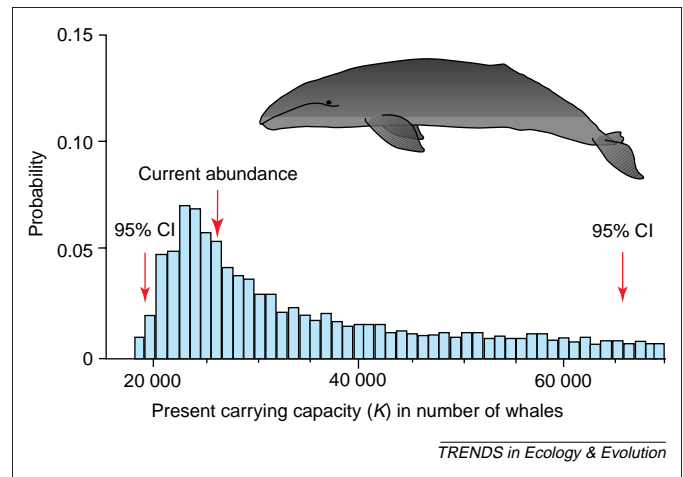


**Figure 3**. Estimated abundance at current carrying capacity ($K$) of the eastern Pacific gray whale. Estimates are based on Bayesian parameter estimation and a generalized logistic population model with an additional variance component previously unaccounted for in the survey trend. The prior distribution was uniform from $N = 17\,000$ to $70\,000$. Small arrows indicate the 95% confidence intervals for estimated current carrying capacity ($N = 19\,980$–$66\,720$). The large arrow indicates the point estimate of abundance ($N = 26\,300$) for the last season of the sighting survey, 1996–1997 (http://www.iwcoffice.org/conservation/estimate.htm). Reproduced, with permission, from [16].

whales (and other exploited species). Neutral genetic diversity reflects population size and changes across deep ecological time because this diversity is directly related to population size for a given mutation rate. Large, stable populations harbour greater diversity than do small or fluctuating populations and, for a given population size, genetic markers with high rates of mutational substitution are more variable than are those with low rates. For the maternally inherited mitochondrial (mt) genome (a commonly used marker in studies of historical demography [17]), this relationship is given by the simple formula $\theta = 2N_{e(f)}\mu$, where $\theta$ is diversity, $N_{e(f)}$ is the long-term historical number of breeding females in a populations, and $\mu$ is the mutational substitution rate per generation [18]. Genetic diversity, in the form of $\theta$, is lost if a population declines, but is not lost as rapidly as the decline in census population size except in an extreme 'bottleneck'.

In an effort to establish restoration goals for exploited whales, Roman and Palumbi [19] used estimates of $N_{e(f)}$ for three species, humpback *Megaptera novaeangliae*, fin *Balaenoptera physalus* and minke *B. acutorostrata* whales, in the North Atlantic Ocean, as an alternative to historical extrapolations from demographic models. From the relationship $\theta = 2N_{e(f)}\mu$, Roman and Palumbi [19] solved for $N_{e(f)}$ by estimating $\theta$ from published population surveys of mtDNA control region sequences and estimating $\mu$ from the observed divergence of mtDNA among baleen whales, assuming a molecular clock calibrated with the fossil record [20,21]. A coalescent-based, maximum-likelihood analysis [22] was used to adjust the estimated $\theta$ for an upward bias resulting from gene flow (i.e. $N_{m}$). Humpback and fin whales are distributed globally but the estimates of maternal gene flow from other oceans were low (less than one female per generation), discounting, although perhaps not eliminating entirely, some historical influence [23,24]. Estimates of $N_{e(f)}$ were then converted to population census size ($N_{C}$) using adjustments for

demographic parameters such as sex ratio, generation time and the proportion of breeding adults [25]. The resulting estimates were surprisingly high, suggesting a long-term population of nearly 1 000 000 for the three species combined in the North Atlantic before whaling. These 'genetic population estimates' are ten- to 20-fold larger than current demographic estimates of fin and humpback whales and >tenfold larger than assumed pre-exploitation abundance of humpbacks based on whaling records [26].

Although admitting the uncertainty of the genetic estimates, Roman and Palumbi [19] suggest that previous historical reconstructions are biased downward by incomplete catch records, intentional underreporting of catches and high struck-but-lost rates. Some whale biologists, however, find these genetic estimates implausibly high given trends in current populations, and some whaling historians reject Roman and Palumbi's argument as based upon a misunderstanding of the nature of historical catch records [6,27].

## Future directions

An improved understanding of the dynamics of whale populations and pre-exploitation abundance will require refinements in parameter estimation and a better integration of genetic and demographic approaches. For demographic models, an important place to start would be a comprehensive review of world whaling records. This is underway (see History of Marine Populations, http://www.hmapcoml.org) but, given known losses of logbooks and ambiguous recording practices (e.g. failure to record species or reporting only quantities of extracted oil, rather than numbers of whales taken), some of this history will never be recovered. Where whaling records are incomplete, estimation of historical adjustments could be improved by examination of multiple historical sources. These adjustments can have a dramatic impact on model extrapolations. For example, the extrapolated pre-exploitation abundance for the southern right whale would nearly double by assuming a struck-but-lost rate of 2.35 calculated for the North Pacific right whale hunt [28], rather than the rate of 1.35 used in the assessment.

Improved estimates of life-history parameters are also crucial to demographic models and have greater potential for verification through ongoing studies of living whales. In the southern right whale assessment, for example, the upper value of 7.5% $y^{-1}$ for $r_{max}$ was based on studies of only three of the 11 known stocks. Some of the other eight stocks have shown little or no evidence of recovery and might be functionally extinct. To avoid this overrepresentation of rapidly recovering stock, greater emphasis is needed on weakly recovering or declining stocks [11,29]. Studies of these struggling populations can provide clues to the slow and variable recovery of other stocks, particularly the possibility that rates of net reproduction might decrease, rather than increase, at very low levels of abundance, a phenomenon referred to as depensation or the Allee effect [30,31]. In sperm whales, for example, there is evidence that past hunting directed at the largest (and oldest) males resulted in diminished reproductive

success because mature females do not accept younger males as 'substitute' mates [32]. These effects, and the influence of cultural traditions and metapopulation structure (Box 3), require further attention in models of exploited whale populations.

Regardless of model refinements, backwards extrapolations from current estimates of demographic parameters are, in effect, untestable when historical catch records are uncertain [16]. Here, genetic information can play a crucial role by providing independent estimates of historical parameters to test the fit of trajectories. Long-term effective population size, as estimated by Roman and Palumbi [19], is one such parameter. Although genetic and demographic estimates are far apart for the fin and humpback whale, inclusion of a wider range of values for mutational substitution and gene flow, as well as demographic adjustments, might result in overlap, if not close agreement of the approaches. For example, Roman and Palumbi [19] considered substitution rates for baleen whale control region to be in the range of $1-7\%$ million $y^{-1}$ but rates estimated from the well studied human–chimpanzee divergence are higher and more variable (from 2.5% to 26% million $y^{-1}$) [33]. These higher substitution rates would result in proportionately lower genetic estimates of effective population size for whales. Conversely, lower rates of net reproduction and higher

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**Box 3. The dynamics of whale populations and ecological restoration**

Results of the early models of whale population dynamics by the International Whaling Commission stimulated the first efforts to consider the impact on the marine ecosystem of these removals. Mackintosh [61] and Laws [62] used historical trajectories to provide rough approximations of the total standing biomass of whales in the Southern Ocean and the approximate food consumption before and after exploitation. However, these estimates were based on whaling records that included falsified (greatly underreported) Soviet data. These early efforts must be revised using improved models and estimates of krill consumption if we are to understand the ecological impact of the removal of these primary consumers and the fate of 'surplus krill' released by the decline of baleen whales [63,64]. Similarly, Whitehead [10] notes his revised estimates of current sperm whale abundance and level of recovery are considerably lower than generally assumed and, consequently, that consideration of the past and current ecological role of sperm whales requires revision.

More recently, Springer *et al.* [65] have suggested that depletion of baleen whales by commercial hunting forced killer whales *Orcinus orca* in the North Pacific to switch to other prey, causing sequential declines in populations of pinnipeds and sea otters. Although other evidence for this hypothesis is weak, it underscores the need to consider the impact of whaling on other predator-prey relationships, and to examine trends in population declines as well as total removals [66]. Finally, some species of baleen whales are structured into complex metapopulations as a result of maternal fidelity to migratory destinations [43,67]. Some regional subpopulations or stocks were essentially extirpated by whaling (such as blue whales around South Georgia, right whales in much of the North Atlantic and humpback whales off New Zealand), with no recovery evident over periods ranging from 40 to 400 years [68]. Did whaling eradicate the cultural memory of migratory connections to such habitats? Will these empty habitats be rediscovered and colonized as adjacent populations recover and expand? Such populations represent fascinating long-term experiments in both ecological restoration and metapopulation dynamics.

struck-but-lost rates would result in proportionately larger demographic estimate of pre-exploitation abundance [19].

## Conclusions

Reconciling demographic and genetic approaches to the reconstruction of whale population dynamics could serve as a useful case study with broad application to modelling both historical and contemporary population dynamics in a range of organisms, from exploited marine fish to emerging infectious diseases. This will require a common analytical framework to link demographic and genetic models and to evaluate uncertainty in key parameters, such as rates of maximum increase, struck-but-loss rates, mutation rates and gene flow. A promising direction for future development is suggested by recent efforts to model the demographic history of viral populations by integrating gene genealogies and genetic diversity using the coalescent process within a Bayesian framework [34–36]. This has many parallels with the use of a Bayesian framework in models of whale population dynamics and uses many of the same parameters [16,37].

A synthetic model could extract more information from recent demographic history by incorporating multiple indices of genetic diversity and multiple nuclear genetic markers. These respond differently to the timing and intensity of population change, a property exploited in tests to detect selection and population bottlenecks [38,39]. Haplotype diversity of mtDNA, for example, decreases more rapidly than $\theta$ during population decline and the number of extant haplotypes provides an absolute minimum value for the number of females ($N_{min}$) surviving a population bottleneck (N.J. Patenaude, PhD thesis, University of Auckland, 2002). Jointly fitting alternate indices for multiple genetic markers along the entire historical trajectory of these populations should better explain the range of genetic diversity observed among baleen whale populations, including low levels consistent with intensive exploitation [40–42], as well as high levels consistent with large long-term population sizes [21,43].

Ultimately, however, backward and forward extrapolations of demographic, genetic or synthetic models of whale population dynamics must stand the test of time. Predictions of historical carrying capacity can be tested only by observing the dynamics of whale populations over the many decades (or centuries) required for a full recovery. Arguably, an experiment in recovery is underway, but not yet complete, for the eastern Pacific gray and western North Atlantic humpback whales. However, these ecosystems have been subject to considerable perturbations from human activities [4,44], potentially affecting the present environmental carrying capacity for whales. The primal state of the oceans is somewhat better represented in the southern hemisphere, where the krill-based ecosystem is less complex and has a shorter history of perturbation. Here, recovery of the great southern stocks of whales could be allowed to continue unimpeded, offering a chance to document ecological restoration on a scale that is a fitting match to its past disruption.

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