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Selection-delayed population dynamics in baleen whales and beyond

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Abstract While it is known that population cycles are driven by delayed density-dependent feedbacks, the search for a common feedback mechanism in natural populations with cyclic dynamics has remained unresolved for almost a century. To identify the existence and cause of delayed feedbacks I apply six age- and sex-structured population dynamics models to seven species of baleen whales (suborder *Mysticeti*) that were heavily depleted by past commercial whaling. The six models include a predator-prey model with killer whale (*Orcinus orca*) as the predator, and five singe-species models based on i) exponential growth, ii) density-regulated growth, iii) density-regulated growth with depensation, iv) delayed density-regulated growth and v) selection-delayed dynamics. The latter model has a density-regulated growth rate that is accelerated and decelerated by the intra-specific natural selection that arises from the density-dependent competitive interactions between the individuals in the population. Essential parameters are estimated by a Bayesian statistical framework, and it is shown that baleen whales have a delayed recovery relative to density-regulated growth. The time-lag is not explained by depensation, or by interactions with prey or predators. It is instead resolved by a selection-delayed acceleration of the intrinsic growth rate. The results are discussed in relation to the literature on cyclic dynamics, and it is noted i) that selection-delayed dynamics is both theoretically and empirically sufficient for cyclic population dynamics, ii) that it is widespread in natural populations owing to the widespread occurrence of otherwise unexplained phenotypic cycles in populations with cyclic dynamics, and iii) that there is a lack of empirical evidence showing that predator-prey interactions is a sufficient cause for the cyclic dynamics of natural populations. The conclusion stresses the importance of intra-specific delays in cyclic dynamics, and suggests that it is the acceleration of the growth rate, and not the growth rate itself, that is determined by the density-dependent environment.

Keywords: Density regulation, depensation, eco-evolutionary dynamics, inertial dynamics, population cycles, predator-prey.

1 Introduction

Many studies on the causes of cyclic population dynamics have focussed on predator-prey interactions (reviewed by Norrdahl 1995; Berryman 1996; Krebs 1996) instead of intra-specific delays. This may likely reflect that predator-prey cycles were predicted theoretically by Lotka (1925) and Volterra (1926), while the intra-specific hypothesis (Voipio 1950; Chitty 1960) was not well supported mathematically for several decades (Stenseth 1981, 1995). But natural selection in one generation changes the average phenotype in the next, and when selection is density-dependent it creates a density-dependent feedback that is delayed by a single generation. More recent theory have shown that this may induce selection-delayed population cycles owing to the intra-specific natural selection that arises from the density-dependent competitive interactions between the individuals in the population (Witting 1997, 2000a, 2002a). This reopens the never settled quest for a common cause for population cycles in natural populations, and more essentially it questions the generality of density-regulated growth as the appropriate model for single-species dynamics. In an attempt to approach a general answer to these important questions, I examine the relative influence of density regulation, depensation, predator-prey interactions and selection-delayed responses in the population dynamics of baleen whales.

1.1 Selection-delayed dynamics

I define selection-delayed dynamics as population dynamics that is shaped by delayed feedback responses to intra-specific natural selection. Inter-specific selection is not considered because this does not in itself create a feedback from the population upon itself.

Selection delays may not only arise from genetic and epigenetic responses to selection. Maternal effects (Ginzburg and Taneyhill 1994; Ginzburg 1998; Ginzburg and Colyvan 2004) and other plastic phenotypic responses, including changes in behaviour, may

also generate population dynamic delays, and they will generally have a selection origin where they have evolved over longer time-scales in order to allow the organism to respond more directly and fast to changes in ecological selection pressures (Svanbäck et al. 2009). I deal with selection-delayed dynamics in the broadest definition, where it includes all sorts of responses to intra-specific selection; responses that induce delayed feedback and cause the dynamics to deviate from density-regulated growth.

Recent findings have shown that population dynamics and evolutionary changes often occur on similar time-scales (Thompson 1998; Hairston et al. 2005; Saccheri and Hanski 2006; Schoener 2011), and it is thus increasingly essential that the population dynamic impacts of evolutionary processes are explored as a natural component of our population dynamic investigations. So far there has been a general interest in the population dynamic consequences of evolution caused by fishery induced selection (e.g., Law 2000; Browman 2000; Bromaghin et al. 2011; Scott and Sampson 2011). Base case evolution, however, occurs by natural selection and not by anthropogenetic selection. This does not imply that direct anthropogenetic selection, such as size selective fishing, may not affect population dynamics, but it does suggest that natural population dynamics is shaped by evolution even in the absence of direct anthropogenetic selection. Removal of individuals by harvest does not induce direct anthropogenetic selection unless the harvest is selective on some phenotypic trait. Nevertheless, even a non-selective harvest will induce natural selection because it changes the density-dependent selection pressure in the population.

If cyclic population dynamics is indeed induced by selection responses, then the most likely selection mechanism will have to be intra-specific and density-dependent in order to generate the required feedback. The essential question is how this modifies the average life history, which is the phenotypic component that defines the population dynamic growth. Classical life history theory (reviewed by Stearns 1992; Charlesworth 1994; Roff 2002) is based on constant relative fitnesses, which implies pure exploitative competition, and it defines density-dependent selection on the well-known r to k continuum (Anderson 1971; Roughgarden 1971; Clarke 1972). But r- and k-selection is inherently problematic because it always increases the growth potential of the population, even when the population is at carrying capacity. Not only does this require very special conditions to generate cyclic population dynamics, but more essentially the increased quantity of increased population growth will come at a phenotypic quality cost, generating long-term selection for the evolutionary existence of only negligible sized organisms (see Witting 1997, 2008 for details).

In order to generate long-term selection for a realistic scenario, where organisms may evolve large body masses and other organised life history traits like sexual and eusocial reproduction, we need only add interactive competition to the selection equation (Witting 1997, 2002b, 2003a, 2008). Interactive competition is inherently density-dependent because the number of competitive encounters per individual per unit time depends upon the absolute number of individuals in the population. Quite generally, due to the energetic quality-quantity trade-off, density-dependent competitive interactions generate selection for interactive quality (which may include body mass, metabolic rate, interactive behaviour, group size, interacting individuals such as males, and sexual reproduction) at the cost of selection for increased population growth. The evolutionary equilibrium, which includes the population dynamic equilibrium, is defined by a competitive interaction fix-point where the level of interactive competition is exactly so large that the increased reproductive potential of the smaller individuals in the population is balanced against the resource monopolisation of the larger individuals so that the actual reproductive rate is similar across the variation in body mass.

When the abundance is above the evolutionary population equilibrium there is increased interference competition with selection for increased competitive quality at the cost of population growth, while the opposite is the case when the abundance is below the equilibrium. This produces selection-delayed dynamics, where the density-regulated exponential growth rate is decelerated and accelerated by intra-specific selection (Witting 2000a,b; Witting 2002a). Apart from these theoretical arguments in its favour, selection by density-dependent competitive interactions is now being identified in an increasing number of species (e.g., Sinervo et al. 2000; Goss-Custard et al. 2001; Bolnick 2004; Einum et al. 2008; Mappes et al. 2008; Calsbeek and Cox 2010), indicating that its evolutionary effects may be essential for the dynamics of natural populations.

Selection-delayed dynamics is characterised by damped to stable population dynamic cycles (Witting 2000a), in line with the original proposals by Voipio (1950) and Chitty (1960) on the importance of natural selection in cyclic dynamics. Even though selection-delayed dynamics can be so damped that it is practically impossible to distinguish from the monotonic increase of density-regulated growth, it should carry with it at least a small signal of over-compensatory cyclic dy-

namics. Relating to the Voipio and Chitty hypothesis it has been argued that evident spacing behaviour like territoriality is essential for this mechanism to work (e.g., Krebs 1996). While spacing behaviour is likely to influence the dynamics of many natural populations and have been incorporated into models of selection-delayed dynamics (Kapeller et al. 2011), it is not necessary for population cycles by intra-specific delays because selection-delayed dynamics can be deduced from population models with no explicit spatial structure (Witting 1997, 2000a).

Evidence for selection-delayed dynamics include profound genetic changes over few generations in cyclic populations (Semeonoff and Robertson 1968; Krebs et al. 1973; Sinervo et al. 2000), and these responses to selection can be enhanced by maternal effects as observed in cyclic rodents (Boonstra and Hochachka 1997), snowshoe hare (*Lepus americanus*) (Boonstra and Singleton 1993; Krebs 2011), and forest insects (Rossiter 1994). Delayed life history changes are found consistently in natural populations (Mousseau and Fox 1998; Beckerman et al. 2002), and fast evolution can cause large heritable differences in the birth rate between individuals from the low and increasing phase of a cycle (Mihok and Boonstra 1992), and an acceleration of the population dynamic growth rate by up to 40 % within few generations (Turcotte et al. 2011a,b). Finally, selection by density-dependent competitive interactions have been found to generate a two-generation cycle in the abundance of side-blotched lizard (*Uta stansburiana*) (Sinervo et al. 2000). Given this wide range of evidence for evolutionary change on population dynamic time scales, it is prudent to examine selection-delayed dynamics as one of the ecological processes that changes the exponential growth rate.

1.2 Predator-prey dynamics

With empirical and theoretical findings showing that selection-delayed responses can be important, it is essential to note that the underlying mechanisms of cyclic dynamics have remained unresolved for basically all species, with population cycles tending to be in-principle consistent with both the inter- and intra-specific hypotheses (Norrdahl 1995; Berryman 1996; Ginzburg and Colyvan 2004). Relating to the inter-specific hypothesis, the widespread cycles of snowshoe hare and canada lynx (*Lynx canadensis*) seems to be the obvious candidate for a predator-prey cycle. Nevertheless, the strongest development of the predator-prey hypothesis comes from studies of voles in Fennoscandia. This case developed into the hypothesis that limit cycles are generated by specialist predation by the least weasel (*Mustela nivalis*) (Henttonen et al. 1987; Hanski et al. 1991). A gradual disappearance of cycles southwards should be caused by a decline in the relative influence of destabilising specialist predation and an increase in stabilising generalist predation, with snow cover in the north isolating the small specialist predator with its prey hence avoiding the stabilising influence from predation by larger generalists. Theoretical modelling and empirical evidence have shown that the Fennoscandian cycles are unlikely to be induced by prey-resource interactions (Klemola et al. 2000, 2003), although the influence of these interactions may be more important in other systems, such as in high-arctic lemmings (Turchin et al. 2000; Turchin and Batzli 2001).

A large number of field, laboratory and model studies have investigated the Fennoscandian cycles (see Norrdahl 1995 for review), and some of the best empirical evidence for a predator-prey driven cycle comes from Korpimäki and Norrdahl (1998) that found that the removal off all predator species could reverse a decline, and from Korpimäki et al. (2002) that found that a corresponding removal increased the density during the peak phase with an apparent delay of the decline.

The essential test for the strict predator-prey cycle (which is caused by predator-prey interactions with no intra-specific delays), however, is not whether the removal of all predators may reverse a decline, but whether the removal of predators down to the predator density at the corresponding prey density during the increasing phase of the cycle will cause a change from decline to increase in prey density. This test has not been conducted, and the removal of only specialist predators did not stop the decline (Korpimäki and Norrdahl 1998). Generally it remains to be shown that predator-prey interactions is a sufficient mechanism for the cyclic dynamics of natural population, e.g., by showing that predator removal will cause a cyclic prey population to become non-cyclic. In fact, predator removals have often been found to have no impact on the cyclic dynamics of the prey (e.g., Norrdahl and Korpimäki 1995; Krebs 1996; Graham and Lambin 2002), and based on a predator removal experiment that spanned all phases of a population cycle, Graham and Lambin (2002) concluded that specialist predators are neither sufficient nor necessary for the cyclic dynamics of field vole (*Microtus agrestis*) in Kielder Forest in northern England (but see discussion Oli 2003a,b; Korpimäki et al. 2003).

Quite generally, predator-prey cycles are stabilised by density regulation in the prey, and in the predator from other factors than the exploitation of the

prey species that is explicitly included in the equations. Predator-prey models for Fennoscandia do not include stabilising effects in the predator from density regulation by intra-specific interference and dependence upon multiple species of prey (Hanski et al. 1991; Oksanen et al. 2001; Klemola et al. 2003). It is thus unclear whether the predator-prey hypothesis is consistent with observed cycles. With density dependent intra-specific interference competition being the rule in predator populations, and with practically all predators being dependent upon several species of prey (even for specialist predators), the idea that predator-prey interactions generate stable limit cycles in natural populations may not be well supported.

In order to test the predator-prey hypothesis, in this paper I construct predator-prey models between killer whale [*Orcinus orca* (Linnaeus 1758)] and baleen whales where the dependence of the killer whale upon the other species of prey, that are not directly included in the modelling, is explicitly quantified.

1.3 Baleen whale dynamics

In my attempt to disentangle the relative importance of intra- and inter-specific delays in population dynamics, I analyze one of the largest population dynamic experiments on Earth; the worldwide over-exploitation of baleen whales by commercial whaling in past centuries. Baleen whales are particularly useful for population dynamic studies of predator-prey interactions, because their trophic interactions to copepods, krill, and small fishes below, and to killer whale above, make the delayed feed-back signal from the two trophical levels distinctively different. Having generation times from few months to a few years, baleen whale prey will induce a short time-lag. A long time-lag is instead induced by interactions with the predator because the killer whale has a mean lifetime expectancy around 50 years (Olesiuk et al. 2005).

Not only is it possible to distinguish between signals from prey and predators, but the baleen whale suborder (*Mysticeti*) seems also to be the only case on Earth where we have a similar historical perturbation of almost all the natural populations of an entire taxonomic group. Starting with the Basque over-exploitation of the North Atlantic right whale *Eubalaena glacialis* in the eastern North Atlantic in the 15th century, whaling accelerated into industrial operations in the 20th century, with one species after another being brought to the verge of extinction until a moratorium was placed on commercial whaling in 1986. Except for the toothed sperm whale [*Physeter macroephalus* (Linnaeus 1758)], it was especially baleen whales that were targeted, with all the larger species being heavily depleted worldwide. Most populations were exposed to a short-term perturbation, in the sense that the historical harvest shows a single larger peak with almost no current take. This allows us to compare the current population trajectories across species, and to generalise on common results.

Out of ten depleted species of large baleen whales (excluding the smaller minke whales and pygmy forms) I analyse the dynamics of seven (Table 1) with sufficient data to determine the current trends in abundance. The periods with abundance data are unfortunately so short that they are largely unable to differentiate the dynamics on the continuum from an over-compensatory increase to stable population cycles. Nevertheless, the relationships between the historical catches and the recent trends in abundance have proven sufficient to conclude that gray whales [*Eschrichtius robustus* (Lilljeborg 1861)] in the eastern North Pacific seem not to follow simple density-regulated growth (Butterworth et al. 2002; Witting 2003b), and the same is the case for humpback whales [*Megaptera novaeangliae* (Borowski 1781)] in the North Atlantic (IWC 2003a). This raises the question whether baleen whale populations violate density-regulated growth in general, and if so, is it then because of interactions with prey or predators, or because of intra-specific time-lags?

2 Material and methods

2.1 Overall approach

My primary goal was to estimate which of the four plausible mechanisms (density regulation, depensation, predator-prey and selection-delayed) that most likely cause the population dynamics of baleen whales, assuming that the true population trajectories were strongly shaped by the historical catches and that the current rates of increase is captured by time-series of abundance estimates. I wanted to focus on the baleen whale suborder *Mysticeti*, so I constructed only one set of popu-

Species	Area
Bowhead whale	Bering-Chukchi-Beaufort Seas
Gray whale	Eastern North Pacific
North Atlantic right whale	Western North Atlantic
southern right whale	Southern Hemisphere
Humpback whale	Central North Atlantic
Fin whale	Central North Atlantic
Blue whale	Antarctic

Table 1: The baleen whale species of the study.

lation models for each species to avoid over- or under-representation of some species. In order to have a similar experimental setup across all species, I included only the larger species that were heavily depleted by past whaling.

The population dynamic analyses of all species were the same, with six different age- and sex-structured models being constructed for each species. These included a single predator-prey model with killer whale as the predator, and five single-species models based on i) exponential growth, ii) density-regulated growth, ii) density-regulated growth with depensation, iv) delayed density-regulated growth and v) selection-delayed dynamics.

All the non-exponential models except the delayed density-dependent model have explicit biological mechanisms that cause r to change over time. The delayed density-dependent model has only a mathematical relationship with no biological mechanism associated with it. Hence, this model was used only to estimate the existence of time-lags, and to illustrate how biological models with delayed density-dependent feedbacks (such as selection-delayed and predator-prey models) may perform relative to models with no time-lag.

All models were initialised with a stable age structure; the exponential model ten years before the first available abundance estimate; other models on the first year with commercial whaling (from 1632 to 1900 dependent upon species), assuming a pre-whaling population at population dynamic equilibrium. As a sensitivity run, the density-regulated model was applied also with a pre-whaling population that was not at carrying capacity and an initial stable age structure given the growth rate of the initial abundance. Population trajectories were projected to the present by subtracting the historical catches from the dynamics, and the likelihood of the different models was determined from recent abundance estimates.

To provide statistical estimates of parameters and population trajectories given the catch and abundance data, I applied a Bayesian statistical framework as developed for baleen whales in the Scientific Committee of the International Whaling Commission (Punt and Butterworth 1999; Wade 2002; Witting 2003b). Prior distributions were obtained from literature estimates, and the likelihood of each parameterisation drawn from the joint prior was calculated from the resulting trajectory and the abundance data assuming log-normally distributed errors (De la Mare 1986). The integration from prior to posterior distributions was obtained by the sampling-importance-resampling method (Rubin 1988). A total of 145 million population trajectories, with 2.5 million on average per model, were analysed to obtain smooth posterior distributions, with sampling statistics for all models given in Table S1 in the Electronic Supplementary Material (ESM).

To estimate the relative consistency between the different mechanisms and the true dynamics of baleen whales, I focussed on comparisons of the best parameterisations with the highest likelihood, by applying an approximate maximum likelihood (MLE) method with model comparisons based on the Akaike information criterion (AIC, Akaike 1974). I preferred this method over a Bayes factor comparison, because the latter would depend on my priors, while I wanted my comparisons to be as independent of my prior assumptions as possible. Unfortunately, I was unable to construct a multi-parameter MLE optimisation routine for the predator-prey model with up to 23 parameters. So instead I chose the parameterisation with the highest likelihood in the Bayesian sampling to represent the best estimate. I tested whether this method was representative as MLE estimates for the different models, by applying multi-parameter MLE optimisation on the exponential, density-regulated, and selection-delayed models using the three parameterisations with the three highest likelihoods from the Bayesian sampling as the initial starting points of the optimisation routine. These optimisations provided only a few percentages increase in the likelihood, and in no case did it change the order of the two most optimal models. Hence, I concluded that my approximate MLE method was sufficient, especially since my main method of analysis was not based directly on an AIC comparison, but on comparisons between population estimates and model constraints (see below).

My analysis focused on the species distribution because the available data were insufficient for several of the species to distinguish between the different models when analysed in isolation. For essential population dynamic relationships, I analysed whether the joint distribution of the seven species was consistent with the constraints of the different models, assuming implicitly that the dynamics of the seven species are driven by similar factors. In particular, I focussed on the relationship between the relative growth rate (r/r_{max}) and the relative abundance (N/N^*). All the non-exponential single-species models define functional relationships between the relative growth rate and some measure of relative abundance, and it was examined whether these relationships are consistent with the data. To do this, for each model, I compared the species distribution of the model-dependent estimates of the functional dependence of r/r_{max} on N/N^* (as defined by the best pa-

rameterisation for each species) to model-independent estimates of the relative growth rate (best parameterisation of exponential model) during the period of the abundance data (relative abundance estimated by best parameterisation of non-exponential model). If a model is completely consistent with the data, all the model-independent estimates of relative growth should fall within the distribution of the model-dependent estimates of the relationship between r/r_{max} and N/N^*.

In addition to this I examined the consistency between the model-dependent population trajectories and the recent abundance estimates. This was done by comparing model-dependent (best parameterisations of non-exponential model) and model-independent (best parameterisations of exponential model) estimates of the exponential growth rate during the periods of the abundance data. A correct model should show a strong positive correlation between the species distributions of the best estimates of these growth rates.

Finally, I examined the more traditional method of model selection by AIC comparison, which estimates the relative likelihood of the different models given the data. This method not only rewards goodness of fit, but it also includes a penalty that is an increasing function of the number of estimated parameters. Hence, from an AIC point of view the age-structured predator-prey model is hopeless because it includes approximately twice as many parameters as the selection-delayed model. However, as my main focus was not on the construction of an efficient model, e.g., by adding one extra parameter at the time, but on testing the relevance of the different biological hypotheses, it can be argued that a predator-prey model that explained the data equally well as a selection-delayed model should be given the same credit despite of its excess of parameters. Hence, in addition to the parameter dependent AIC, I also made an AIC-like comparison with the parameter penalty removed.

2.2 Populations and data

The selected population segment differed slightly between species, owing to species differences in population structure and the availability of abundance data and catch histories. I generally focussed on the area where I could obtain the best abundance data from the literature. Only segments with at least one time-series of either absolute, or relative, abundance estimates that were informative on trend were selected, and at least one absolute estimate was needed to provide information on total abundance.

The bowhead whale *Balaena mysticetus* in the Bering-Chuckchi-Beaufort Seas, gray whale in the eastern North Pacific, and North Atlantic right whale in the western North Atlantic were the obvious choices for these species owing to the amount of data from these areas. For bowhead whales in the Bering-Chukchi-Beaufort Seas I used nine absolute abundance estimates from 1978 to 2003 (Zeh and Punt 2005), and a catch history that started in 1848 was obtained from the International Whaling Commission (IWC). A catch history for gray whales (starting in 1846) was also obtained from IWC, and for this species I used re-analysed absolute abundance estimates from the southbound migration surveys running from 1967 to 2006 (Laake et al. 2009). The latter time-series was truncated in 1998, partly to avoid the disturbance from a mass mortality event in 1999-2000 (inclusion of later estimates would require a more detailed and time specific model on survival), but also to focus on the period with an increasing population in order to make the data more comparable with those of the other species. For the North Atlantic right whale I used calf count data (Kraus et al. 2007) as a time-series of the relative abundance in age-class zero, together with an absolute abundance estimate from 1996 (IWC 2001a), and a catch history starting in 1770 (IWC 2001b).

For the humpback whale there are several well studied populations, both in the Atlantic, the Pacific, and on the northern and southern part of the globe. I chose to focus on humpback whales in the central North Atlantic owing to the long time series of abundance estimates for this region [18 relative estimates from 1970 to 1988 (Sigurjonsson and Gunnlaugsson 1990), and three absolute estimates from 1995, 2001 and 2007 (NAMMCO 2011)] and a well documented catch history that starts in 1825 (Smith and Reeves 2010). For fin whale *Balaenoptera physalus* I chose to focus on the western part of the central North Atlantic owing to the existence of four absolute abundance estimates from 1988 to 2007 from the East Greenland–West Iceland area (IWC 2010) and a well documented catch history from IWC starting in 1884.

For the blue whale *Balaenoptera musculus* and southern right whale *Eubalaena australis* I chose larger population segments on the Southern Hemisphere. Inspired by Mori and Butterworth (2004), and by the existence of three absolute abundance estimates from 1981 to 1998 (Branch 2007), I focussed on blue whales around Antarctic using a catch history that started in 1900 (Mori and Butterworth 2004). For southern right whales there are several breeding units. Given the modelling constraint of an absolute abundance estimate combined with time series on trend and catch history,

in line with IWC (2001b), I chose to focus on the entire Southern Hemisphere. Here, I used a catch history that started in 1770 and a single absolute abundance estimate, both obtained from IWC (2001b). To capture the overall trend in abundance I used three times series of relative abundance from Argentina (Cooke et al. 2001), South Africa (Best et al. 2001) and West Australia (Bannister 2008).

For nearly all chosen population segments there were a rather straightforward relationship between the area of the catches and the area covered by the population, in some cases because hunting occurred mainly on summering grounds. North Atlantic humpback whales, however, were hunted also during winter in the West Indies and around Cape Verde. Western North Atlantic summer aggregations overwinter in the West Indices, but 87 % of the Norwegian and 40 % of the central North Atlantic (CNA; Icelandic and Faroese areas) animals overwinter around Cape Verde (IWC 2002). Based on abundance estimates from 2001 [Norway: 1.450 (CV:0.29, Øien 2009); CNA: 14.622 (CV:0.36, Paxton et al. 2009)] this indicates that 82 % of the Cape Verde catches may have been from CNA animals. With the remaining 13 % Norwegian and 60 % CNA animals wintering in the West Indices together with animals from the western North Atlantic, based on abundance estimates from all summer areas [2001 estimate from Norway (Øien 2009); 2007 estimates from all other areas (NAMMCO 2011)], it is indicated that 47 % of the West Indies catches may have been from CNA animals. Hence, for my model of CNA humpback whales I applied all the CNA catches plus 47 % of the catches from the West Indies and 82 % from Cape Verde.

All the catch histories are shown in Fig. S1 in ESM, and for most model runs they were assumed to be exact. This assumption was relaxed in sensitivity runs of the density-regulated model, where the applied catch history was allowed to vary from one to two times the known catch history. This was done to test for the influence of uncertain catch histories due to under reporting and insufficient correction for whales that were struck and lost.

2.3 Population dynamics

Selection-delayed dynamics

In traditional models of population dynamic it is assumed that changes imposed by natural selection necessarily occur much slower than population growth, so that the intrinsic growth rate ($\tilde{r}$) can be assumed to be constant over time. This implies the well-known concept of density-regulated growth, where the per capita rate of increase is

$$\frac{1}{N}\frac{dN}{dt} = \tilde{r} - f(N), \tag{1}$$

$f(N)$ is the density regulation function that increases monotonically from $f(0) = 0$, the carrying capacity is defined as $N^* = f^{-1}(\tilde{r})$, and $\tilde{r} > 0$.

Whenever there is natural selection it is likely to affect $\tilde{r}$, and this implies that the density-regulated growth of eqn 1 evolves into selection-delayed dynamics (Witting 1997, 2000a,b, 2002a), where the intrinsic growth rate $\tilde{r}$ of eqn 1 is accelerated and decelerated by intra-specific and density-dependent natural selection

$$\frac{d\tilde{r}}{dt} = \sigma^2\frac{\partial r}{\partial \tilde{r}} = \sigma^2 g(N) \tag{2}$$

where is σ^2 is the response potential (equal to the additive genetic variance when all responses are genetic), $\frac{\partial r}{\partial \tilde{r}} = g(N)$ is the selection gradient on $\tilde{r}$, and $N^{**} = g^{-1}(0) = f^{-1}(\tilde{r})$ defines the evolutionarily determined population dynamic equilibrium, with $g^{-1}(0)$ specifying the absence of selection at the equilibrium. Given selection by density-dependent competitive interactions (Witting 1997, 2000a,b, 2002a), the selection gradient is monotonic with $g < 0$ for $N > N^{**}$ and $g > 0$ for $N < N^{**}$, so that the intrinsic growth rate increases whenever the abundance is below the equilibrium abundance, while it declines whenever the abundance is above the equilibrium. Note, that the joint model of eqns 1 and 2 reduces into density-regulated growth when there is no selection response, i.e., when $\sigma^2 = 0$.

If these equations are taken to the limit of zero density, it is well known that density-regulated growth reduced into the Malthusian law of exponential increase ($dN/dt = \tilde{r}N$; Malthus 1798). Probably less well known to population ecologists, it can be noted that eqn 2 is the secondary theorem of natural selection (Robertson 1968), which says that the rate of change in a trait (here the trait is the intrinsic growth rate) is the selection gradient on the trait multiplied by the additive genetic variance in that trait. Generally, and contrary to the assumption in life history theory based on constant relative fitnesses, the intrinsic growth rate do not represent the genetic coding for fitness, because interactive quality is an equally important component whenever there is interactive competition. However, at the $N = 0$ limit, there is no interactive competition, and $\tilde{r}$ becomes the trait of fitness so that the selection gradient reduces to one ($\partial r/\partial \tilde{r} = 1$) and eqn 2 reduces into Fisher's (1930) fundamental theorem of natural selection, which says that the rate of increase in fitness

is equal to the additive genetic variance in fitness. The result is a hyper-exponential $[dN/dt = (\tilde{r}_0 + \sigma^2 t)N]$, instead of exponential, increase in abundance. In this way, the fundamental theorem can be seen to replace the Malthusian law as the limit theorem of population dynamics (see Witting 2000a,b, 2002b for details).

Population responses to natural selection include, but are generally not limited to, genetic changes. They may also include responses by epigenetic inheritance, maternal effects, phenotypic plasticity, and/or between generation changes in the way that individuals interact with one-another and the environment. Hence, the response potential include several components, i.e., $\sigma^2 = \sigma_g^2 + \sigma_e^2 + \sigma_p^2$ to include the joint genetic (σ_g^2), epigenetic (σ_e^2) and plastic (σ_p^2, including maternal effect & behaviour) responses. The case where the response is mediated through maternal effects is known as inertial dynamics (Ginzburg and Taneyhill 1994; Ginzburg 1998; Ginzburg and Colyvan 2004), where similar population dynamic equations have been developed independently of the selection-delayed hypothesis.

Equations 1 and 2 show selection-delayed dynamics for the continuous case, and the original deduction was based on a discrete model (Witting 1997, 2000a). A full specification of the age- and sex-structured models that are applied to baleen whales is given in the subsection below.

Single species models

With x being the maximum lumped age-class, let the number $N^g_{a,t+1}$ of males ($g = m$) and females ($g = f$) in age-classes $0 < a < x$ in year $t + 1$ be

$$N^g_{a+1,t+1} = p_a N^g_{a,t} - c^g_{a,t} \tag{3}$$

and the number of animals in age-class x

$$N^g_{x,t+1} = p_x N^g_{x,t} + p_{x-1} N^g_{x-1,t} - c^g_{x,t} - c^g_{x-1,t} \tag{4}$$

where p_a is the age specific survival rate, and $c^g_{a,t}$ the age specific catch in year t. The age dependent survival rates $p_a = p\tilde{p}_a$ are given as a product between a survival scalar p and a relative ($0 < \tilde{p}_a \leq 1$) survival rate, with $\tilde{p}_0 < 1$ and $\tilde{p}_{a\geq 1} = 1$. The age and gender (g) specific catches

$$c^g_{a,t} = c^g_t \tilde{c}^g_a N^g_{a,t} / \sum_{i=0}^{x} \tilde{c}^g_i N^g_{i,t} \tag{5}$$

in year t is given as a function of the total catch (c^g_t), as specified by the catch history, and the age-specific abundance ($N^g_{a,t}$) and catch selectivity ($\tilde{c}^g_a$), with $\tilde{c}^g_0 = 0$ and $\tilde{c}^g_a = 1$ for $a > 0$.

The number of females and males in age-class zero is $N^f_{0,t} = \vartheta N_{0,t}$ and $N^m_{0,t} = (1 - \vartheta)N_{0,t}$, where ϑ is the fraction of females at birth, and $N_{0,t} = \sum_{a=a_m}^{x} B_{a,t}$ with a_m being the age of the first reproductive event. The number of births from females in age class a, is

$$B_{a,t} = b_t \, M^f_{a,t} \tag{6}$$

where b_t is the birth rate in year t, and $M^f_{a,t}$ the number of mature females in age-class a in year t, defined as

$$M^f_{a,t} = \begin{cases} 0 & \text{if } a < a_m \\ N^f_{a,t} & \text{if } a \geq a_m \end{cases} \tag{7}$$

Let, for the exponential and the three models of density-regulated growth, b_t be independent of the age of the mature females and given as

$$\begin{aligned} b_t &= b && \text{for exponential,} \quad (8) \\ b_t &= b^* + \tfrac{b_{max} - b^*}{1-(\hat{N}_t/\hat{N}^*)^\gamma} && \text{density-regulated,} \\ b_t &= \tfrac{b^* + [b_{max} - b^*][1-(\hat{N}_t/\hat{N}^*)^\gamma]}{1-[1-\hat{N}_t/\tilde{d}\hat{N}^*]^\gamma} && \text{depensation } (d_t < \tilde{d}), \\ b_t &= b^* + \tfrac{b_{max} - b^*}{1-(\hat{N}_{t-\tau}/\hat{N}^*)^\gamma} && \text{and delayed,} \end{aligned}$$

where b is a constant birth rate, b^* is the birth rate at population dynamic equilibrium (assuming zero catch), b_{max} is the maximal birth rate, γ is the density dependence parameter, $\tilde{d}$ the critical abundance level below which depensation is operating (for abundance levels $d_t = \hat{N}_t/\hat{N}^* > \tilde{d}$ the standard density regulation model applies), and τ the time-lag of density regulation in the delayed density-dependent model. The abundance component that imposes density dependence is set to the one-plus component

$$\hat{N}_t = \sum_{a=1}^{x} N_{a,t} \tag{9}$$

For the selection-delayed model the birth rate is both time and age dependent

$$b_{a,t} = \min[b_{max}, \dot{b}_{a,t}(\hat{N}_t/\hat{N}^{**})^{-\gamma}] \tag{10}$$

with $\dot{b}_{a,t}$ being the average intrinsic birth rate for females in age-class a in year t, initially set to b^* for all age-classes. The average intrinsic birth rate of offspring (age-class zero) born by age-class a females

$$\dot{b}_{0,t+1|a} = \min[b_{max}, \dot{b}_{a,t}(\hat{N}_t/\hat{N}^{**})^{-\iota}] \tag{11}$$

is the average intrinsic birth rate of the parents $\dot{b}_{a,t}$ plus a proportional response to density-dependent natural selection, with the birth rate being truncated here at

b_{max} and ι defining the response to selection. Hence, the average intrinsic birth rate of age-class zero is the weighted average across all offspring

$$\dot{b}_{0,t+1} = \frac{\sum_{a=a_m}^{x} b_{a,t} N_{a,t}\ \dot{b}_{0,t+1|a}}{\sum_{a=a_m}^{x} b_{a,t} N_{a,t}} \tag{12}$$

Assuming that there is no change in the intrinsic fecundity rate of a cohort over time, $\dot{b}_{a+1,t+1} = \dot{b}_{a,t}$ and

$$\dot{b}_{x,t+1} = \frac{\dot{b}_{x,t}(p_x N^f_{x,t} - c^f_{x,t}) + \dot{b}_{x-1,t}(p_{x-1} N^f_{x-1,t} - c^f_{x-1,t})}{N^f_{x,t+1}} \tag{13}$$

Predator-prey model

The density-regulated model is extended to include potential killer whale predation, with eqn 3 extending to

$$N^g_{a+1,t+1} = p_a N^g_{a,t} - c^g_{a,t} - c^{p,g}_{a,t} \tag{14}$$

where $c^{p,g}_{a,t}$ is the number of age-class a male/females whales caught by killer whale in year t. Let this number be

$$c^{p,g}_{a,t} = c^p_t \tilde{c}^p_a N^g_{a,t} / \sum_{i=0}^{x} \tilde{c}^p_i N_{i,t} \tag{15}$$

where $N_{a,t}$ is the number of prey in age-class a, c^p_t the total catch of prey by the predator population, and $\tilde{c}^p_a$ the relative age-specific selectivity of prey by the predator.

The total catch of prey by the predator population is

$$c^p_t = c^{p,**} \hat{P}_t (\hat{N}_t / \hat{N}^{**})^{\mu} \tag{16}$$

where $\hat{P}_t$ is the one-plus component of the predator population in year t, $c^{**,p}$ is the number of baleen whale individuals taken per predator per year given a predator-prey system at population dynamic equilibrium ($**$ denotes that both species are in population dynamic equilibrium given zero catches of baleen whales by humans), and μ defines the functional response of the predator to prey abundance ($\hat{N}_t$).

The killer whale model resembles the baleen whale model except for a few changes. No catches of killer whale are included, and the density regulation on the birth rate is

$$b_t = b_{max,t}\ e^{-\gamma \hat{P}_t / \hat{P}^{**}} \tag{17}$$

where $b_{max,t}$ is the maximal birth rate in year t, $\hat{P}_t$ the one plus abundance of predators in year t, and $\hat{P}^{**}$ the one plus abundance at the joint population dynamic equilibrium with no catches of baleen whales. Contrary to the Pella-Tomlinson density regulation model of eqn 8, this model allows the γ parameter to be calculated from the b^{**}_{max}/b^{**} ratio, making the parameterisation of the predator-prey model more straight forward (see next section).

The functional response of the predator to the prey is assumed to regulate both the survival scalar and the maximal birth rate of the predator in a similar way

$$\begin{aligned} p_t &= p^{**}(\hat{N}_t/\hat{N}^*)^{\mu}\phi + (1-\phi)p^{**} \\ b_{max,t} &= b^{**}_{max}(\hat{N}_t/\hat{N}^*)^{\mu}\phi + (1-\phi)b^{**}_{max} \end{aligned} \tag{18}$$

where p^{**} is the survival scalar and b^{**}_{max} the maximal birth rate at the joint population dynamic equilibrium, and ϕ is a prey specialisation parameter that defines the dependence of the predator on the explicit prey relative to all other prey species, with $(1-\phi)p^{**}$ and $(1-\phi)b^{**}_{max}$ giving the survival and birth rates in the complete absence of the explicit prey. The responses of the birth and the survival rates are assumed the same in order to keep the model simple, and to allow for a more drastic relative response in the mortality rate relative to the birth rate, in line with evidence from killer whale in the north-eastern Pacific Ocean (Ford et al. 2010).

2.4 Parameterisation

A list of the parameters for the different models and their parameterisation is given in Table 2. Parameters were either drawn from a prior distribution, or calculated from the prior parameters and the constraints of the models. The prior parameters for all models include the initial and/or equilibrium abundance (N_0 for exponential model; $N_0 = N^*$ for other models, except that N_0 and N^* differ for the $N_0 \neq N^*$ sensitivity runs of the density-regulated model), the exponential growth rate (realised r for exponential model; r_{max} for other models), the age of the first reproductive event (a_m), the birth rate (realised b for exponential growth; b_{max} for other models, i.e., b^{**}_{max} for the predator), the female fraction at birth (ϑ), and the relative survival of age-class zero individuals ($\tilde{p}_0$). Adult survival (p; for the predator p^{**}) was calculated from the exponential growth rate by the Euler equation. Then, for all models, except the exponential, the birth rate at population dynamic equilibrium (b^*; for the predator b^{**}) was estimated numerically given the $r^* = 0$ constraint in the absence of harvest.

For all models, except the exponential, selection-delayed and the predator of the predator-prey model, the density regulation parameter γ was drawn from a prior. For the predator, γ was calculated as $\gamma = \ln(b^{**}_{max}/b^{**})$ from eqn 17. For the selection-delayed model, density regulation was set to match the selection

Parameter	S	E	D	N	C	A	T	S	PP
Equilibrium ($*$ or $**$) abundance	N^*	-	l	l	l	l	l	l	l|l
Initial abundance	N_0	l	c	l	c	c	c	c	c|c
Maximal growth rate	r_{max}	-	u	u	u	u	u	u	u|u
Exponential growth rate	r	u	c	c	c	c	c	c	c|c
First year survival	p_0	u	u	u	u	u	u	u	u|u
Adult survival	p	c	c	c	c	c	c	c	c|c
Age of maturity	a_m	u	u	u	u	u	u	u	u|u
Realised birth rate	b	u	c	c	c	c	c	c	c|c
Equilibrium ($*$ or $**$) birth rate	b^*	-	c	c	c	c	c	c	c|c
Maximal birth rate	b_{max}	-	u	u	u	u	u	u	u|u
Female fraction at birth	ϑ	f	f	f	f	f	f	f	f|f
Density regulation	γ	-	u	u	u	u	u	c	u|c
Catch history	c_h	f	f	f	u	f	f	f	f|-
Allee effect	$\tilde{d}$	-	-	-	-	u	-	-	-|-
Density regulation time-lag	τ	-	-	-	-	-	l	-	-|-
Selection response	ι	-	-	-	-	-	-	l	-|-
Functional response	μ	-	-	-	-	-	-	-	-|u
Whales eaten per predator at $**$	$c^{**,p}$	-	-	-	-	-	-	-	-|u
Age-selective predation	$\tilde{c}_a^p$	-	-	-	-	-	-	-	-|f
Predator N^* with no baleen whale	$P^*(0)$	-	-	-	-	-	-	-	-|u
Prey specialisation of predator	ϕ	-	-	-	-	-	-	-	-|c
Abundance bias†	β	l	l	l	l	l	l	l	l|-
Additional variance†	CV_a^2	u	u	u	u	u	u	u	u|-

Table 2: Parameters their symbols (S), and their parameterisations for the different models. Models are exponential growth (E), density regulation (D), density regulation with $N_0 \neq N^*$ (N), density regulation with catch uncertainty (C), density regulation with depensation (A, Allee effect), delayed density regulation (T), selection-delayed (S), and predator-prey (PP) with left representing the prey (baleen whale) and right the predator (killer whale). Parameters that are non-existing for a model is indicated by $-$, and existing parameters are set either as a uniform prior (u), log-uniform prior (l), calculated from model constraints and other parameters (c), or as a fixed value or vector (f). †: Data dependent.

response $\gamma = \iota$, with ι drawn from a prior. By fixing γ at ι I constrain the set of options that the selection-delayed model have to explain the relationship between the catch and abundance data. The value of ι relative to γ determines the degree to which the cyclic dynamics is stable or damped, with $\gamma = \iota$ generating stable cycles for a discrete model (Witting 2000a). Hence, I focus only on the fraction of the selection-delayed dynamics that is clearly over-compensatory cyclic relative to density-regulated growth, realising that the time-series of baleen whale abundance data are too short to actually estimate the degree of cyclic stability. While this assumption will affect my estimates of historical abundance to some degree, it is a pragmatic solution to the problem that it may require extremely large sampling to produce smooth posterior distributions with the sampling-importance-resampling routing for these kind of selection-delayed models when there are independent priors on both ι and γ (L. Witting, unpublished).

The depensation $\tilde{d}$ parameter for the density-regulated model with depensation, as well as the time-lag τ for the delayed density-dependent model, were also drawn from priors. For the predator-prey model, the number of prey eaten per predator ($c^{**,p}$) at the joint population dynamic equilibrium was drawn from a prior, and so was the functional response μ. Prey specialisation ϕ was calculated from the prior parameter

$$P^*(0) = P^*(N = 0)/P^{**} \tag{19}$$

that describes the equilibrium abundance of the predator in the absence of the baleen whale [$P^*(N = 0)$] relative to the equilibrium abundance of the predator in the presence of the prey (P^{**}). Given $P^*(0)$ and the absence of the explicit baleen whale prey ($N = 0$), the survival part of eqn 18 reduces to $p_t = (1-\phi)p^{**}$ allowing for a numerical ϕ-dependent estimate of $b^*(N = 0)$, so that ϕ can be estimated numerically by the following model constraint $b^*(N = 0) - (1-\phi)b^{**}_{max}\, e^{-\gamma P^*(0)} = 0$ from eqn 17. Just as r_{max} is not an explicit model parameter but a quantity that can be calculated from the model, so is $P^*(0)$. This quantity is introduced only

Species	Maturity	Birth rate	Survival rate	r_{max}
Bowhead	22 (14–26)[1]	- (0.25–0.50)[1]	0.99 (0.98-0.999)[2]	0.061
Gray	7 (6–12)[3]	- (0.3–0.6)[3]	0.98 (0.96–0.997)[3]	0.099
N right	11 (5–21)[4]	0.24 (0.17–0.5)[4]	0.99 (0.98–0.997)[5]	0.093
S right	8.5 (6–13)[6]	- (0.3–0.5)[6]	0.99 (0.98–0.997)[6]	0.095
Humpback	7 (5–13)[7]	0.42 (0.3–1.0)[8]	0.97[9]	0.14
Fin	- (5–15)[10]	- (0.3–0.6)[10]	0.96[11]	0.086
Blue	- (5–15)[12]	- (0.3–0.5)[12]	0.98 (0.96–0.985)[13]	0.087
Killer	14 (10–21)[14]	0.21 (0.15–0.5)[14]	0.99 (0.98–0.997)[14]	0.061

Table 3: Literature estimates for the age of maturity in females (first reproductive event), the yearly birth rate, and adult survival. Estimates of r_{max} were calculated by the Euler equation from the minimum age of maturity, the maximum birth rate, and the point estimate of survival, assuming an age class zero survival of 75 % of adult survival. Literature estimates, if possible from relevant areas, if not from other areas: 1:IWC (2003b); 2:Zeh et al. (2002); 3:Punt and Wade (2010); 4:Kraus et al. (2007); 5:Kraus 2002; 6:Best et al. (2001); Cooke et al. (2001); 7:Robbins (2007); 8:Barlow and Clapham (1997); 9:Larsen and Hammond (2004); IWC (2011); 10:Lockyer and Sigurjonsson (1992); Mizroch et al. (1984a); 11: Allen (1980); Arrigoni et al. (2011); 12: Mizroch et al. (1984b); 13: Ramp et al. (2006); 14: Olesiuk et al. (2005);

for the purpose of calculating ϕ from a $P^*(0)$ prior that provides more ecological insight than a direct prior on ϕ.

The parameters of the prey and predator population were first drawn from priors and calculated from constraints, and then the two models were connected by readjusting the survival rates of the prey to the presence of the predator, assuming a joint population dynamic equilibrium prior to whaling. With p_a being the survival rate of age-class a prey in the absence of human catches, the number of naturally dying age-class a individuals $[(1-p_a)N_a^{**}]$ can also be given with explicit killer whale predation $[(1-\tilde{p}_a)N_a^{**}+c_a^p]$, where c_a^p is given by eqn 15, $1-\tilde{p}_a$ is natural mortality by other causes than killer whale predation, and $\tilde{p}_a$ is estimated as

$$\tilde{p}_a = (p_a N_a^{**} + c_a^p)/N_a^{**} \tag{20}$$

Relating to the abundance data, a prior was placed on a bias parameter (β) when models were fitted to relative abundance data. This parameter defines the relationship $\tilde{N}_A = \beta N_A$ between the abundance estimate ($\tilde{N}_A$) and the abundance of the model (N_A), with A being the age-component, i.e., 1+ or 0 dependent upon the data.

An extra prior on an additional coefficient of variation $\text{CV}_{a,i}^2$ was placed on time-series of absolute and relative abundance estimates. This parameter estimates variance that is not accounted for by the variance estimates of the abundance estimates (Wade 2002). It was assumed that the variance has a Gaussian distribution so that the total coefficient of variation for abundance estimate $N_{i,t}$ in data set i is

$$\text{CV}_{i,t} = \sqrt{\hat{\text{CV}}_{i,t}^2 + \text{CV}_{a,i}^2} \tag{21}$$

where $\hat{\text{CV}}_{i,t}$ is the coefficient of variation of the abundance estimate $N_{i,t}$. This prior was placed on all time-series except the absolute estimates for the humpback and fin whale, where the confidence intervals of all estimates in the absence of additional variance were well overlapping with the estimated distributions of population trajectories.

2.5 Prior distributions

Uniform priors on the age of the first reproductive event and the realised or maximal yearly birth rate was applied to all models, with the lower and upper limits on the prior set to the limits of estimates obtained from the literature (Table 3).

In the absence of evidence for sex biased offspring in baleen whales, the fraction of females at birth was set to 1/2 for all models. The prior on the relative survival of age-class zero individuals was set to cover a range (0.50 to 0.95) believed to be slightly wider than realistic. In the Gulf of Maine, humpback whale calf survival is estimated to 0.66 (95 % CI from 0.52 to 0.78). And with a yearly adult survival of 0.99 (95 % CI from 0.92 to 0.99); when excluding animals younger than five years of age (Robbins 2007), this indicates a range from $0.52 = 0.52/0.99$ to $0.85 = 0.78/0.92$.

Given the above parameters, adult survival was estimated from draws from a uniform prior on the exponential growth rate [realised growth (r) for the exponential model and maximal growth (r_{max}) for all other models]. The lower and upper limits on the growth rate prior for the exponential model were set to be wider than the expected posterior dirtsibution. For all other models, the priors on r_{max} were set to range from $\max(0.01, r_{max}^l)$ to $\max(r_{max}^t, r_{max}^u)$, where 0.01 was considered as an

absolute minimum, r^l_{max} is the lower, and r^u_{max} the upper, limit of the 95 % credibility interval on the posterior estimate of the growth rate for the exponential model, and r^t_{max} is the estimated r_{max} value from Table 3.

The density regulation parameter (γ) was given a uniform prior from 1.5 to 5 in the density-regulated models to mimic a maximum sustainable yield level in a range from approximately 0.5 to 0.7, as often assumed in density-regulated models of baleen whales. The depensation $\tilde{d}$ parameter of density-regulated growth with depensation was given a uniform prior from zero to 0.3, to span from Allee effects at very low abundance only to effects over a quite large abundance range. A log uniform prior was placed on the regulation time-lag (τ) in the delayed density-regulated model, with τ ranging from zero to the number of years in the catch history.

The catch history sensitivity version of the density-regulated model had a uniform prior on the catch history, ranging from one to two times the known catch history. The initial carrying capacity sensitivity version of the density-regulated model had a uniform prior on the pre-whaling abundance N_0 from $0.5N^*$ to $1.5N^*$ in order to relax the assumption of N_0 at carrying capacity.

Uniform priors were applied to the selection response (ι) in the selection-delayed model (log scale), the initial (N_0) and/or equilibrium (N^*) abundance (log scale) and, when needed, on additional variance ($\text{CV}^2_{a,i}$) and the bias (β) of the relative abundance estimates (log scale). For most of these parameters I had no strong prior expectations. Initial sampling-importance-resampling runs were thus conduced with wide priors to mimic the case of infinitely wide priors. These wide priors, however, required very large sampling to generate posterior convergence. So, to increase the efficiency of the sampling-importance-resampling routine, for the final runs I narrowed these uniform priors by removing some of boundary space with no, or almost, no weight in the posteriors of the initial runs. For strongly updated parameters (all cases of N_0, N^*, β; $\text{CV}^2_{a,i}$ for some time-series; ι for bowhead, gray, humpback and fin whale) this resulted in uniform priors that were clearly wider than the posterior distributions. For weakly updated parameters ($\text{CV}^2_{a,i}$ for some time-series, and ι for the blue whale and the right whales) it resulted in uniform priors that were narrowing the width the posterior distribution. While this narrowing indicates insufficient data for accurate parameter estimation, the priors were set to be so wide that they allowed for what was considered a sufficient parameter search to have covered the true parameter space of the population and/or the data generation process. Hence, the expected parameter space of the optimal parameterisation of all models was covered by the priors.

Predator-prey

Although small calves of some species of baleen whales may be vulnerable to attacks from sharks (Weller 2002), the killer whale is the only predator that poses a real risk to large whales. Ford and Reeves (2008) conclude that there is evidence that Antarctic minke whale [*Balaenoptera bonaerensis* (Burmeister 1867)] are important prey of killer whale (Yukhov et al. 1975; Budylenko 1981), and numerous successful attacks on common minke whale [*Balaenoptera acutorostrata* (Lacépède 1804)] have been documented (Ford et al. 2005). These two species are the smallest baleen whales and they are not included in this study. However, there is also evidence that young calves of several large whale species are frequent targets of killer whale attacks. Gray whale calves migrating northward with their mothers are regularly hunted (Ford and Reeves 2008), scars from attacks from killer whale are found on as many as 20 to 40 % of individuals in some populations of humpback whale and evidence is strong that such scars are acquired when animals are calves (Naessig and Lanyon 2004; Reeves et al. 2006; Mehta et al. 2007). Reviews conclude that successful predation by killer whale on baleen whales other than calves is fairly rare except possibly in the case of Antarctic minke whale and common minke whale (Reeves et al. 2006; Mehta et al. 2007; Ford and Reeves 2008). To reflect this I assume age-selective predation, and set somewhat arbitrary a relative selectivity of $\tilde{c}^p_0 = 1.0$ for baleen whale calves in their first year, of $\tilde{c}^p_1 = 0.2$ and $\tilde{c}^p_2 = 0.05$ for whales in their second and third year, and of zero for older individuals.

The dependence of the killer whale population upon the baleen whale population is parameterised by the ratio of the carrying capacity of the killer whale in the absence versus presence of the baleen whale [$0 \leq P^*(0) \leq 1$]. While there are no literature estimates of this ratio, only individuals of some populations of killer whale are known to take marine mammals on a regular basic. For 767 individuals of observed marine mammal killer whale prey worldwide, 11 % were large baleen whales (excluding Antarctic minke whale and common minke whale), with the gray whale being the most often caught species in 3 % of the observed cases (Jefferson et al. 1991). While this comparison does not allow for an estimation of the relative importance of the different species of prey for killer whale, it does illustrate that

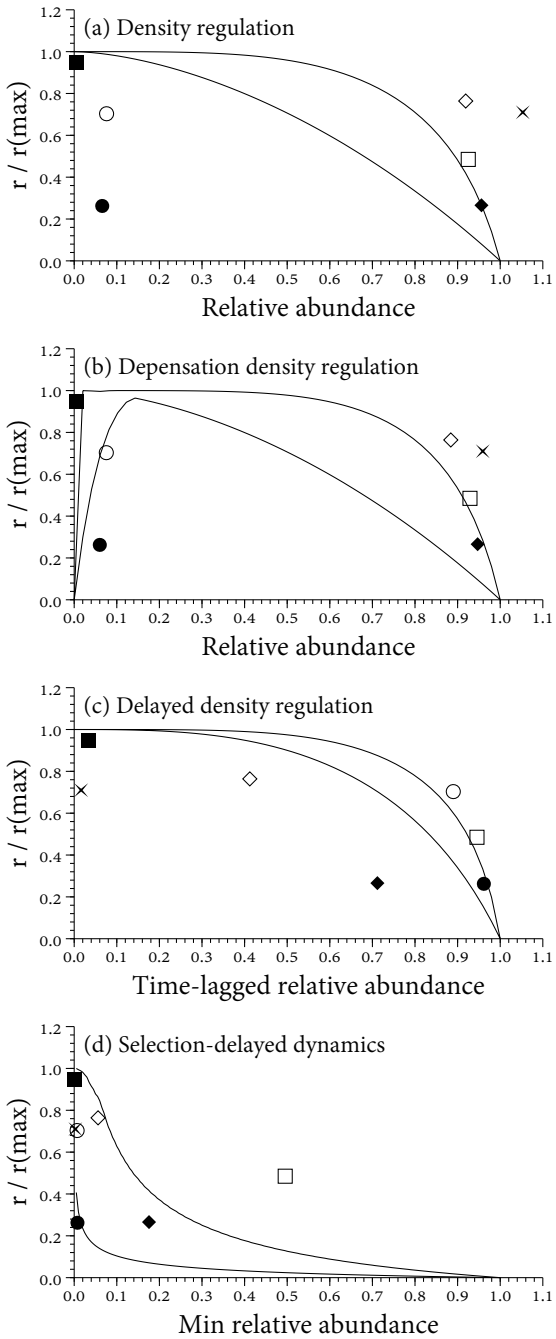

Figure 1: The relative exponential growth rate (r/r_{max}) as a function of the relative abundance (N/N^* or N/N^{**} dependent upon model) for *a*) density regulation, *b*) density regulation with depensation, *c*) delayed density regulation (time-lagged abundance), and *d*) selection-delayed dynamics (minimum historical abundance). **Open diamond**: bowhead whale; **Filled diamond**: gray whale; **Open circle**: southern right whale; **Filled circle**: North Atlantic right whale; **Open square**: fin whale; **Filled square**: blue whale; **Star**: humpback whale.

Model	+ H	− H
Density regulation	0.19	0.82
Density regulation ($N_0 \neq N^*$)	0.29	0.81
Density regulation (Catch prior)	0.49	0.79
Density regulation (Depensation)	0.21	0.85
Delayed density regulation	0.87	0.73
Selection-delayed dynamics	**0.97**	**0.94**
Predator − prey	0.14	0.83

Table 4: Correlation coefficients between the model-dependent and the model-independent estimates of the exponential growth rate, with (+ H) and without (− H) humpback whale included. The strongest correlations are shown in bold.

populations of killer whale are only marginally dependent upon specific species of baleen whales. By setting a uniform prior on $P^*(0)$ from 0.01 to 0.1 it is most likely that I assume a stronger than realistic dependence of killer whale on baleen whales. By doing this I allow for a stronger rejection of the hypothesis of natural population cycles by predator-prey interactions. This is because it is the parameterisations with the stronger dependence that produce the more cyclic dynamics.

A uniform prior on the strength of the functional response of the predator (μ) was set as log uniform from 0.3 to 3 to allow for both concave and convex responses. A uniform prior on $c^{**,p}$, the number of caught baleen whale prey per year per killer whale individual at the joint population dynamic equilibrium, was set quite wide ranging from 0.01 to 100 on logarithmic scale, and a uniform prior on the equilibrium abundance was set following the method described for the other models.

3 Results

3.1 Density-regulated growth

An essential feature of density-regulated growth is that the actual growth rate relative to the maximal growth rate (r/r_{max}) monotonically declines from one to zero as the relative abundance (N/N^*) increases from zero to one. The area between the curves in Fig. 1a represents the distribution of the best estimates of these density regulation curves across the seven species. Only one of the best model-independent estimates of relative growth fall within this area, suggesting that density-regulated growth is an insufficient model. This conclusion is echoed by the absence of a significant negative correlation (-0.18; $n = 7$; one-tailed $P = 0.35$) between the relative abundance and the model independent estimates of the relative growth rate. The result does not

Model	Bowhead	Gray	S right	N right	Humpback	Fin	Blue
Exponential growth	1.062 2.886	0.048 0.130	0.852 2.316	1.051 2.858	0.787 2.138	1.553 4.221	1.221 3.320
Density regulation	0.795 **0.795**	0.000 0.000	0.357 0.357	0.517 **0.517**	0.000 0.000	0.259 0.259	0.613 **0.613**
Density regulation ($N_0 \neq N^*$)	0.932 0.343	0.005 0.002	0.403 0.148	0.600 0.221	0.000 0.000	0.357 0.131	**1.062** 0.391
Density regulation (Catch prior)	0.970 0.357	0.044 0.016	0.357 0.131	0.844 0.310	0.000 0.000	0.748 0.275	0.803 0.295
Density regulation (Depensation)	0.827 0.304	0.000 0.000	0.549 0.202	0.705 0.259	0.000 0.000	0.262 0.096	0.613 0.225
Delayed density regulation	**1.062** 0.391	**0.247** **0.091**	**1.716** **0.631**	**1.259** 0.463	**0.625** **0.230**	**1.716** **0.631**	**1.062** 0.391
Selection-delayed dynamics	**1.000** **1.000**	**1.000** **1.000**	**1.000** **1.000**	**1.000** **1.000**	**1.000** **1.000**	**1.000** **1.000**	1.000 **1.000**
Predator-prey	0.869 0.000	0.000 0.000	0.419 0.000	0.827 0.000	0.000 0.000	0.292 0.000	0.560 0.000

Table 5: Model comparisons relative to selection-delayed dynamics, based on the AIC criterion (below the horizontal lines) and the AIC criterion with no parameter penalty (above the line). The two models with the highest relative score among the non-exponential models are shown in bold for each species.

depend upon whether the pre-exploited population is at carrying capacity or not, and it is also not affected by allowance of up to twice as many historical catches to compensate for incomplete catch histories due to underreporting and insufficient correction for whales that were struck and lost (Table 4 & 5; Fig. S2 in ESM).

3.2 Depensation

Dependent upon the species, the estimated density-regulated growth following whaling was either slower than expected from the prior (bowhead whale, North Atlantic right whale, southern right whale, and blue whale Fig. S3 in ESM), or it occurred too early to match the recent trend in abundance (gray whale, humpback whale and fin whale Fig. S4 in ESM). The actual growth is thus delayed relative to expectations, and this suggests that baleen whales may perhaps experience depensation, where, below a critical abundance, there is a positive relationship between the growth rate and the abundance. The estimated density dependence curves with depensation were more similar to the model-independent estimates of growth than for the density-regulated model with no depensation (Fig. 1a,b). However, only one of the estimated relative growth rates was contained within the density dependence space of the best estimated depensation models, and the correlation between the best model-dependent and model-independent estimates of the current growth rate remained low (0.21 for depensation and 0.19 for density regulation, Table 4).

3.3 Delayed feed-back

The limited success of the depensation model suggests a delayed density-dependent feed-back in the population dynamics of baleen whales. The delayed density-regulated model showed a significant negative correlation (-0.71; $n = 7$; one-tailed $P = 0.036$) between the relative growth rate and the relative abundance of the time-lag (Fig. 1c), and a strong positive correlation (0.87; $n = 7$; one-tailed $P = 0.006$) between the best model-dependent and model-independent estimates of the current growth rate. The average time-lag was 118 years with point estimates ranging from 35 to 290 years (Table 6).

3.4 Predator-prey dynamics

While a density-dependent time-lag may arise from inter-specific interactions, it is implausible that the growth of baleen whale prey would be delayed by hundred years. However, with a killer whale mean lifetime expectancy around 50 years (Olesiuk et al. 2005), a potential density-dependent feedback from killer whale predation would be substantially delayed. The age- and sex-structured killer whale - baleen whale predator-prey models, which allowed the equilibrium abundance of killer whale to decline by up to 99 % in the absence of the baleen whale, did not improve the estimates of the growth rate. The correlation between the best model-dependent and model-independent estimates of the current growth rates of baleen whales declined from 0.19 to 0.14 when killer whale predation was added to the density-regulated model (Table 4).

Species		N^{**}	N_m	d_t	r_t	a_m	b	p_0	p	ι	τ
	$x_{0.5}$	20	1.8	0.56	4.1	18	0.41	0.78	0.98	0.35	88
	$x_{0.025}$	13	0.9	0.34	2.3	14	0.27	0.53	0.96	0.14	2
Bowhead	$x_{0.975}$	24	5.1	0.88	5.2	25	0.52	0.94	0.99	3.72	130
	$x_{0.5}$	20	5.5	0.93	2.6	8	0.47	0.74	0.97	0.47	59
	$x_{0.025}$	14	2.3	0.71	1.8	6	0.31	0.52	0.93	0.11	18
Gray	$x_{0.975}$	25	10.2	1.52	3.5	12	0.61	0.94	0.99	2.11	100
	$x_{0.5}$	8	0.3	0.04	3.0	10	0.41	0.75	0.96	0.00	290
	$x_{0.025}$	7	0.0	0.03	0.0	5	0.22	0.52	0.93	0.00	150
N right†	$x_{0.975}$	8.1	0.3	0.04	5.7	20	0.53	0.94	0.98	0.06	360
	$x_{0.5}$	150	5.6	0.05	6.1	9	0.42	0.81	0.97	0.03	200
	$x_{0.025}$	140	1.3	0.03	1.8	6	0.31	0.51	0.94	0.01	130
S right†	$x_{0.975}$	160	13.3	0.09	8.9	13	0.50	0.94	0.99	0.12	230
	$x_{0.5}$	11	0.5	0.60	10.2	7	0.82	0.80	0.97	0.16	100
	$x_{0.025}$	9	0.1	0.30	6.0	5	0.43	0.53	0.93	0.04	45
Humpback	$x_{0.975}$	19	7.8	1.11	13.1	13	0.99	0.94	0.99	0.50	160
	$x_{0.5}$	19	13.0	0.92	3.9	9	0.48	0.76	0.97	0.41	35
	$x_{0.025}$	12	6.7	0.45	1.0	5	0.32	0.52	0.92	0.00	1
Fin	$x_{0.975}$	34	18.1	1.43	7.3	15	0.59	0.94	0.99	2.02	100
	$x_{0.5}$	390	1.1	0.00	5.3	8	0.43	0.79	0.97	0.02	39
	$x_{0.025}$	330	0.3	0.00	-3.0	5	0.31	0.52	0.92	0.00	1
Blue†	$x_{0.975}$	400	7.4	0.02	9.9	15	0.52	0.95	0.98	0.64	110

Table 6: Posterior updates of selected parameters given by the median ($x_{0.5}$) and the 95 % credibility interval ($x_{0.025}$ - $x_{0.975}$) of the posterior distributions. Estimates are based on selection-delayed dynamics, except that r_t is given by the exponential model, and τ by the delayed density-dependent model. The equilibrium (N^{**}) and historical minimum (N_m) abundance is given in thousands, and the exponential growth rates (r_t) in percent. The relative abundance (d_t) and r_t refer to the following years: 2003 for bowhead whale, 1983 for gray whale, 1995 for North Atlantic right whale, 1997 for southern right whale, 1988 for humpback whale, 2007 for fin whale, and 1998 for blue whale. †: Posterior for ι limited by the prior.

3.5 Selection-delayed dynamics

Age- and sex-structured models of selection-delayed dynamics improved the fit for baleen whales. The correlation between the best model-dependent and model-independent estimates of the current growth rates increased to 0.97 ($n = 7$; one-tailed $P = 0.0002$), and it is only the selection-delayed model and the delayed-density-dependent model that are able to provide reasonable estimates of the growth rate of humpback whale (Table 4). If the humpback whale was removed from the set of species, the correlation between the model-dependent and model-independent growth rate estimates increased quite drastically for the different density-regulated models and the predator-prey model (Table 4). Nevertheless, the strongest correlation was still obtained by the selection-delayed model.

Selection-delayed dynamics provide also a close resemblance between the model-dependent and model-independent estimates of the relative growth rate as a function of the historical minimum in relative abundance (Fig. 1d). The central North Atlantic fin whale is the only outlier from the curves in the figure, which show the growth rate at N^{**} following a point perturbation with all removals in a single year. This mimics the removals for most species, however, the fin whale was exposed to two distinct harvest peaks (Fig. S1 in ESM). This prolonged the time spent below N^{**} and extended the period with selection for increased growth. As expected, we find a fin whale with a higher relative growth rate than indicated by the curves in Fig. 1d.

Parameter estimates for the selection-delayed models are given in Table 6, with the estimated population trajectories shown in Fig. 2. The populations fall in three sets; those that are estimated to have recovered to near historical levels (gray whale, fin whale, and humpback whale), the bowhead whale that has recovered to approximately half the historical abundance, and those that are still heavily depleted (North Atlantic right whale, southern right whale, and Antarctic blue whale). All populations are estimated to increase, with annual growth rates ranging from 2.6 % (95 % CI from 1.8 to 3.5) in gray whales to 10 % (95 % CI from 6.0 to 13) in humpback whales.

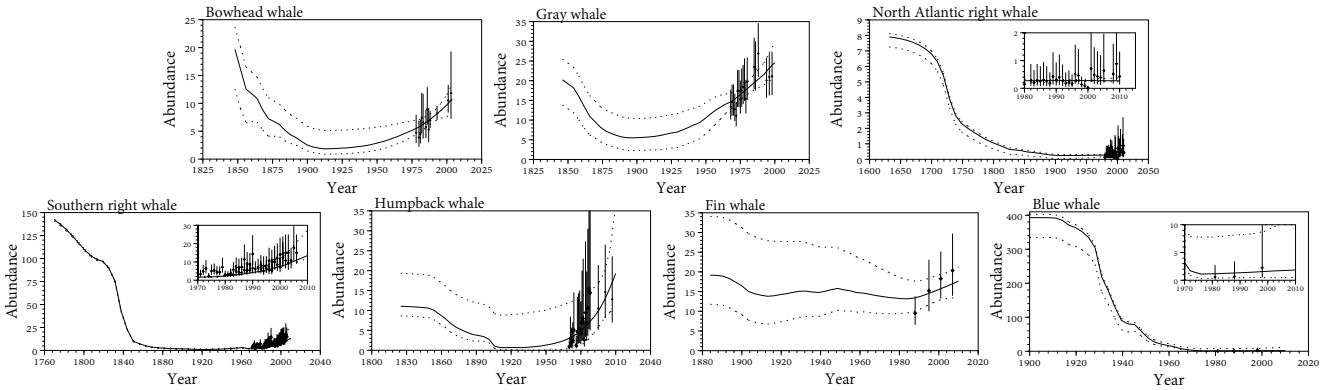

Figure 2: The projected 1+ abundance (in thousands) of the selection-delayed model for the seven species, with the last part of the trajectories being shown also in insert figures for the North Atlantic right, southern right, and blue whale. The solid lines are the median and dashed lines the 95 % credibility intervals. Scaled data with 95 % credibility intervals are also shown (blue whale data hardly visible in the main figure). The scales of both axes differ between the panels.

3.6 Model comparisons

Among the six models with a mechanistic change in the growth rate, the selection-delayed model had the highest AIC for all species, and the best fit (parameter independent AIC) for all species except the blue whale, where it had the second best fit (Table 5). There are two species (gray and humpback whale) for which the AIC, and the parameter independent AIC, identifies a statistically significant best model. In both cases, selection-delayed dynamics is optimal. For the gray whale the second best model is density-regulated growth with an uncertain catch history, but it is only between 1.6 % and 4.4 % as likely as selection-delayed dynamics. For the humpback whale the relative weight of all the other models is basically zero.

Owing to the high number of parameters, the AIC criterion identifies the predator-prey model as a completely ineffective model, having relative AIC values below 0.05 % for all species. When judged solely on its ability to explain the data, independently of the parameter penalty, the predator-prey model is generally equally suited as some of the density-regulated variants.

The projections of the best estimates of the four mechanistic models (density regulation, depensation, predator-prey and selection-delayed) are shown in Fig. 3 for the seven species of baleen whales. The trajectories of the density regulation, depensation and predator-prey models are relatively similar for most species. The selection-delayed model estimates instead i) higher rates of current growth for all species, ii) a more severe historical depletion for the gray whale, humpback whale and fin whale, iii) a higher initial abundance for the bowhead, North Atlantic right, southern right and blue whale, and iv) a lower initial abundance for the fin and gray whale.

4 Discussion

With the selection-delayed model and the delayed density-regulated model providing the best explanations for the current rates of increase, it is concluded that baleen whales have a delayed over-compensatory increase relative to density-regulated growth. Owing to the relative shortness of the time-series of abundance estimates, I did not attempt to estimate the degree to which this cyclic dynamics is damped.

Status estimates for baleen whale populations has usually assumed density-regulated growth, and a move to selection-delayed dynamics implies some changes in status (Fig. 3). The apparent long-term dynamics of the gray whale cannot be estimated by traditional density-regulated growth, which is unable to estimate the increase that has been documented since 1968 (Butterworth et al. 2002; Witting 2003b; Fig. S4 in ESM). To circumvent this problem, density-regulated models have been used to estimate the recent dynamics only (Wade 2002; Punt and Wade 2010), but selection-delayed models provide alternatives that can estimate also the long-term dynamics of the species (Witting 2003b; Punt et al. 2004; Fig. 2).

The humpback whale in the North Atlantic is another case where density-regulated growth cannot reconcile catch histories with recent abundance estimates, and tend to estimate recovered populations with too little current growth (IWC 2003a; Fig. 3; Fig. S4 in ESM). Selection-delayed models provide an alternative with the historical trajectories and current growth in general agreement (Fig. 2). For fin whales there is an absence of

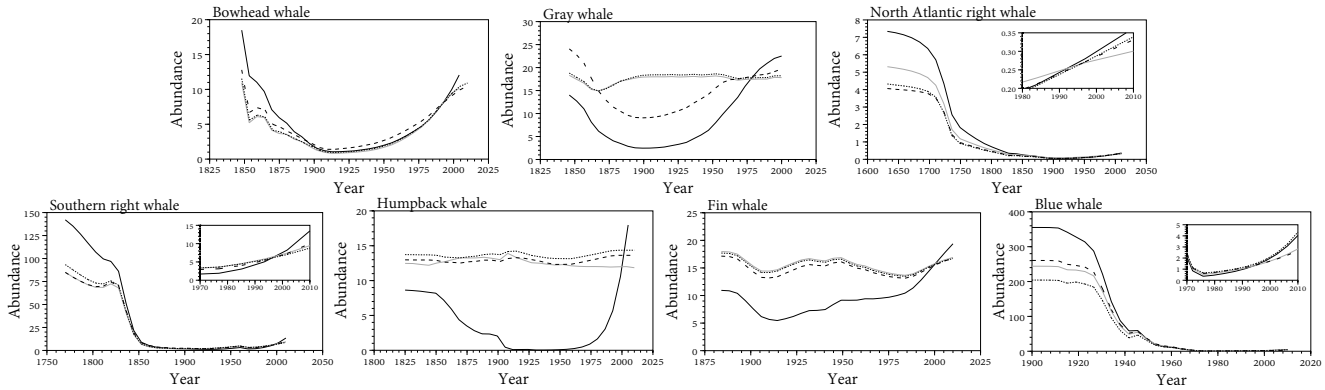

Figure 3: The projected 1+ abundance (in thousands) for the best estimates of four non-exponential models, with the last part of the trajectories being shown also in insert figures for the North Atlantic right, southern right, and blue whale. **Solid black line**: selection-delayed dynamics; **solid gray line**: density-regulated growth; **dotted line**: density-regulated growth with depensation; **dashed line**: killer whale predator-prey dynamics. The scales of both axes differ between the panels.

published assessments, but the selection-delayed model provides a better estimate of current growth than the density-regulated model (Fig. 3,2; Fig. S4 in ESM).

For the bowhead whale, long-term models based on density-regulated growth estimate a population that is almost recovered with a rate of increase that is about to decline (Fig. 3; Givens et al. 1995; Brandon and Wade 2006; Punt 2006). The selection-delayed model estimates a continued increase and a population that has recovered only to approximately 60 % of it pre-whaling abundance.

For the three remaining species that are still strongly depleted, the density-regulated and selection-delayed models estimate rather similar trajectories (Fig. 3), with the major difference being that density regulation estimates a pre-whaling abundance around 70 % of the selection-delayed model. Also for these three species, selection-delayed dynamics estimates higher rates of current increase than density-regulated growth (Fig. 3).

A negative annual growth of 2 % was estimated for North Atlantic right whale in 1995 (Fujiwara and Caswell 2001). This estimate is not directly comparable with the 3 % (95 % CI from 0.0 to 5.7) increase that I estimated. The 3 % is an average estimates for 1980 to 2010 in the absence of known anthropogenetic mortality, whereas the 2 % decline is specific for 1995 with anthropogenetic mortality included. For 1980 to 1995, Fujiwara and Caswell (2001) estimated an average increase of 1 %, and the expected growth is larger for 1980 to 2010 because there has been a strong increase in the number of sighted calfs after 1995 (average calf number: 11.1 from 1980 to 1995; 19.2 from 1996 to 2010; Kraus et al. 2007).

Unfortunately, the estimated historical trajectories are hard to impossible to check. Genetic based estimates of the abundance of whales prior to whaling (Roman and Palumbi 2003; Alter et al. 2012) are surprisingly high and apparently not directly comparable with estimates based on population modelling (Holt 2004; Baker and Clapham 2004). Alternative genetic estimates of the minimum abundance during the historical trajectories are strongly dependent upon the assumed richness of haplotypes prior to whaling (Jackson et al. 2008), and they may not offer much independent control. Nevertheless, my minimum estimate of 23 humpback whales in 1932 for the best parameterisation of the selection-delayed model may seem unreasonably low. The estimated minimum is though expected to be somewhat negatively biased because the absolute abundance estimates are subject to perception and availability bias, and I may have allocated too many winter catches from the West Indices and Cape Verde to the summer aggregation in the central North Atlantic.

4.1 Sufficient, necessary and contributing factors

Density regulation, depensation and predator-prey interactions were found not to be sufficient mechanisms for the estimated over-compensatory dynamics in baleen whales. Selection-delayed dynamics, on the other hand, was sufficient. That intra-specific delays can be sufficient for cyclic dynamics was maybe first shown by Murdoch and McCauley (1985), who found that *Daphnia* isolated in the laboratory may cycle with a relatively fixed period independently of the presence versus absence of a cycle in its prey. For natural populations, Sinervo et al. (2000) found an abundance cycle in side-blotched lizard caused by selection by density

and frequency dependent interactive competition.

The positive findings for intra-specific delays stand out against an absence of results that show that predator-prey interactions can be a sufficient mechanism for the cyclic dynamics of natural populations. There are studies that conclude that predation affects the growth and abundance of prey species with cyclic dynamics (e.g., Korpimäki and Norrdahl 1998; Korpimäki et al. 2002), but this does not in itself imply that the cycle is caused by predation. There is an absence of removal experiments that show that natural and cyclic prey populations become non-cyclic when predators are removed (Krebs 1996; Oli 2003a,b); instead there are removal experiments that conclude that predator-prey interactions are neither sufficient nor necessary to explain the observed cycles (Graham and Lambin 2002).

Population modelling that has been used to explain apparent predator-prey cycles (Hanski et al. 1991; Oksanen et al. 2001; Klemola et al. 2003) do not include the stabilising effects of the density regulation in the predator that is caused by other factors than the prey species that is explicitly included in the model. My initial killer whale - baleen whale models that did not include these stabilising terms were able to provide reasonable estimates of the current growth rates in baleen whales (results not shown), but when corrected to include predator dependence on other species the models were no longer sufficient to explain the delayed recovery of baleen whales.

While intra-specific delays have been found to be sufficient, it is unlikely that they are always necessary for the cyclic dynamics of natural population. However, by finding that predator-prey interactions are insufficient, and that intra-specific delays are sufficient, it is suggested that intra-specific delays are also necessary in order to explain the dynamics of baleen whales.

Nevertheless, even if predator-prey interactions are not sufficient to cause cyclic dynamics by themselves, they may be an important contributing or even necessary factor for the existence of an apparent predator-prey cycle. If a damped selection-delayed prey cycle is initiated by an environmental perturbation, then relative to cases with a constant predation rate, the delayed population growth of a specialist predator relative to the growth of its prey implies increased prey mortality at the low phase of the prey cycle, and decreased predation at the peak phase. Hence, specialist predation ensures a continued downward perturbation during the low phase, and a continued upward perturbation at the peak phase, and this might be sufficient to keep a damped selection-delayed cycle running instead of damping out.

Predation responses by generalist, on the other hand, may not be delayed if generalist predators concentrate on the cyclic prey during its peak phase, and prey predominately on other species during the low phase. If this is the case, generalist predation will stabilise the damped selection-delayed cycle even more by inducing a downward perturbation during the peak, and an upward perturbation during the low, phase of the prey cycle. A fading out of cyclic dynamics on a cline from specialist to generalist predation [as proposed for Fennoscandia (Henttonen et al. 1987; Hanski et al. 1991) and other areas (Oksanen et al. 2001)] may thus result from the interaction between selection-delayed dynamics and predator-prey interactions. A laboratory example of an apparent predator-prey cycle between rotifer and algal that exists only when the prey population can respond to selection is given by Yoshida et al. (2003).

4.2 How common is selection-delayed dynamics?

Selection-delayed dynamics is characterised not only by cyclic population dynamics, but also by cycles in the phenotypic characters that are used as competitive traits (Witting 1997, 2000a). The phase of these cycles are roughly opposite to expectations from density regulation (e.g., largest average body mass during the late peak phase where we would expect the smallest body mass from density regulation), and they may therefore be used as an indicator of natural populations with selection delayed dynamics.

A projected example of a cycle in body mass relative to the cycle in population density is illustrated in Fig. 4, showing that a lower than average mass can be expected during the late low / early increasing phase of a cycle, and that a larger than average mass can be expected during the late peak / early declining phase. A phase opposite to the predicted (e.g., smaller body masses at peak abundance), is not necessarily evidence against selection-delayed dynamics, as argued by Klemola et al. (2004). Selection-delayed dynamics include both the effects of density regulation and selection, and even with selection for an increased intrinsic mass, the phenotypic mass might decline due to an overriding effect from a deteriorating environment.

Size, or body mass, is one example of a possible competitive trait cycle in a population with selection-delayed dynamics. Other traits include the group size of the reproducing unit (with cooperation among kin being more favourable at large abundance) and the sex ratio when males act as interfering individuals

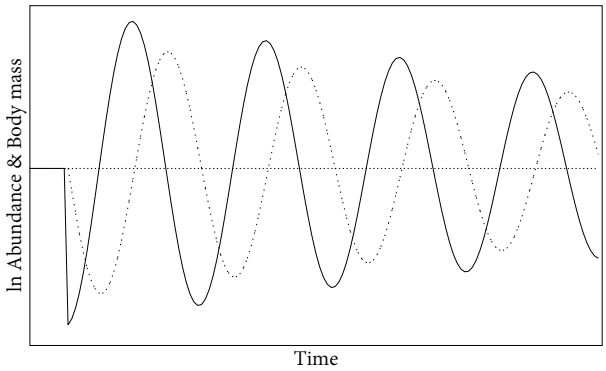

Figure 4: The projected body mass (dotted line) and abundance (solid line) on log scale for damped selection-delayed dynamics using the discrete model in Witting (2000a). The horizontal broken line indicates the evolutionary equilibrium.

and females as reproducing individuals (Witting 1997, 2000a).

There are no publications that investigate a phenotypic response in baleen whales in relation to cyclic dynamics, but there are plenty of studies from other species. Cycles in competitive quality occur in side-blotched lizard with selection-delayed dynamics (Sinervo et al. 2000), and the abundance cycle in the *Daphnia* experiments of Murdoch and McCauley (1985) had an associated cycle in body mass, with the larger *Daphnia* occurring mainly during the late peak phase of the cycle (Witting 2000a). In fact, such body mass cycles appear to be the rule, rather than the exception, in species with cyclic population dynamics. They are widespread in voles and lemmings with cyclic dynamics (Chitty 1952; Hansson 1969; Krebs and Myers 1974; Boonstra and Krebs 1979; Mihok et al. 1985; Lidicker and Ostfeld 1991; Stenseth and Ims 1993; Ergon et al. 2001; Norrdahl and Korpimäki 2002; Lambin et al. 2006), and they have been observed in snowshoe hare (Hodges et al. 1999) and cyclic forest insects (Myers 1990; Simchuk et al. 1999). Quite generally, it is observed that voles and lemmings are small, non-aggressive, and that they have a high reproductive rate when the abundance is low and increasing. When instead the abundance is high and declining, they are aggressive, and 20 to 30 % larger having a delayed and low reproductive rate.

Cycles in other traits have been reported by Naumov et al. (1969) who found that the percentage of males increased in small rodents when densities are high, while females predominate during the low phase. Other cases of an increased male fraction with increased density include white-tailed deer (*Odocoileus virginianus*) (McCullough 1979) and northern elephant seal (*Mirounga angustirostris*) (Le Boeuf and Briggs 1977). And the abundance cycles in red grouse (*Lagopus lagopus scotica*) are associated with cycles in kin structure, with larger kin groups evolving during the increasing phase of a cycle (Watson et al. 1994; Matthiopoulos et al. 2003; Piertney et al. 2008).

In conclusion we note i) that selection-delayed dynamics is both theoretically (Witting 1997, 2000a) and empirically (Murdoch and McCauley 1985; Sinervo et al. 2000) sufficient for cyclic population dynamics, ii) that it is widespread in natural populations owing to the widespread occurrence of otherwise unexplained phenotypic cycles in populations with cyclic dynamics, iii) that there appears to be a lack of empirical evidence showing that predator-prey interactions can be a sufficient mechanism for the cyclic dynamics of natural populations, and iv) that the present study is the first that differentiates between the inter- and intra-specific hypotheses across the species of a taxonomic group, by supporting the selection-delayed hypothesis in baleen whales over the hypotheses of density regulation, depensation and predator-prey interactions. It seems that selection-delayed intra-specific feed-backs is a much more general cause for cyclic population dynamics than previously thought.

4.3 Implications of selection-delayed dynamics

Cyclic dynamics

With selection for increased growth when the abundance is below the population equilibrium, and selection for decreased growth when the abundance is above the equilibrium, selection-delayed dynamics may generate damped or neutrally stable cycles (Witting 2000a). This suggests that the amplitude of cycles in natural populations may be defined more by the magnitude of perturbations than by an intrinsic cyclic property (as for limit cycles), as illustrated in Fig(1d) that shows the maximal archived growth as a function of the magnitude of the perturbation. This dependence on perturbations is likely to cause Moran effects (Moran 1953), where different populations and species have cycles that are synchronised by similar responses to spatially and temporally correlated environmental perturbations.

Given a dependence on external perturbations, we may expect population cycles to show a cline, where they become more common, widespread and with larger amplitudes in more marginal and fluctuating environments. Furthermore, if these environments are associ-

ated with more specialist predation relative to generalist predation, the continued perturbations imposed by specialist predation would contribute to the existence of more stable cycles with larger amplitudes. These expectations coincide with evidence where northern cycles relative to southern cycles have larger amplitudes, with high-arctic cycles tending to extreme amplitudes (Hanski et al. 1991; Oksanen and Oksanen 1992; Lambin et al. 2000), including more species often with synchronized dynamics (Henttonen et al. 1987; Korpimäki et al. 2005; Hansen et al. 2013), and are synchronous at larger spatial scales (Lambin et al. 1998; Huitu et al. 2003; Sundell et al. 2004). It is also in agreement with a widespread collapse of cycles in the south as an apparent response to shorter winters, with a lower frequency of environmental perturbations and maybe more generalist predation (reviewed by Ims et al. 2008).

Korpimäki et al. (2003) and Korpimäki et al. (2005), however, argue that small mammal cycles in Fennoscandia are mechanistically different from cycles elsewhere and in other species, but this is questioned by Lambin et al. (2006) who note that the patterns argued to be special for Fennoscandia cycles (long-term changes in relative abundance and type of dynamics; geographical synchrony over large areas; inter-specific synchrony; phenotypic cycles) are observed also for common vole (*Microtus arvalis*) in western, central and eastern Europe. Indeed, although maybe on different scales, these patterns are often observed world-wide (Leirs et al. 1997; Lima et al. 2002; Stenseth et al. 2003; Lambin et al. 2006; Holmengen et al. 2009) not only for voles and lemmings, but also for snowshoe hare (Roth et al. 2007) and insects (Berryman 1996; Myers 1998; Klemola et al. 2006). This indicates that the underlying mechanisms may be the same although the exact parameterisation differ between cases. For baleen whales that have been extensively depleted by past whaling, it is important to recognise that they may now have the potential to greatly overshoot their equilibrium abundance.

Cyclic carrying capacity

Another consequence of selection delayed dynamics is a re-definition of the population dynamic equilibrium. The carrying capacity of density-regulated growth (N^*) is sometimes seen as a capacity of the environment, even though it is a tension where the increase of exponential growth is balanced against a deterioration of the environment (Fisher 1930). Being defined where this deterioration results in zero population growth, the carrying capacity is positively related to the maximal (intrinsic) growth rate, which is defined for optimal zero-density conditions. For the population dynamic equilibrium of selection-delayed dynamics (N^{**}) there is the additional requirement that selection on the intrinsic growth rate is absent.

During a population dynamic cycle, there is selection for an increase in the intrinsic growth rate, and thus an increase in carrying capacity (as traditionally defined), when the abundance is below the equilibrium, while there is selection for a decline when the population is above the equilibrium. Hence, selection-delayed population cycles include a cycle in carrying capacity and during the course of a cycle, the population is at carrying capacity at both the peak and bottom density (see Fig. 1 in Witting 2000a). However, these densities have density-frequency-dependent selection for changes in the carrying capacity, and these changes causes the population to continue its cycle. In comparison, the population takes both a positive, and a negative, growth rate at the density of the population dynamic equilibrium. At this density, there is no selection pressure for a change in the intrinsic growth rate and carrying capacity, but past selection has caused the carrying capacity N^* to be higher than N^{**} during the increasing phase of the cycle, and less than N^{**} during the declining phase.

In order to reconcile the historical catches and recent growth rates of baleen whales with density-regulated growth, it has been suggested that there has been an increase in the environmental component of the carrying capacity over time (Butterworth et al. 2002). While it may seem unrealistic that the ecological conditions of all oceans should have improved over past centuries, we note that selection-delayed dynamics actually predicts the increasing carrying capacities over time as a logical consequence of density-frequency-dependent selection in depleted populations. This increase, however, is not caused by improved environmental conditions, but by a selection induced increase in the intrinsic growth rate.

Harvest dynamics

This paper considered selection consequences on population dynamics following a short-term perturbation of otherwise relatively undisturbed natural populations. A continued anthropogenetic disturbance is expected to cause other changes. A continued harvest will cause some longer-term depression in the abundance and level of interactive competition relative to the undisturbed state. This will change the density-frequency-dependent selection pressure generating selection for

a decline in competitive traits so that the population abundance is re-established and the increased mortality rate is compensated for by an increased reproductive rate (Witting 2002a). While the time-scale of such responses are unclear, there is plenty of evidence showing that populations with increased anthropogenetic or natural mortality evolve lower body masses and an increased reproductive rate (e.g., Reznick et al. 1996; Haugen and Vøllestad 2001; Sinclair et al. 2002; Coltman et al. 2003; Carlson et al. 2007; Herczeg et al. 2009; Rossetto et al. 2012).

Several life history responses to fisheries are consistent with density-frequency-dependent natural selection in depleted populations, but some of these responses may also arise from direct harvest selection from a fishery that takes predominately the larger individuals (e.g., Browman 2000; Sinclair et al. 2002; Olsen et al. 2004). So far the relative importance of indirect versus direct harvest selection has not been quantified, although the relative influence of harvest versus natural selection has been examined in pike (*Esox lucius*) (Carlson et al. 2007; Edeline et al. 2007).

Growth rate acceleration

Finally, it is essential to note that under selection-delayed dynamics, it is no longer possible to determine the per capita growth rate, but only the acceleration of the growth rate, as a function of the density-dependent environment. Traditional ecological thinking based on density-regulated growth assumes that given environmental conditions (including density and predation) set a specific growth rate for a population. But selection-delayed dynamics implies that a population can have a large, if not infinite, number of growth rates, often with opposite signs, associated with the same environmental conditions. This conceptual transition was first proposed by Ginzburg (1972) from analogy to Newton's laws of motion (Newton 1687). By rejecting the alternative hypotheses of density regulation, depensation and predator-prey interactions, it is suggested that baleen whale population dynamics is determined by a selection-delayed acceleration of the growth rate.

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