

Reconstructing the population dynamics of eastern Pacific gray whales over the past 150 to 400 years

LARS WITTING

Greenland Institute of Natural Resources, PO Box 570, DK-3900 Nuuk, Greenland
Contact e-mail: larsw@natur.gl

ABSTRACT

Reconstructing the historic trajectory of the eastern North Pacific gray whale (*Eschrichtius robustus*) is important for the understanding of whale population dynamics and for management of the hunt on the population. Interestingly, the density-regulated BALEEN II model (Punt, 1999) will generally not reconstruct the trajectory because it does not reconcile catch history and abundance data unless additional *ad hoc* hypotheses are added to the model. Here, an alternative model of inertial dynamics is used to estimate the population trajectory over the past 150 to 400 years. This model is a traditional density-regulated model with superimposed density-dependent changes in the intrinsic life history. Nine different versions of the model are examined and Bayesian assessments performed for the complete catch histories from 1600 and 1846. This reconciles the data, can explain an independent abundance estimate from 1885 and it predicts an over-compensatory population that has increased steadily above the equilibrium abundance for the last three decades. The model predicts that gray whale abundance will begin to decline in a more or less drastic manner in the near future.

KEYWORDS: GRAY WHALE; MODELLING; FISHERIES; INERTIAL DYNAMICS; DENSITY-REGULATION; NATURAL SELECTION

INTRODUCTION

For the majority of species, including large whales, it has been the consensus among population ecologists that Malthusian (exponential) increase and density-dependent regulation are the essential population dynamic mechanisms intrinsic to populations. However, our understanding of population dynamics is not given by consensus *per se*. Instead it depends on plausible models that will reconstruct the dynamics of natural species. For one of the best documented whale populations — the eastern North Pacific gray whale (*Eschrichtius robustus*) — it is well-known that the hypothesis of density-regulated growth does not reconcile the known historical catches with the recent trajectory in abundance estimates (Cooke, 1986; Lankester and Beddington, 1986; IWC, 1993; Butterworth *et al.*, 2002). When, as is customarily done in whale management research, the historical catches are used to back-calculate current abundance estimates to a pre-exploited population in dynamic equilibrium, the estimated trajectory does not show the observed increase that has occurred in the population since the 1960s. To reconcile the density-regulation hypothesis and the abundance estimates from 1968 to 1988, the carrying capacity in 1988 needs to be at least twice that in 1846, the commercial catches from 1846 to 1900 need to be at least 2.5 times those accepted by IWC (1993) or the annual aboriginal catches prior to the commercial catches need to be at least 3 times larger; these limits weaken if the factors are considered in combination (Butterworth *et al.*, 2002).

Although the density-regulated model tends not to explain the data, the coarse history of the three gray whale populations have been reconstructed during the last decades. The reason for the disappearance of the gray whale in the North Atlantic (Mead and Mitchell, 1984) is unclear but hunting may have been the cause; it certainly reduced the North Pacific populations to very low numbers. Since the halt of the commercial harvest, the western North Pacific gray whale population has remained small (Weller *et al.*, 1999), while the eastern North Pacific (hereafter 'eastern') population has increased substantially. For the eastern

population, which is the only population to be considered in detail here, the historical catches apparently reduced a population of 10,000–20,000 animals in the 1840s (Lankester and Beddington, 1986) to an approximate estimate of 160 whales in 1885 (Townsend, 1886). In the early 20th century, the population was believed extinct (Andrews, 1914), but in the 1930s migrating gray whales were again commonly observed off California (Rice *et al.*, 1981). Some 20 surveys over the last 30 years have shown a steady increase at 2.5% (SE=0.3%) per annum (Reilly, 1984; Buckland and Breiwick, 2002) while on average 155 whales were taken each year (Punt, 2001), predominately in a local subsistence hunt along the Chukotka Peninsula. A total of 26,600 whales (CV=10%) were estimated in 1997/98 (Hobbs and Rugh, 1999), and a combination of recent mass mortality (Le Boeuf *et al.*, 2000) and a decline in more recent abundance estimates (Rugh *et al.*, 2002) indicate that the population might be close to carrying capacity.

One possible reason for the lack of fit of the density-regulated model could be that the gray whale has cyclic population dynamics. Direct density-regulation cannot explain the widespread tendency for cyclic dynamics in natural species (Turchin, 1990; Witteman *et al.*, 1990; Turchin and Taylor, 1992; Ginzburg and Taneyhill, 1994). However, delayed density-regulation can explain both cyclic dynamics and the fact that delayed density-dependence is documented in many species (e.g. Turchin, 1990; Turchin and Taylor, 1992; Berryman, 1996). But delayed density-regulation does not represent a realistic single-species model; there is no strong theoretical basis to explain how this mechanism would work within a species. In this paper, the alternative single-species model of inertial dynamics (Ginzburg, 1980; 1998; Ginzburg and Taneyhill, 1994; Witting, 1997; 2000; 2002a; c; Inchausti and Ginzburg, 1998) is used to examine whether the gray whale data can be explained by cyclic population dynamics.

Inertial dynamics resemble traditional density-regulated models with superimposed density-dependent changes in the intrinsic life history. Such models may be compared with older models of delayed density-regulation in the sense that

both can explain the cyclic dynamics in many natural species, and that both models include delayed density-dependence, although the delay in inertia models is restricted to one generation. However, where the delayed density-dependence is given by assumption in the delayed density-regulated models, the delay in the inertia models arises from plausible natural selection-based mechanisms that operate within the population. Another essential difference is that the intrinsic growth rate is a parameter in delayed, as well as direct, density-regulated models, while it is an initial condition in inertia models.

To examine whether inertial dynamics can explain the gray whale data the trajectories of the traditional density-regulated model are compared with the trajectories of the inertia model for three different life histories. A larger span of variation in the inertia model is also examined by comparing different inertia models with the gray whale data. The inertia models covered include variation in life history parameters (e.g. reproduction and survival), variation in catch histories, variation in the sex ratio of the catches and the population, and variation in the intrinsic life history parameters that are allowed to change in time. All these comparisons are made to a baseline model by changing one component at a time comparing the abundance data to the projections of the best fits of the different models. Finally, a Bayesian assessment based on the inertia model and two different catch histories is presented.

METHOD

Population dynamics model

One of the more realistic density-regulated models for the gray whale is the age- and sex-structured BALEEN II model (Punt, 1999) that the IWC applies to baleen whales. A discrete variant of the model may take the form:

$$N_{t+1} = \lambda N_t f(N_t) - c_t \quad (1)$$

where subscript t is time, N abundance, λ the intrinsic growth rate, $f(N)$ the density-regulation function that declines monotonically with N and c the catch.

Using density- and frequency-dependent game theory, it has been shown (Witting, 1997; 2000; 2002a) that selection by intra-specific density-dependent competitive interactions can extend the density-regulated model of Equation (1) into:

$$\begin{aligned} \lambda_{t+1} &= \lambda_t g(N_t) \\ N_{t+1} &= \lambda_t N_t f(N_t) - c_t \end{aligned} \quad (2)$$

where the selection response function $g(N)$ monotonically declines with N , being one at equilibrium $N^* = g^{inv}(1)$. This function reflects between generation changes in the intrinsic life history as they arise from genotypic and epigenetic responses to selection. A g function that is constant in time reflects the simplistic case where the selection response at a given abundance is time independent. Population models like Equation (2) have also been deduced from epigenetic maternal effects independently of natural selection (Ginzburg and Taneyhill, 1994; Ginzburg, 1998; Inchausti and Ginzburg, 1998).

From Equation (2), the intrinsic growth rate λ will increase in populations below the equilibrium and decline in populations above the equilibrium. The result is inertial dynamics where, relative to traditional density-regulated dynamics, the actual growth rate is being maintained when the population approaches the population dynamic equilibrium, generating cyclic dynamics in abundance, life

history and carrying capacity $k_t = f^{inv}(1/\lambda_t)$. These cycles arise from selection processes intrinsic to the population and they may be damped, stable, or repelling with periods ranging from two to an infinite number of generations. Since λ and k are initial conditions in Equation (2) k will generally differ from the equilibrium abundance N^* unless the population is in dynamic equilibrium.

An age-structured inertia model based on BALEEN II was developed by Witting (2002c). The present study is based on a slightly modified version as described in the Appendix. This model can operate with density-regulation and selection responses in the fecundity rate (b) and in the age of reproductive maturity (a_m).

Model comparisons

The inertia model used as a baseline case has life history parameters that are close to the average of the generally accepted priors for the eastern gray whale. To examine how sensitive the fit of the inertia model is to the life history parameters, the model is also applied for a fast and a slow life history that lie at the boundaries of the gray whale priors (fast and slow refer to a faster and slower turnover rate of individuals in the population). Using the average, lower and upper limits to the priors in Punt (2000), this gives adult survival of $S_{ad} \in \{0.95, 0.97, 0.99\}$, an age of reproductive maturity of $a_m \in \{5, 7, 9\}$, and a maximal fecundity of $b_{max} \in \{0.60, 0.45, 0.30\}$ for respectively the fast, baseline and slow life histories. For the baseline case, the rate of juvenile survival (S_{juv}) is estimated from a traditional Pella-Tomlinson density-regulated model with no inertia under the assumption that the maximum sustainable yield (MSY) rate is 0.05 and the MSY level is 0.6 (see Punt, 1999 and Appendix for detail). For the fast and slow life history, juvenile survival is adjusted such that the ratio of juvenile to adult survival is similar to the ratio of the baseline model. This gives the following survival estimates $S_{juv} \in \{0.92, 0.94, 0.96\}$, and the following estimate of MSY rate $\in \{0.04, 0.05, 0.06\}$ for the fast, baseline and slow Pella-Tomlinson models with no inertia.

To illustrate the difference between the fit of the traditional density-regulated model and the inertia model, trajectories are also calculated for the baseline, fast and slow life histories for the Pella-Tomlinson density-regulated model with no inertia. Together with the Appendix, for the Pella-Tomlinson density-regulated model with no inertia, the above mentioned parameters specify the complete parameterisation of the life history leaving the equilibrium abundance (N^*) as the only free parameter in the model. This contrasts to the inertia models that have four free parameters: the strength of density-regulation (γ); the level of selection response (ι), also referred to as the level of inertia; the level of density-regulation and inertia in the age of reproductive maturity relative to that of the fecundity rate (α); and the equilibrium abundance (N^*).

The baseline catch history used includes the aboriginal and commercial catches from the beginning of the commercial harvest in 1846 (IWC, 2002), assuming a post-1998 catch of 61 females and 61 males per year. To reflect some of the uncertainty in the catch history, two alternative catch histories were examined: the complete catch history from the beginning of the aboriginal harvest in 1600 as estimated by IWC (1993), and the catch history from 1846 including only the commercial catches and the post-1943 aboriginal catches.

The commercial harvest of gray whales reported more females than males. For the complete catch history from 1846, including aboriginal catches with an assumed equal

sex ratio, the fraction of females in the catch is 0.66. For the baseline model, the sex ratio at birth is even and, thus, it is assumed that the female biased catch reflects a disproportionally large catch of females. To examine the alternative where the sex ratio of the catch reflects the sex ratio of the population, the case where the sex ratio in the harvest is even assuming the same total number of catches is considered, and so is the case where the female fraction at birth is 0.66.

In the baseline model, it is also assumed that the density-regulation and selection responses are restricted to the fecundity rate, i.e. α is set to zero in Equations (15) and (20). There are, nevertheless, plenty of reasons to believe that such responses will operate on a much larger set of life history parameters (e.g. Witting, 1997; 2002b). To reflect this, the dynamics are also examined when there is an additional density-regulation and selection response in the age of reproductive maturity (a_m), assuming that this response is half, or equal to, the response in b , i.e. α is set to respectively 0.5 and 1.

To find an optimal parameterisation for each of these models, the models were fitted to the shore-based survey estimates of the 1+ abundance from 1968 (the 1967/68 count) to 2002 (the 2001/02 count) obtained from IWC (2002) and Rugh *et al.* (2002). This was carried out by projecting the population from a pre-exploited abundance in population dynamics equilibrium, and by using the method of de la Mare (1986) to calculate the likelihood under the assumption that the observation errors are log-normally distributed (Buckland, 1992). This gives the likelihood function:

$$L = \prod_t \exp\left(-\frac{[\ln(\hat{N}_t^{obs} / \hat{N}_t)]^2}{2cv_t^2}\right) / cv_t \quad (3)$$

where \hat{N}_t^{obs} is an estimate of the 1+ abundance at time t , \hat{N}_t is the 1+ abundance of the model projection at time t , and cv_t is the coefficient of variation of the abundance estimate at time t .

To find an optimal parameterisation, the three-dimensional parameter space of ι , γ and N^* was searched. The level of inertia was searched by 0.1 steps within the range $0 \leq \iota \leq 5$, that cover dynamics from a traditional density-regulated model with no inertia ($\iota=0$), over inertia models with damped cyclic dynamics ($0 < \iota < \approx 3-4$), to inertia models with unstable dynamics ($\approx 3-5 < \iota$). Trajectories that cycle too fast were discarded during the search. For the trajectories that are initiated in 1846, the following were discarded: (1) all trajectories that before 2005 cross the equilibrium abundance in an upward direction more than once; and (2) all the trajectories that cross the equilibrium abundance in the downward direction, except for the initial decline starting in 1846. For the trajectories that were initiated in 1600, the trajectories that before 2005 cross the equilibrium abundance in an upward direction more than twice and all the trajectories that cross the equilibrium abundance in the downward direction more than once were discarded. This allows for one full population cycle in the 1846 to 2005 trajectories, and for two full cycles in the 1600 to 2005 trajectories.

For each 0.1 step within the inertia range $0 \leq \iota \leq 5$, 60 steps were used to search the γ parameter over one order of magnitude around the values that an initial and more crude search has indicated to contain the optimal parameterisation. For each $\iota - \gamma$ combination, all N^* within the range $7,000 \leq N^* \leq 22,000$ that will hit the point estimate of the abundance in 1977 were found. Among these, all the parameterisations

that lead to dynamics with too fast cycles were discarded, as described above. From the remaining hits, the hit with the highest likelihood was optimised by Brent's method (Brent, 1973) for γ and N^* in order to find a local optimum in the likelihood function. The best estimate was then the parameterisation with the highest likelihood chosen among these potentially 3,060 different local optima. This routine will not necessarily find the global likelihood optimum but it is likely to find a parameterisation that is close to the global optimum.

Bayesian assessment

A Bayesian method was used to estimate the parameters of the inertia model for two cases with a density-regulation and selection response in the fecundity rate only, aboriginal and commercial catches starting from 1600 and 1846 respectively, and an even sex ratio in age-class zero. The technical method resembles that of Wade (2002), where the sampling-resampling routine of Rubin (1988) was used to estimate the posterior distribution. Initially, n_1 random parameterisations θ_i ($1 \leq i \leq n_1$), with dynamics that contain no more than one (two) full cycle(s) in the period from 1846 (1600) to 2005, were sampled from the joint prior distribution (Table 1). For each set the population was projected from the pre-exploited equilibrium until 2005 and the likelihood $L(\theta_i)$ was calculated. The n_1 parameter sets were then re-sampled n_2 times with replacement, with the sampling probability of the i th parameter set being:

$$q_i = \frac{L(\theta_i)}{\sum_{j=1}^{n_1} L(\theta_j)} \quad (4)$$

This will generate a random sample of the posterior distribution of size n_2 . The sample of the posterior distribution was set to $n_2 = 5,000$, and the initial sampling to $n_1 > 2,000,000$ in order to produce a smooth posterior distribution.

Table 1

The prior distributions: b_{max} is the maximal fecundity rate; a_m the age of reproductive maturity; S_{ad} adult survival; S_{juv} juvenile survival; ι the level of inertia; γ the strength of density-regulation; N^* the equilibrium abundance; and cv_{ad} the additional variance in the abundance estimates, given as a coefficient of variation. The 1600 and 1846 in parentheses indicate distributions that apply only to the catch histories from 1600 and 1846 respectively. U indicates a uniform distribution, and DU a discrete uniform distribution.

Parameter	Dist.	Min.	Max.
b_{max} (1600)	U	0.20	0.60
b_{max} (1846)	U	0.30	0.60
a_m	DU	5	9
S_{ad}	U	0.95	1.00
S_{juv}	U	0.80	0.99
ι	U	0.00	5.00
γ (1600)	U	0.000005	0.0001
γ (1846)	U	0.00001	0.00050
N^*	U	10,000	20,000
cv_{ad}	U	0.00	0.35

Generally the priors (Table 1) resemble those of Wade (2002) and Punt *et al.* (2002) except for the equilibrium abundance that is restricted to much lower values in Table 1. This is because a large equilibrium abundance has virtually no likelihood in the inertia model and, thus, the restricted range was chosen to make the sampling-resampling routine more efficient. Another difference is the maximal birth rate that has a minimum value of 0.2 for the inertia model with

catches starting in 1600, while the minimum is 0.3 in Wade (2002) and Punt *et al.* (2002). This is because an initial estimate indicated an estimate very close to 0.3.

Like Wade (2002), an additional variance term was used. The additional variance was parameterised as a coefficient of variation (cv_a), considered to be constant across years and incorporated into the likelihood function in each year as an additive variance term to the abundance estimate assuming that the additional variance has a Gaussian distribution. Hence, in each year, the cv_t of Equation (3) is given as:

$$cv_t = \sqrt{cv_{n,t}^2 + cv_a^2} \quad (5)$$

where $cv_{n,t}$ is the coefficient of variation of the abundance estimate in year t .

RESULTS

Model comparisons

The parameters and relative likelihood of the best fitting inertia models and the three Pella-Tomlinson models that hit the 1977 abundance are given in Table 2, together with four management-related quantities; the trajectories of the different projections are shown in Fig. 1a-e.

Like in other studies (e.g. Butterworth *et al.*, 2002), the traditional density-regulated models (Fig. 1a) fail to explain the increase in the abundance estimates from 1968, and nor are they consistent with a depleted population around 1900, as indicated in the figure by the abundance estimate of 160 whales in 1885 (Townsend, 1886). This contrasts to the inertia models (Fig. 1b-e) that all explain both the increase in the abundance estimates from 1968 and the depleted population around 1900, although only two of the models indicate depletions to the level of 160 whales. All inertia models predict that the current abundance is much larger than the equilibrium abundance, and that the population will begin a more or less drastic decline in the near future (average year of initial decline 2019, ranging from 1999 to 2046).

The three Pella-Tomlinson models with no inertia (Fig. 1a) have almost zero likelihood compared with the inertia models. Among the inertia models it is especially the trajectories of the slow life history, the commercial catch series from 1846, and the total catch series from 1600 that have the highest relative likelihood. By comparing the

differences in the relative likelihood with the trajectories of the inertia models, it can be seen that the largest fraction of the differences in the relative likelihood is caused by the fit to the high abundance estimates from 1994 to 1998 and the low estimates for 2001 and 2002. None of the inertia models are able to capture the drastic change in the abundance estimates between these two periods, and the differences in the relative likelihood is to a large degree due to the way that the trajectories compromise between the estimates of the two periods.

Nearly all the inertia models give comparable estimates of the historical trajectories, including comparable fits to the data (except 1994-2002), with the largest differences being in the projections from 2000 to 2100. For the three life history models – baseline, fast and slow (Fig. 1b) – the historical trajectories are very similar, while the future trajectories show some differences in the timing and level of the peak abundance, and in the subsequent population decline. All three models show slow declines with the population being above the equilibrium abundance in 2100, with the peak abundance being progressively later and higher in the slow, baseline and fast life history models.

A larger difference is induced by the different catch histories (Fig. 1e). Again the historical trajectories are very similar, but compared with the baseline model, both the catch history from 1600 and the commercial catches from 1846 induce a much more drastic decline in abundance after year 2000. The inclusion of inertia and density-regulation in the age of maturity (Fig. 1c) has the opposite effect, with the abundance continuing to increase at a very slow rate until 2040-45. Again there are only minor differences in the historical trajectories. The models where the sex ratio of the catch reflects the sex ratio of the population (Fig. 1d), however, induce a clear decline in the historical trajectories so that they are comparable with the historical abundance estimate of 160 whales in 1885. For these models, the model with an even sex ratio in the catch induces a more drastic decline in the abundance after year 2000, while the model with a female-biased sex ratio in the newborns produce a future trajectory that is comparable with the trajectory of the baseline model.

For the management related quantities in Table 2 we find that nearly all models estimate a population close to the current carrying capacity. However, for the inertia models with a dynamic carrying capacity, it may be more helpful to

Table 2

The three Pella-Tomlinson models with no inertia ($\iota = 0$) that hit the point estimate of the 1977 abundance, and the best fits of the inertia models ($\iota > 0$). ι is the level of inertia; γ the strength of density-regulation; N^* the equilibrium abundance; and q % the relative likelihood in percent, as estimated by Equation (4) when summed over the best fits of the 12 different models. N_2/N^* is the depletion ration in 2002 relative to the equilibrium abundance N^* , N_2/K_2 the depletion ration in 2002 relative to the carrying capacity K in that year, and Y_2 and Y_{12} are the production of whales in the population in the years 2002 and 2012 respectively.

Model	ι	γ	N^*	q %	N_2/N^*	N_2/K_2	Y_2	Y_{12}
Baseline	0.0	-	16,680	0.0	0.95	0.95	122	126
Fast	0.0	-	16,520	0.0	0.96	0.96	121	128
Slow	0.0	-	16,930	0.0	0.93	0.93	121	124
Baseline	0.2	0.000096	14,670	2.2	1.66	0.86	247	167
Fast	0.2	0.000045	15,730	0.7	1.67	0.78	359	237
Slow	3.4	0.000154	14,540	50.7	1.57	1.00	146	94
Commercial catches	2.2	0.000066	10,880	15.1	2.03	1.17	42	-41
Catches from 1600	1.8	0.000068	10,800	15.2	2.07	1.09	62	-25
Even sex ration in catch	1.4	0.000058	8,390	9.2	2.70	1.06	99	-1
Birth female biased	0.3	0.000082	11,510	3.9	2.07	0.88	226	143
Rep. Maturity $\alpha = 0.5$	0.2	0.000056	15,760	2.8	1.60	0.74	333	259
Rep. Maturity $\alpha = 1.0$	0.3	0.000037	16,560	0.2	1.58	0.61	382	302

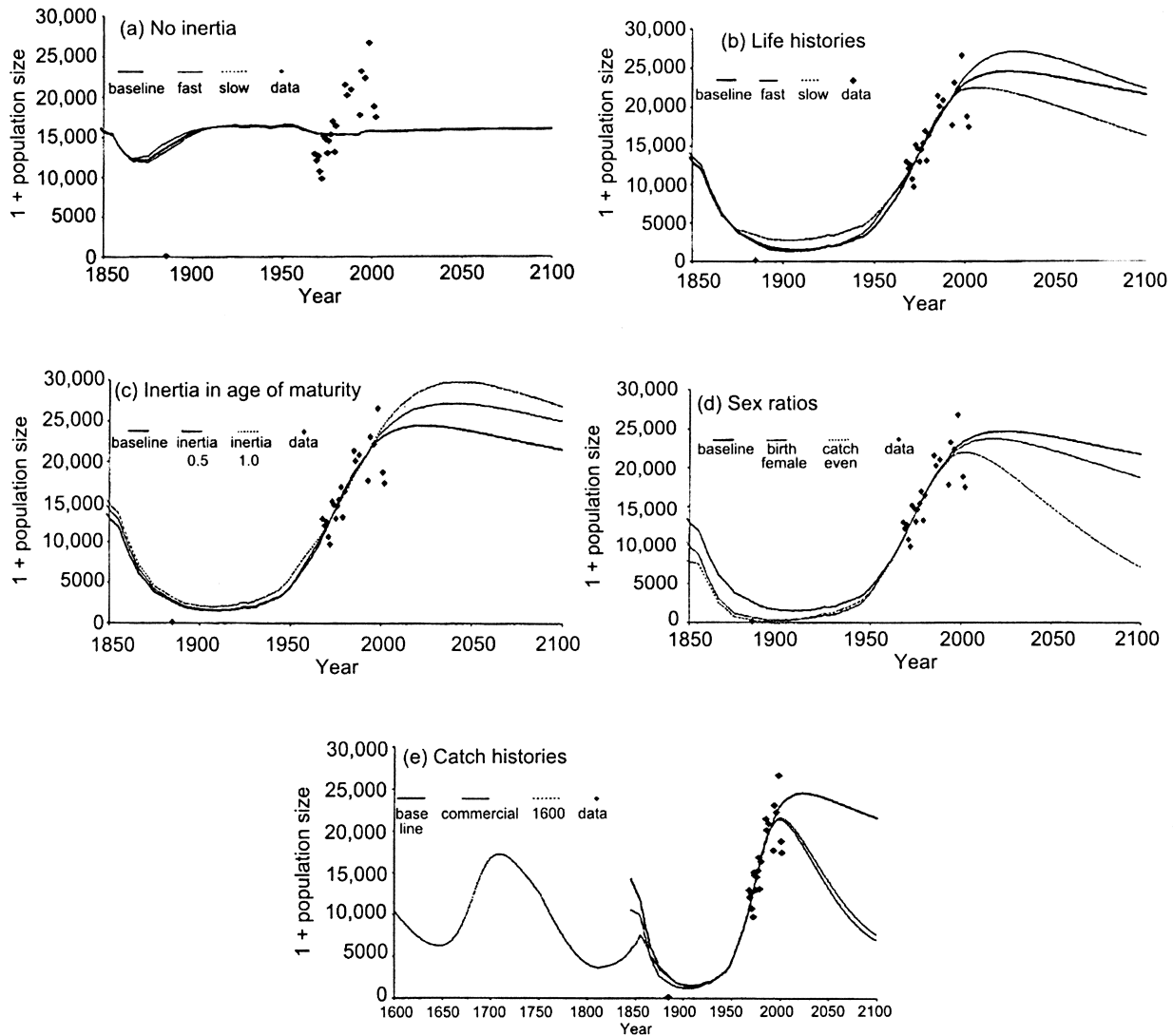


Fig. 1. Comparing gray whale data to models. The diamonds are the point estimates of abundance, and the curves the trajectories of different models. These models are: (a) the Pella-Tomlinson density-regulated model with no inertia, for the baseline, fast and slow life histories under the assumption that the trajectories hit the 1977 abundance estimate; (b) the best fits of the inertia model for the baseline, fast and slow life histories; (c) the baseline and two levels of inertia and density-regulation in the age of reproductive maturity; (d) the baseline, the case with a female biased sex ratio at birth, and an even sex ratio in the catch; and (e) the baseline, the commercial catch history from 1846, and the complete catch history from 1600. All inertia models are fitted to the abundance estimates from 1968 to 2002, and the 1885 estimate is included only for comparison.

define the depletion ratio relative to the equilibrium abundance, where the current population size is 1.6 to 2.7 times the equilibrium abundance.

The production of the population in 2002 is estimated to be 120 whales per year for the Pella-Tomlinson models with no inertia, with a slight increase between 2002 and 2012. For the inertia models, the production in 2002 varies between 42 and 380 whales per year, with all models predicting a decline between 2002 and 2012. On average, the decline in the yearly production between 2002 and 2012 is 85 whales, with the range for the best fits of the different models being a decline between 52 and 120 whales.

Bayesian assessment

The parameter estimates, management quantities and correlation matrices of the Bayesian assessments for the catch histories from 1846 and 1600 are given in Tables 3 and 4 respectively. The median and the 95% credibility intervals (CI) of the posterior distribution of population abundance are shown in Fig. 2a-b, and the corresponding values are shown in Fig. 3a-b for the posterior distribution of the yearly production in the population.

In general, both catch histories give similar parameter estimates, not only for the life histories but more surprisingly also for the equilibrium abundance that is estimated to 15,200 (CI: 13,600-18,900) and 14,600 (CI: 11,200-19,600) for the catch histories starting in 1846 and 1600 respectively. For all parameters, it is the catch history from 1846 that gives the smallest CI. For the posterior distribution of abundance (Fig. 2) and production (Fig. 3) it is generally the historical estimates from 1850 to 2000 that have the smallest CIs, while the projection into the future and the historical estimates prior to 1850 are less accurate.

The estimates of both catch histories suggest that the abundance in 2002 is 1.5-1.7 times the equilibrium abundance (CI: 1.23-1.61) for the 1846 catch history. Whereas the estimates of the 1846 catch history suggest that the 2002 abundance is 0.85 (CI: 0.46-1.75) times the carrying capacity in that year, the 1600 catch history suggests that the 2002 abundance is only 0.68 (CI: 0.21-0.89) times the 2002 carrying capacity. This difference is also reflected in the production levels. Although both models suggest that the yearly production between 2002 and 2012 will decline by approximately 100 whales, the 1600

Table 3

Parameter estimates for the 1846 catch history. Estimates of parameters and four management-related quantities, together with the parameter correlation matrix. The point estimates are given as the posterior mode and medians, followed by the 95% credibility interval.

Parameter estimates								
	Mode	Median	2.5 th	97.5 th				
b_{max}	0.31	0.40	0.31	0.56				
a_m	6	7	5	9				
S_{ad}	0.97	0.96	0.95	0.99				
S_{juv}	0.88	0.89	0.80	0.95				
t	2.88	1.02	0.27	5.00				
γ	0.000059	0.000059	0.000022	0.000136				
N^*	15,200	15,200	13,600	18,900				
cv_{ad}	0.09	0.14	0.09	0.20				

N_2/N^*		1.51	1.23	1.61				
N_2/K_2		0.85	0.46	1.75				
Y_2		195	-36	558				
Y_{12}		117	-116	449				
Correlation matrix								
	b_{max}	a_m	S_{ad}	S_{juv}	t	γ	N^*	cv_{ad}
b_{max}	1.00	-	-	-	-	-	-	-
a_m	0.07	1.00	-	-	-	-	-	-
S_{ad}	0.12	-0.14	1.00	-	-	-	-	-
S_{juv}	-0.33	0.41	0.13	1.00	-	-	-	-
t	-0.19	0.28	-0.14	0.24	1.00	-	-	-
γ	0.19	0.05	0.32	-0.01	-0.27	1.00	-	-
N^*	0.17	-0.18	0.38	-0.08	-0.23	-0.50	1.00	-
cv_{ad}	0.23	0.08	-0.12	-0.06	-0.30	0.15	0.03	1.00

Table 4

Parameter estimates for the 1600 catch history. For detail see Table 3.

Parameter estimates								
	Mode	Median	2.5 th	97.5 th				
b_{max}	0.53	0.38	0.21	0.55				
a_m	9	8	5	9				
S_{ad}	0.96	0.97	0.95	0.99				
S_{juv}	0.83	0.86	0.80	0.95				
t	1.08	1.08	0.09	4.90				
γ	0.000050	0.000050	0.000009	0.000092				
N^*	14,000	14,600	11,200	19,600				
cv_{ad}	0.13	0.13	0.01	0.34				

N_2/N^*		1.67	1.13	1.93				
N_2/K_2		0.68	0.21	0.89				
Y_2		337	116	739				
Y_{12}		218	19	717				
Correlation matrix								
	b_{max}	a_m	S_{ad}	S_{juv}	t	γ	N^*	cv_{ad}
b_{max}	1.00	-	-	-	-	-	-	-
a_m	0.06	1.00	-	-	-	-	-	-
S_{ad}	-0.48	-0.04	1.00	-	-	-	-	-
S_{juv}	-0.30	-0.11	0.06	1.00	-	-	-	-
t	-0.27	-0.19	0.48	0.10	1.00	-	-	-
γ	0.13	0.17	-0.00	-0.20	-0.69	1.00	-	-
N^*	-0.30	-0.05	0.22	0.02	0.31	-0.47	1.00	-
cv_{ad}	-0.12	0.11	0.04	0.04	0.22	-0.32	0.21	1.00

catch history gives a yearly production of 337 (CI: 116-739) whales in 2002, while the corresponding production for the 1846 catch history is 195 (CI: -36-558) whales. Seen over the longer time span of Fig. 3a-b, the models estimate large cycles in the production level. For the 1846 catch history,

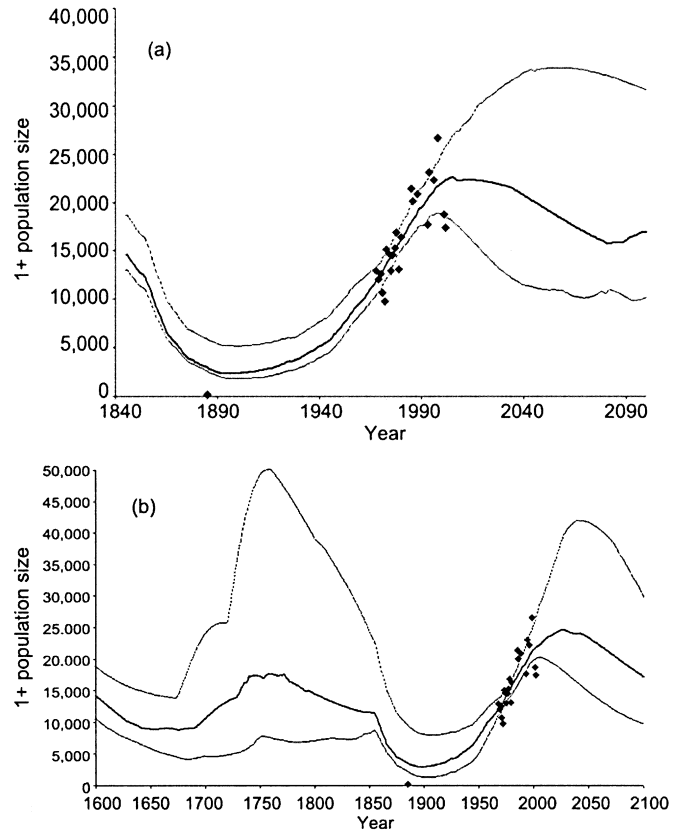


Fig. 2. Comparing gray whale data to Bayesian assessments. The solid curves are the medians and the dashed curves the 95% credibility intervals of the posterior abundance distribution for the complete catch histories from (a) 1846 and (b) 1600. The diamonds are the point estimates of abundance, with the model fitted to the estimates from 1968 to 2002, and the 1885 estimate included only for comparison.

e.g. there is a peak in the yearly production of 596 (CI: 406-683) whales in 1975, and a predicted minimum of -13 (CI: -174-214) whales in 2030.

DISCUSSION

The inertia model is better than traditional density-regulated models in reconciling the catch history and the abundance data of the eastern North Pacific gray whale. Except for the recent decline in the abundance estimates for 2001 and 2002, the inertia model is generally consistent with the data, while a successful fit of the density-regulated model depends on the inclusion of *ad hoc* hypotheses, e.g. that the carrying capacity in 1988 is at least 2.5 times the capacity in 1846 (Butterworth *et al.*, 2002). While such an increase is potentially possible, the density-regulation hypothesis provides no mechanism to explain it. A mechanism is instead provided by the inertia model that predicts that selection induced changes in the intrinsic growth rate implies that the carrying capacity in 1988 is 1.9 (CI: 1.6-3.2) times the capacity in 1846 or 2.5 (CI: 1.6-6.4) times the capacity in 1600.

Other factors that may enable the density-regulated model to fit the estimates of gray whale abundance are commercial catches that are 2.5 times the catches documented by the IWC (1993) for the period 1846-1900, or aboriginal catches prior to 1846 that are three times larger than the current estimates. Although 'the overall data set was the best available', IWC (1993) 'noted that the estimated commercial

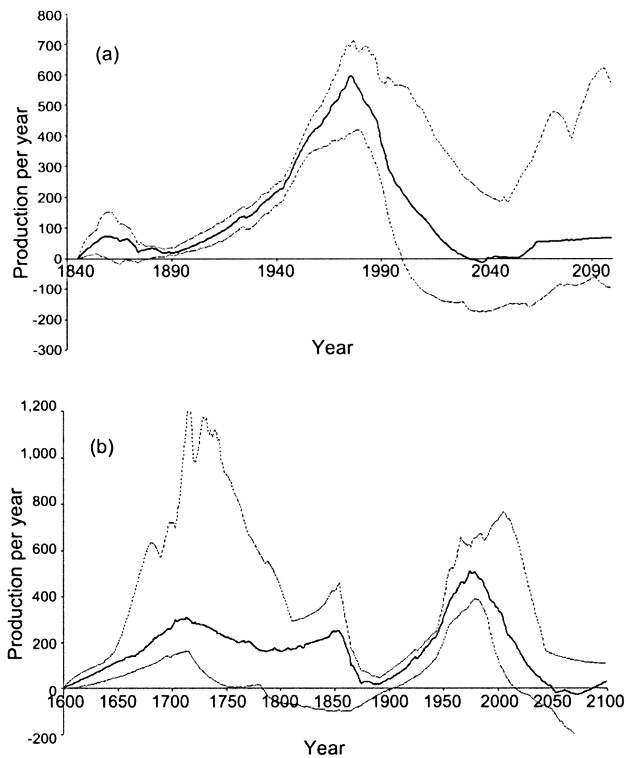


Fig. 3. The yearly production of whales in the eastern North Pacific gray whale population, as estimated by the Bayesian assessment for the complete catch histories from (a) 1846 and (b) 1600. The solid curves are the medians and the dashed curves the 95% credibility intervals.

catches may be underestimates to an unknown degree and possibly up to 1.5 times'. Obtaining estimates for early aboriginal catches is extremely difficult.

The different versions of the inertia model are approximately equally efficient in explaining the data. The major differences between the trajectories of the different models lie in the projections into the future, where some models have a faster and deeper decline in the abundance than other models. The historical trajectories, on the other hand, are generally very similar between the different models suggesting that the abundance in historical time is rather accurately estimated should the gray whale population be driven by inertial dynamics.

It could be argued that the inertia model is too robust because the different models are approximately equally efficient in explaining the data despite the fact that only one model can be the true model. This may, however, reflect that the cyclic dynamics of the inertia model are comparable to those of the gray whale, and that the three free parameters by which the model is fitted to the data allow for sufficient flexibility in the dynamics despite the differences in model structure and catch histories. The indication that the gray whale may have cyclic dynamics is also compatible with the fact that the traditional density-regulated models with a monotonic return to equilibrium cannot easily fit the data unless additional *ad hoc* factors are added to the models.

If the dynamics of the gray whale is truly cyclic it does not necessarily imply that the underlying mechanism is that of inertial dynamics. The dynamics might instead be driven by other factors that can induce delayed density-dependence, with the most obvious alternative being predator-prey interactions. The essential predator-prey interaction may, at least in principle, be both with the prey or predators of the gray whale. However, as the delay in the density-dependence

more probably needs to be comparable with the generation time of the gray whale before the estimated cycles will arise, the essential interaction may unlikely be with gray whale prey. Of other explanations, interactions with the killer whale (*Orcinus orca*) is the main potential predator.

The recent high mortality in the gray whale population (Le Boeuf *et al.*, 2000; Pérez-Cortés *et al.*, 2000) and the abrupt decline between the abundance estimates of 1994-98 and 2001-02 may indicate that the population is about to experience a major decline in abundance, although IWC (2002) suggests lower mortality and healthier animals in 2001. While the traditional density-regulated model will not be able to explain such a decline without additional *ad hoc* hypotheses such as decline in carrying capacity, the inertia model predicts that a decline in abundance and carrying capacity is about to occur. However, even the decline in the fastest declining inertia model cannot keep up with the decline in the recent abundance estimates. There may be several reasons for this. The abundance estimates for 2001 and 2002 might be negatively biased, they might be the result of a 'catastrophic' event that generated the recent mass mortality independently of the mechanisms that usually drive the gray whale dynamics, the gray whale may not have inertial dynamics, or the gray whale may have inertial dynamics while the models investigated here do not fully capture the dynamics of the species.

At present, there is no particular reason to expect that the two abundance estimates of 2001 and 2002 are negatively biased compared with the earlier estimates (Rugh *et al.*, 2002). The recent high mortality, which seems to be a likely cause for a recent decline, might have been caused by some catastrophic event, but it might also be a reflection of more general population dynamics mechanisms that operate at peak densities in species with cyclic dynamics. Such mechanisms may include increased sensitivities to infections by parasites due to high densities and/or malnourished individuals. But, the mechanisms may also be more directly linked to a cause of cyclic dynamics. For example, the inertia models investigated in this paper are all based on the assumption that the within population bias in the distribution of resource between individuals is a linear function of the population density, which for most cases imply that the competitive game that distributes the resource among the individuals is assumed to be the same over all population densities; this may not be the case. The competitive games are to a large degree determined by the strongest individuals and if at high population densities these individuals experience a shortage in the availability of resource it is likely that they will change the game in their favour so that they will dominate the access to the resource even more than they do at lower densities with less resource shortage. If this is the case, one can expect density-dependent transitions in the competitive game with the resource becoming increasingly monopolised at the highest densities at the cost of the competitively inferior, or even the majority of, individuals in the population. In such cases, one would generally expect a population decline that is faster than for the models presented here, where the cycles are symmetrical in the sense that the declining phase of the cycle is comparable with the increasing phase.

The Standing Working Group on the Development of an Aboriginal Subsistence Whaling Management Procedure (AWMP) is presently developing a *Strike Limit Algorithm* (SLA) for the eastern North Pacific gray whale (see e.g. IWC, 2002). This is done in a simulation framework where candidates SLAs are tested over a number of trials, with each trial representing *inter alia* a different hypothesis on the

population dynamics of gray whales. Although at present a few of the trials are based on inertial dynamics, the majority are variants of the density-regulated hypothesis that does not reconcile the historical catches and the recent abundance estimates. This problem is circumvented in the trials by discarding the majority of the historical catches and initiating the trials in 1930 assuming that the age-structure is stable and that the population is not in dynamic equilibrium at that time. While this allows for a good fit of the density-regulated hypothesis to the estimates of gray whale abundance, it does not allow for trials with cyclic dynamics, nor does it explain the discrepancy between the data and the model.

With the abundance estimates and catch histories being consistent with cyclic population dynamics it would seem to be a wise strategy if candidate *SLAs* were tested firmly against the hypothesis of cyclic dynamics, particularly as the abundance data indicates a decline that is faster than the decline of the fastest declining inertia model applied in this paper. It could be argued that an accepted *SLA* for the eastern gray whale must be able to cope even with a crashing gray whale population. Unfortunately, such *SLAs* would necessarily, at least to some degree, compromise the number of allowable strikes if the gray whale would stabilise at approximately the current abundance, as assumed by most of the density-regulated trials. This trade-off is probably unavoidable if the objective is to develop an *SLA* that will work also for the apparently likely scenario where the gray whale abundance is declining.

The development of an *SLA* designed also for cyclic dynamics might be a somewhat tedious process. Both the management objectives of the IWC and the framework used to evaluate candidate *SLAs* have been developed only for traditional density-regulated dynamics. Traditional management objectives are often defined relative to the *MSY* and the *MSY* level, which are concepts that apply only to cases where the intrinsic growth rate is constant. For inertial dynamics, the intrinsic growth rate is an initial condition so that most population abundances are associated with a suite of both positive and negative realised population dynamic growth rates. Among other things, this implies that there is no single curve of sustainable yields and, thus, no well-defined harvest optimum as assumed by the IWC.

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Appendix ABUNDANCE DYNAMICS

Let age- and sex-structure resemble the BALEEN II model (Punt, 1999), where the dynamics in the number of animals in age classes larger than zero is:

$$\begin{aligned}
 R_{t+1,a+1}^{m/f} &= (R_{t,a}^{m/f} - C_{t,a}^{m/f})S_a + U_{t,a}^{m/f}S_a\delta_{a+1} & 0 \leq a \leq x-2 \\
 R_{t+1,x}^{m/f} &= (R_{t,x}^{m/f} - C_{t,x}^{m/f})S_x + (R_{t,x-1}^{m/f} - C_{t,x-1}^{m/f})S_x - 1 & (6) \\
 U_{t+1,a+1}^{m/f} &= U_{t,a}^{m/f}S_a(1 - \delta_{a+1}) & 0 \leq a \leq x-2
 \end{aligned}$$

where $R_{t,a}^{m/f}$ is the number of recruited males/females of age a at the start of year t , $U_{t,a}^{m/f}$ is the number of unrecruited males/females of age a at the start of year t , δ_a is the fraction of unrecruited animals of age $a-1$ which recruit at age a (assumed to be independent of sex), $C_{t,a}^{m/f}$ is the catch of males/females of age a during year t (whaling is assumed to take place in a pulse at the start of each year), S_a is the annual survival rate of animals of age a :

$$S_a = \begin{cases} S_{\text{juv}}S_{\text{adult}} & \text{if } a = 0 \\ S_{\text{juv}} & \text{if } 1 \leq a \leq a_{\text{adult}} \\ S_{\text{adult}} & \text{if } a > a_{\text{adult}} \end{cases} \quad (7)$$

where S_{juv} is the survival rate for 'juveniles', S_{adult} is the survival rate for adults, a_{adult} is the greatest age at which the 'juvenile' survival rate applies, and x is the maximum (lumped) age-class (all animals in this and the $x-1$ class are to be recruited and to have reached the age of reproductive maturity). In this paper $a_{\text{adult}} = 0$ and $\delta_a = 1$ for $a \geq 1$.

The number of births at the start of year $t+1$, B_{t+1} , is:

$$B_{t+1} = \sum_{a=a_{m,\text{min}}}^x B_{t+1,a} \quad (8)$$

where $a_{m,\text{min}}$ is the potential lower limit to the age of reproductive maturity a_m , and $B_{t+1,a}$, the number of births in age class a , is:

$$B_{t+1,a} = b_{t+1,a}N_{t+1,a}^f \quad (9)$$

where $b_{t,a}$ is the fecundity rate for mature females (at time t in age class a), and $N_{t,a}^f$ is the number of mature females in age class a at the start of year t , defined as:

$$N_{t,a}^f = \begin{cases} 0 & \text{if } a_{m,t,a} > a \\ R_{t,a}^f + U_{t,a}^f & \text{if } a_{m,t,a} \leq a \end{cases} \quad (10)$$

where $a_{m,t,a}$ is the age of reproductive maturity for individuals in age class a at time t .

Density-regulation

Let \hat{N} be the component of the population that imposes density-regulation, and let it be the one plus component

$$\hat{N} = \sum_{a=1}^x U_a^f + U_a^m + R_a^f + R_a^m \quad (11)$$

Let density-regulation operate on the fecundity rate b and on the age of reproductive maturity a_m , with:

$$\beta_{t+1,a} = \beta_{t,t+1,a}f_\beta(\hat{N}_{t+1}) \quad (12)$$

where $\beta = b$ and $\beta = a_m$ respectively, $\beta_{t,t+1,a}$ is the intrinsic parameter b_t or $a_{m,t}$ in age class a at time $t+1$, and the density-regulation function $f_\beta(\hat{N}_t)$ is monotonically declining with \hat{N}_t for $\beta = b$ and monotonically increasing with \hat{N}_t for $\beta = a_m$. Both density-regulation functions f_b and f_{a_m} take the age specific limits:

$$\beta_{\text{min}} / \beta_{t,t,a} \leq f_\beta(\hat{N}_t) \leq \beta_{\text{max}} / \beta_{t,t,a} \quad (13)$$

where $\beta_{\text{min}} \in \{b_{\text{min}}, a_{m,\text{min}}\}$ is the lower and $\beta_{\text{max}} \in \{b_{\text{max}}, a_{m,\text{max}}\}$ the upper limits for b and a_m . At the population dynamic equilibrium (\hat{N}^*), the density-regulation functions take the value of one [$f_\beta(\hat{N}^*) = 1$], the age-structure is stable, the realised parameters are identical to the intrinsic parameters ($\beta_a^* = \beta_{t,a}^*$) being the same over all age classes.

For the traditional density-regulated model with no inertia and density-regulation operating only on the fecundity rate b , let the density-regulation function take the Pella-Tomlinson form:

$$f(\hat{N}_{t+1}) = \max(1 + A[1 - (\hat{N}_{t+1}/\hat{N}^*)^z], 0) \quad (14)$$

where $A = (b_{max} - b^*)/b^*$ because there is no age structure in the fecundity rate of mature females. Then, as b^* can be estimated from age structured survival (S_a), and as the MSY rate and the MSY level is given by S_a , b^* , A and z , provided estimates/assumptions of MSY rate, MSY level and S_{adult} it is possible to calculate S_{juv} .

For density-regulation in the inertia models the exponential Ricker functions are used:

$$\begin{aligned} f_b(\hat{N}_{t+1}) &= e^{-\gamma(\hat{N}_{t+1} - \hat{N}^*)} \\ f_{a_m}(\hat{N}_{t+1}) &= e^{\alpha\gamma(\hat{N}_{t+1} - \hat{N}^*)} \end{aligned} \quad (15)$$

to avoid that $f_\beta(\hat{N}) = 0$ for abundances above the population dynamic equilibrium N^* and to avoid that $f_\beta(\hat{N})$ is discontinuous at N^* (γ and $\alpha\gamma$ define the strength of the density-regulation functions f_b and f_{a_m} respectively).

Life history dynamics

Let the intrinsic life history parameters b_t and $a_{m,t}$ be stable during the lifespan of the individual, and let the average intrinsic component of a cohort be stable as the individuals of the cohort is dying. Hence, for $0 \leq a \leq x - 2$:

$$\begin{aligned} b_{t,t+1,a+1} &= b_{t,t,a} \\ a_{m,t,t+1,a+1} &= a_{m,t,t,a} \end{aligned} \quad (16)$$

Let the intrinsic components of age class \times be the weighted average of the cohorts within this class:

$$\beta_{t,t+1,x} = \frac{\beta_{t,t,x}(N_{t,x}^f - C_{t,x}^f)S_x + \beta_{t,t,x-1}(N_{t,x-1}^f - C_{t,x-1}^f)S_{x-1}}{(N_{t,x}^f - C_{t,x}^f)S_x + (N_{t,x-1}^f - C_{t,x-1}^f)S_{x-1}} \quad (17)$$

where $\beta = b$ and $\beta = a_m$ respectively.

Let the intrinsic components of new-borns be the components of the parents multiplied by a density-dependent selection response $g_\beta(\hat{N})$, so that the average intrinsic components of a new-born cohort is:

$$\beta_{t,t+1,0} = \frac{g_\beta(\hat{N}_{t+1}) \sum_{a=a_{m,min}}^x \beta_{t,t+1,a} B_{t+1,a}}{B_{t+1}} \quad (18)$$

with $\beta = b$ and $\beta = a_m$, and where B_t is given by Equation 8, $B_{t,a}$ by Equation 9, and the selection response functions $g_\beta(\hat{N}_t)$ are positive, monotonically declining with \hat{N}_t for $\beta = b$, and monotonically increasing with \hat{N}_t for $\beta = a_m$, taking the value of one at equilibrium [$g_\beta(\hat{N}^*) = 1$]

Let the intrinsic parameters be constrained between a lower ($b_{t,min}$ and $a_{m,t,min}$) and an upper ($b_{t,max}$ and $a_{m,t,max}$) limit. Let the upper intrinsic limits be estimated from the upper limits of the actual parameters (b_{max} and $a_{m,max}$) and a maximal abundance (\hat{N}_{max}) above which the population cannot reproduce at the maximal rate. Likewise, let the lower intrinsic limit be estimated from the lower limit on the actual parameters (b_{min} and $a_{m,min}$) and a minimum abundance (\hat{N}_{min}) below which the population cannot reproduce at the minimum rate. Hence, the intrinsic parameters are constrained within:

$$\begin{aligned} b_{min} / f_b(\hat{N}_{min}) &\leq b_t \leq b_{max} / f_b(\hat{N}_{max}) \\ a_{m,min} / f_{a_m}(\hat{N}_{min}) &\leq a_{m,t} \leq a_{m,max} / f_{a_m}(\hat{N}_{max}) \end{aligned} \quad (19)$$

In this paper it is assumed that $b_{min} = 0$ and that $\hat{N}_{min} = \hat{N}_{max} = \hat{N}^*$, while the remaining limits b_{max} , $a_{m,min}$ and $a_{m,max}$ are given by the parameterisation of the model.

Let the selection response functions be comparable with the density-regulation functions, and defined as:

$$\begin{aligned} g_b(\hat{N}_{t+1}) &= e^{-i\delta(\hat{N}_{t+1} - \hat{N}^*)} \\ g_{a_m}(\hat{N}_{t+1}) &= e^{\alpha i\delta(\hat{N}_{t+1} - \hat{N}^*)} \end{aligned} \quad (20)$$

where the i parameter scales g_β relative to f_β . Thus, the inertia model reduces into a traditional density-regulated model with no inertia at the limit $i = 0$.

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