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SEASONAL GRAY WHALES IN THE PACIFIC NORTHWEST: AN ASSESSMENT OF OPTIMUM SUSTAINABLE POPULATION LEVEL FOR THE PACIFIC COAST FEEDING GROUP

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Seasonal gray whales in the Pacific Northwest: An assessment of optimum sustainable population level for the Pacific Coast Feeding Group

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Summary

A single population stock of gray whales referred to as the eastern North Pacific (ENP) stock is presently recognized in U.S. waters (Carretta *et al.* 2013). A small group of gray whales, known as the Pacific Coast Feeding Group, or PCFG spends the summer and autumn along the Pacific coast of North America, where they overlap with the Makah Tribe's Usual and Accustomed (U&A) fishing grounds off the coast of Washington. In 2005, the Makah requested that NOAA/NMFS waive the MMPA take moratorium and adopt regulations that would authorize the tribe to hunt ENP gray whales within their U&A. As part of its review of this proposed hunt, NMFS continues to evaluate information relevant to ENP stock structure and status, including the population dynamics of the PCFG. Assessing whether the PCFG is currently at Optimum Sustainable Population (OSP) (i.e., not depleted) was the objective of the analysis described in this report[1]. The assessment is based on modifications to an existing population dynamics model used by the International Whaling Commission (IWC) to conduct projections of gray whale abundance. The model is deterministic, age- and sex-structured, and consists of two groups (the 'north' group and the PCFG), which are assumed to be separate for purposes of the analysis, but with possible immigration between them. Parameter estimation is based on Bayesian methods. Thirteen variants of the model were run (models A – M); these differed with respect to how priors were specified and the number of parameters estimated. Ultimately it was not possible to draw a definitive conclusion as to whether the PCFG is within OSP. Across all 13 model variants, the estimated probability of the PCFG being above its Maximum Net Productivity Level (*MNPL*) and hence within OSP ranged from ≈ 0.35 on the low end (models F and G) to 0.83 (model M) and 0.88 (model K) on the high end. In the latter two models (K and M), bycatch mortality[2] was fixed at zero, which is not realistic. For the remaining 11 models, the probability was ≤ 0.70, which is fairly equivocal. This stems from the PCFG abundance time series being largely uninformative regarding population rate parameters since it is relatively flat (no information about growth rate or density-dependence), apart from the short period of growth explained by an atypical pulse immigration event. Given the limited available information, the apparent stability of the PCFG population size for the past decade has several possible explanations. One explanation is that the population is at or near its carrying capacity and thus above *MNPL* and within OSP. However, it is also possible, given different potential rates of intrinsic population growth, that the PCFG area could support more whales and that current numbers are regulated by a combination of bycatch mortality and emigration that offsets immigration and internal production (recruitment of calves born to known PCFG females). Obtaining better empirical estimates of bycatch mortality, net annual immigration rates, and reducing prior uncertainty in Maximum Sustainable Yield Rate (*MSYR)* and *MNPL* could potentially improve inference about the likelihood of the PCFG being within OSP.

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[1] This is a continuation of work first considered during the gray whale stock identification workshop described in Weller *et al*. (2013).
[2] "Bycatch mortality" refers to human-caused fisheries-related mortality (e.g., from entanglement in gear) as summarized in U.S. marine mammal stock assessment reports (e.g., Carretta *et al*. 2013).

Introduction

The National Marine Fisheries Service (NMFS) recognizes a single population stock of gray whales (*Eschrichtius robustus*) within U.S. waters, termed the Eastern North Pacific (ENP) stock (Carretta *et al.* 2013). This stock ranges from wintering areas in Baja California, Mexico, to summer/autumn feeding areas in the Bering, Beaufort, and Chukchi Seas. A relatively small number (100s) of these whales, referred to as the Pacific Coast Feeding Group (PCFG), spend the summer/autumn along the Pacific coast of North America, between Kodiak Island, Alaska, and northern California (Calambokidis *et al*. 2012). In 2010, the International Whaling Commission (IWC) Standing Working Group on Aboriginal Whaling Management Procedure noted that different names had been used to refer to gray whales feeding along the Pacific coast, and agreed to standardize the terminology referring to animals that spend the summer and autumn feeding in coastal waters of the Pacific coast of North America from California to southeast Alaska as the PCFG (IWC 2011). This definition was further refined for purposes of abundance estimation, limiting the geographic range to the area from northern California to northern British Columbia (from 41°N to 52°N), limiting the temporal range to the period from June 1 to November 30, and counting only those whales seen in more than one year within this geographic and temporal range (IWC 2012) for abundance estimation purposes. The IWC adopted this definition, but noted that "not all whales seen within the PCFG area at this time will be PCFG whales and some PCFG whales will be found outside of the PCFG area at various times during the year." (IWC 2012).

The range of the PCFG overlaps with the Makah Tribe's Usual and Accustomed (U&A) fishing grounds off the coast of Washington. In 2005, the Makah requested that NOAA/NMFS waive the U.S. Marine Mammal Protection Act (MMPA) take moratorium and adopt regulations that would authorize the tribe to hunt ENP gray whales within their U&A. As part of its review of this proposed hunt, NMFS continues to evaluate information relevant to ENP stock structure and status, including the population dynamics of the PCFG. This paper evaluates whether the PCFG is likely to be within its Optimum Sustainable Population level, or OSP. Under the MMPA, OSP means, "with respect to any population stock, the number of animals which will result in the maximum productivity of the population or the species, keeping in mind the carrying capacity of the habitat and the health of the ecosystem of which they form a constituent element." Federal regulations implementing the MMPA describe OSP as a population size within a range that is at or above the level where the population's maximum net productivity occurs (termed the Maximum Net Productivity Level, or MNPL).[3] Populations below OSP are considered 'depleted' under the MMPA. Assessing whether the PCFG is currently within OSP (not depleted) was the objective of the analysis described in this report.

[3] Regulations implementing the MMPA at 50 CFR 216.3 state that "Optimum sustainable population is a population size which falls within a range from the population level of a given species or stock which is the largest supportable within the ecosystem to the population level that results in maximum net productivity. Maximum net productivity is the greatest net annual increment in population numbers or biomass resulting from additions to the population due to reproduction and/or growth less losses due to natural mortality."

Methods

Population Model

The assessment of ENP gray whales is based on a population dynamics model with two groups, a 'north' group and the PCFG. These two groups are assumed to be separate for purposes of the analysis, but with possible immigration between them. The model considers four strata (north of 52^0N, south of 41^0N, PCFG area December – May, and PCFG area June – November) because the relative vulnerability of the two groups to whaling and bycatch mortality differs among these strata.

The parameters of the model are estimated using Bayesian methods. Unlike IWC (2013), the analysis allows for uncertainty in the amount of 'pulse' immigration from the north group to the PCFG in 1999 and 2000, uncertainty in the annual level of immigration from the north group to the PCFG, and in $MSYL_{1+}$[4] and $MSYR_{1+}$[5] (the subscript 1+ refers to animals 1-year old and older). In contrast, IWC (2013) conducted analyses for pre-specified values for the level of 'pulse' immigration, the annual level of immigration, and $MSYL_{1+}$ and $MSYR_{1+}$. Note that the terms *MSYL* and *MSYR* reflect IWC terminology; within an MMPA context MSYL is the same as MNPL.

The underlying population dynamics model is deterministic, age- and sex-structured, and based on a two-stock version of the Baleen II model (Punt, 1999). Reference to 'stock' or 'population' below means either the north group or the PCFG, noting that usage of the term 'stock' with the model descriptions refers generically to a population unit and does not imply a formally recognized stock as defined under the MMPA.

Basic dynamics

Equation 1 provides the underlying 1+ dynamics.

$$\begin{aligned}
R^{s,m/f}_{t+1,a+1} &= (R^{s,m/f}_{t,a} + I^{s,m/f}_{t,a} - C^{s,m/f}_{t,a})\, \tilde{S}^s_t\, S^s_a + U^{s,m/f}_{t,a}\, \tilde{S}^s_t\, S^s_a\, \delta_{a+1} && 0 \le a \le x-2 \\
R^{s,m/f}_{t+1,x} &= (R^{s,m/f}_{t,x} + I^{s,m/f}_{t,x} - C^{s,m/f}_{t,x})\, \tilde{S}^s_t\, S^s_x + (R^{s,m/f}_{t,x-1} + I^{s,m/f}_{t,x-1} - C^{s,m/f}_{t,x-1})\, \tilde{S}^s_t S^s_{x-1} && (1) \\
U^{s,m/f}_{t+1,a+1} &= U^{s,m/f}_{t,a}\, \tilde{S}^s_t\, S^s_a\, (1-\delta_{a+1}) && 0 \le a \le x-2
\end{aligned}$$

where $R^{s,m/f}_{t,a}$ is the number of recruited males/females of age *a* in stock *s* at the start of year *t*; $U^{s,m/f}_{t,a}$ is the number of unrecruited males/females of age *a* in stock *s* at the start of year *t*; $C^{s,m/f}_{t,a}$ is the catch of males/females of age *a* from stock *s* during year *t* (whaling and bycatch mortality is assumed to take place in a pulse at the start of each year); δ_a is the fraction of unrecruited animals of age *a*-1 which recruit at age *a* (assumed to be independent of sex, time, and stock); S^s_a is the annual survival rate of animals of stock *s* and age *a* in the absence of catastrophic mortality events (assumed to be the same for males and females):

$$S^s_a = \begin{cases} S^s_0 & \text{if } a = 0 \\ S^s_{1+} & \text{if } 1 < a \end{cases} \tag{2}$$

[4] MSYL (Maximum Sustainable Yield Level) is the population size relative to carrying capacity at which surplus production is maximized; this is the same as MNPL under the MMPA.

[5] MSYR is the ratio of MSY to the population size at which MSY is achieved.

S_0^s is the calf survival rate for animals of stock *s*; S_{1+}^s is the survival rate for animals aged 1 and older for animals of stock *s*; $\tilde{S}_t^s$ is the amount of catastrophic mortality (represented in the form of a survival rate) for stock *s* during year *t* (catastrophic events are assumed to occur at the start of the year before mortality due to whaling, bycatch and natural causes; in general $\tilde{S}_t^s=1$, i.e. there is no catastrophic mortality); $I_{t,a}^{s,m/f}$ is the net migration of female/male animals of age *a* into stock *s* during year *t*; and x is the maximum (lumped) age-class (all animals in this and the *x*-1 class are assumed to be recruited and to have reached the age of first parturition). *x* is taken to be 15 for these trials.

Catastrophic mortality is assumed to be zero (i.e., $\tilde{S}_t^s=1$) except for the north group in 1999 and 2000 when it is assumed to be equal to the parameter $\tilde{S}$ (Punt and Wade, 2012). This assumption reflects the large number of dead ENP gray whales observed stranded along the coasts of Oregon and Washington during 1999 and 2000 relative to annual numbers stranding there historically (Gulland *et al*. 2005; Brownell *et al*. 2007). The mortality event is assumed to have only impacted the north group because the abundance estimates for the PCFG increased when the mortality event occurred, in contrast to those for the north group which declined substantially.

Immigration only occurs from the north group to the PCFG, and only animals aged 1+ immigrate. The annual number of animals immigrating is $I_t=\bar{I}\,N_t^{\text{north},1+}/20000$ where $\bar{I}$ is the hypothesized recent average number of individuals recruiting into the PCFG and 20000 is the approximate 1+ population size for the north group during those years (i.e., recent $N_t^{\text{north},1+}/20000 \approx 1$ (Laake *et al*. 2012) and thus recent $I_t = \bar{I}$). The annual number of immigrants by age and sex is given by:

$$I_{t,a}^{s,m/f}=I_t\frac{(R_{t,a}^{\text{north},\text{m/f}}+U_{t,a}^{\text{north},\text{m/f}})}{N_t^{\text{north},1+}} \tag{3}$$

Emigration from the PCFG is modelled by implementing an extra survival rate, $\tilde{\tilde{S}}$ after 1930 (immigration or emigration are ignored when carrying capacity and the parameters which determine the productivity of the population are calculated). Owing to the different sizes of the two groups, emigrants from the PCFG are assumed to die rather than join the north group. The value of $\tilde{\tilde{S}}$ is set so that at carrying capacity immigration and emigration are balanced, i.e.:

$$\frac{\bar{I}\,K_{1+}^{\text{north}}}{20000}=K_{0+}^{\text{PCFG}}(1-\tilde{\tilde{S}}) \tag{4}$$

Births

The number of births to stock *s* at the start of year *t*+1, B_{t+1}^s, is given by:

$$B_{t+1}^s=b_{t+1}^s\,N_{t+1}^{s,f} \tag{5}$$

where $N_t^{s,f}$ is the number of mature females in stock *s* at the start of year *t*:

$$N_t^{s,f} = \sum_{a=a_m}^{x} (R_{t,a}^{s,f} + U_{t,a}^{s,f}) \tag{6}$$

a_{m} is the age-at-maturity (the convention of referring to the mature population is used here, although this actually refers to animals that have reached the age of first parturition); b_{t+1}^{s} is the probability of birth/calf survival for mature females:

$$b_{t+1}^{s} = b_{-\infty}^{s}\{1 + A^{s}(1 - (N_{t+1}^{s,1+} / K^{s,1+})^{z^s})\} \tag{6}$$

$b_{-\infty}^{s}$ is the average number of live births per year per mature female in the pristine (pre-exploitation) population for stock *s*; A^s is the resilience parameter for stock *s* (A^s determines how much birth rate can increase from $b_{-\infty}^{s}$ when resources are not limiting); z^s is the degree of compensation for stock *s* (determines the population size – relative to carrying capacity – at which MNPL occurs); and $N_t^{s,1+}$ and $K^{s,1+}$ are defined according to the equations:

$$N_t^{s,1+} = \sum_{a=1}^{x} (R_{t,a}^{s,\mathrm{f}} + U_{t,a}^{s,\mathrm{f}} + R_{t,a}^{s,\mathrm{m}} + U_{t,a}^{s,\mathrm{m}}) \qquad K^{s,1+} = \sum_{a=1}^{x} (R_{-\infty,a}^{s,\mathrm{f}} + U_{-\infty,a}^{s,\mathrm{f}} + R_{-\infty,a}^{s,\mathrm{m}} + U_{-\infty,a}^{s,\mathrm{m}}) \tag{7}$$

The number of female births, $B_t^{s,f}$, is computed from the total number of the births during year *t* according to the equation:

$$B_t^{s,f} = 0.5 B_t^{s} \tag{8}$$

The numbers of recruited/unrecruited calves is given by:

$$\begin{aligned} R_t^{s,f} &= \pi_0\, B_t^{s,f} & \qquad R_t^{s,m} &= \pi_0\, (B_t^{s} - B_t^{s,f}) \\ U_t^{s,f} &= (1-\pi_0)\, B_t^{s,f} & \qquad U_t^{s,m} &= (1-\pi_0)(B_t^{s} - B_t^{s,f}) \end{aligned} \tag{9}$$

π_0 is the proportion of animals of age 0 which are recruited ($\pi_0 = 0$ for the analyses of this report).

Catches

The historical ($t < 2010$) catches by stratum (north, south, PCFG December – May, and PCFG June – November) are taken to be equal to the reported catches (IWC 2011; Table 1). The historical catches are allocated to the north group or PCFG in fixed proportions as follows:

(1) North area catches: all north animals;
(2) PCFG area catches in December – May: PCFG animals with probability ϕ_{PCFG} (base-case value 0.3, as determined by the photo-ID data; Calambokidis *et al*. 2012);
(3) PCFG area catches in June – November: all PCFG animals; and
(4) South area catches: PCFG animals with probability ϕ_{south} (base-case value 0.01, as determined by relative abundance).

The bycatch estimates by stratum for the historical period are computed using the equation (IWC 2013):

$$C_y^{\mathrm{I}/s} = 0.5\begin{cases}\left\{1-\frac{0.5}{69}[1999-y]\right\}\bar{C}^I & \text{if } y \le 1999 \\ \bar{C}^I N_y^{1+} / \bar{N}^{1+} & \text{otherwise}\end{cases} \tag{10}$$

where $C_y^{\mathrm{I}/s}$ is the bycatch of animals of sex *s* during year *y*; $\bar{C}^I$ is the mean catch in the stratum (see Table 2); and $\bar{N}^{1+}$ is the mean 1+ abundance (in the stratum concerned from 2000-2009). The catches from the PCFG and the north group are then allocated to age and size using the formula:

$$C_{t,a}^{s,m} = C_t^{s,m} R_{y,a}^{s,m} / \sum_{a''} R_{y,a''}^{s,m}; \qquad C_{t,a}^{s,\mathrm{f}} = C_t^{s,\mathrm{f}} R_{y,a}^{s,\mathrm{f}} / \sum_{a''} R_{y,a''}^{s,\mathrm{f}}; \tag{11}$$

Recruitment

The proportion of animals of age *a* that would be recruited if the population was pristine is a knife-edged function of age at age 0, i.e.:

$$\pi_a = \begin{cases} 0 & \text{if} \quad a = 0 \\ 1 & \text{otherwise}\end{cases} \tag{12}$$

The (expected) number of unrecruited animals of age *a* that survive to age *a*+1 is $U_{t,a}^{s,m/f}\ S_a$. The fraction of these that then recruit is:

$$\delta_{a+1} = \begin{cases} [\pi_{a+1} - \pi_a]/[1-\pi_a] & \text{if } 0 \le \alpha_a < 1 \\ 1 & \text{otherwise}\end{cases} \tag{13}$$

Maturity

Maturity is assumed to be a knife-edged function of age at age a_{m}.

Initialising the population vector

The numbers at age in the pristine population are given by:

$$\begin{aligned} R_{-\infty,a}^{s,\mathrm{m/f}} &= 0.5 \quad N_{-\infty,0}^{s} \quad \pi_a \prod_{a'=0}^{a-1} S_{a'}^{s} && \text{if} \quad 0 \le a < x \\ U_{-\infty,a}^{s,\mathrm{m/f}} &= 0.5 \quad N_{-\infty,0}^{s} \quad (1-\pi_a) \prod_{a'=0}^{a-1} S_{a'}^{s} && \text{if} \quad 0 \le a < x \\ R_{-\infty,x}^{s,\mathrm{m/f}} &= 0.5 \quad N_{-\infty,0}^{s} \prod_{a'=0}^{x-1} \frac{S_{a'}^{s}}{(1-S_x)} && \text{if} \quad a = x \end{aligned} \tag{14}$$

where $R_{-\infty,a}^{s,\mathrm{m/f}}$ is the number of animals of stock *s* of age *a* that would be recruited in the pristine population; $U_{-\infty,a}^{s,\mathrm{m/f}}$ is the number of animals of stock *s* of age *a* that would be unrecruited in the pristine population; and $N_{-\infty,0}^{s}$ is the total number of animals of stock *s* of age 0 in the pristine population.

The value for $N^s_{-\infty,0}$ is determined from the value for the pre-exploitation size of the 1+ component of the population using the equation:

$$N^s_{-\infty,0} = K^{s,1+} / \left(\sum_{a=1}^{x-1} \prod_{a'=1}^{a-1} S^s_a + \frac{1}{1-S_x} \prod_{a'=0}^{x-1} S^s_{a'} \right) \qquad (15)$$

It is not possible to make a simple density-dependent population dynamics model consistent with the abundance estimates for ENP gray whales (Reilly 1981; 1984; Cooke 1986; Lankester and Beddington 1986; Butterworth *et al.* 2002). This is why recent assessments of this stock (e.g. Punt and Wade 2012) have been based on starting population projections from a more recent year (denoted as τ) than that in which the first recorded catch occurred. The analyses are therefore based on the assumption that the age-structure at the start of τ = 1930 is stable rather than that the populations were at their pre-exploitation equilibrium sizes at the start of some much earlier year. The choice of 1930 for the first year of the simulation is motivated by the fact that the key assessment results are not sensitive to a choice for this year from 1930-1968 (Punt and Butterworth 2002; Punt and Wade 2012). The determination of the age-structure at the start of 1930 involves specifying the effective 'rate of increase', γ, that applies to each age-class. There are two components contributing to γ, one relating to the overall population rate of increase (γ^+) and the other to the exploitation rate. Under the assumption of knife-edge recruitment to the fishery at age 1, only the γ^+ component (assumed to be zero following Punt and Butterworth 2002) applies to ages a of age 0. The number of animals of age a at the start of τ=1930 relative to the number of calves at that time, $N^{s,*}_{\tau,a}$, is therefore given by the equation:

$$N^{s,*}_{\tau,a} = \begin{cases} 1 & \text{if } a = 0 \\ N^{s,*}_{\tau,0} S^s_0 & \text{if } a \le 1 \\ N^{s,*}_{\tau,a-1} S^s_{a-1} (1-\gamma^+) & \text{if } 1 < a < x \\ N^{s,*}_{\tau,x-1} S^s_{x-1} (1-\gamma^+) / (1 - S^s_x (1-\gamma^+)) & \text{if } a = x \end{cases} \qquad (16)$$

where B^s_τ is the number of calves in year τ (=1930) and is derived directly from equations 5 and 6 (for further details see Punt [1999]):

$$B^s_\tau = \left(1 - \left[1/(N^{s,f}_\tau b^s_{-\infty}) - 1\right] / A^s\right)^{1/z^s} \frac{K^{s,1+}}{N^{s,1+*}_\tau} \qquad (17)$$

The effective rate of increase, γ^s, is selected so that if the population dynamics model is projected from 1930 to 1968, the size of the 1+ component of the population (both groups) in 1968 equals a pre-specified value, P^s_{1968}.

z and A

A^s, z^s and S^s_0, are obtained by solving the system of equations that relate $MSYL^s_{1+}$, $MSYR^s_{1+}$, S^s_0, S_{1+}, $f_{\max}$, a_{m}, A^s and z^s, where $f_{\max}$ is the maximum theoretical pregnancy rate (Punt 1999).

Parameter estimation

The method for estimating the parameters of the model (i.e. selecting 5,000 sets of equally likely values for the parameters a_{m}, S_0^s, S_{1+}, $\tilde{S}$, K_{1+}^{north}, K_{1+}^{PCFG}, A^{north}, A^{PCFG}, z^{north}, and z^{PCFG}) is based on a Bayesian assessment (Punt and Butterworth 2002; Wade 2002; Punt and Wade 2012). The algorithm for conducting the Bayesian assessment is as follows:

(a) Draw values for the parameters S_{1+}, f_{max}, a_{m}, K_{1+}^{north}, K_{1+}^{PCFG}, $P_{1968}^{\mathrm{north}}$, P_{1968}^{PCFG}, $\tilde{S}$, $MSYR_{1+}^s$, $MSYL_{1+}^s$, $CV_{add}^{\mathrm{north}}$ (the additional variance for the estimates of 1+ abundance at Carmel, California in 1968), CV_{add}^{PCFG} (the additional variance for the estimates of 1+ abundance from northern California to Southeast Alaska in 1968 – had such a survey taken place) from the priors (see Table 3 for the reference priors).

(b) Solve the system of equations that relate $MSYR_{1+}^s$, $MSYL_{1+}^s$, S_0^s, S_{1+}, f_{max}, a_{m}, A^s and z^s to find values for S_0^s, A^s and z^s.

(c) Calculate the likelihood of the projection for each area, given by[6]:

$$-\ell\mathrm{n}L = 0.5\ell\mathrm{n}\,|\mathbf{V}+\Omega| + 0.5\sum_i\sum_j(\ell\mathrm{n}N_i^{\mathrm{obs}} - \ell\mathrm{n}\hat{P}_i^{1+})[(\mathbf{V}+\Omega)^{-1}]_{i,j}(\ell\mathrm{n}N_j^{\mathrm{obs}} - \ell\mathrm{n}\hat{P}_j^{1+}) \qquad (18)$$

where N_i^{obs} is the i^{th} estimate of abundance[7] (Tables 4a, 4b), $\hat{P}_i^{1+}$ is the model-estimate corresponding to N_i^{obs}, $\mathbf{V}$ is the variance-covariance matrix for the abundance estimates, and Ω is a diagonal matrix with elements given by $E(CV_{add,t}^2)$:

$$E(CV_{add,t}^2) = CV_{add}^2\,\frac{0.1 + 0.013P^*/\hat{P}_t}{0.1 + 0.013P^*/\hat{P}_{1968}} \qquad (19)$$

(d) Steps (a) – (c) are repeated a large number (typically 1,000,000) of times.

(e) 5,000 sets of parameters vectors are selected randomly from those generated using steps (a) – (c), assigning a probability of selecting a particular vector proportional to its likelihood. The number of times steps (a) – (c) are repeated is chosen to ensure that most of the 5,000 parameter vectors are unique.

The expected value for the estimate of abundance of the north area is taken to the total 1+ abundance (north group and PCFG combined) while the abundance estimates for the PCFG area are assumed to pertain to the PCFG only.

Model Scenarios

Thirteen models were run (Table 5). These included a reference model (Table 3) and 12 variants. These models do not represent a comprehensive set of options, but were used to

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6 This formulation assumes that the observed data relate to the medians of sampling distributions for the data. Alternative assumptions (such as that the observed data relate to the means of the sampling distributions) will be inconsequential given the extent of uncertainty associated with the estimates of abundance.

7 The shore-based abundance estimate for year *y*/*y*+1 is assumed to pertain to abundance at the start of year *y*+1.

explore how the model behaved under certain conditions (e.g., parameter constraints) with respect to providing inference about the probability of the PCFG being within OSP.

Results and Discussion

Ultimately it was not possible to draw a definitive conclusion as to whether the PCFG is within OSP. Across all 13 model variants, the estimated probability of the population being above *MSYL* (i.e., *MNPL*), and hence within OSP ranged from ≈ 0.35 on the low end (models F and G) to 0.83 (model M) and 0.88 (model K) on the high end (see Table 6). In the latter two models (K and M), bycatch mortality was fixed at zero, which is not realistic. For the remaining 11 models, the probability was ≤ 0.70, which is fairly equivocal.

The time series of PCFG abundance estimates indicates that a rapid phase of population growth occurred between 1998 and 2001 associated with a pulsed immigration event (≈ 25 – 30 immigrants per year from the north group to the PCFG), followed by no substantial trend in abundance since then (Figure 1). A key reason for the inability to draw definitive conclusions about OSP is because it is unclear whether the stability of the PCFG over the last decade is best explained by it being at or near carrying capacity or whether it has been regulated at a lower level by some other processes.

Unfortunately, the time-series of abundance estimates for the PCFG is largely uninformative regarding population growth rate since it is relatively flat (no information about growth rate or density-dependence) apart from the short period of growth explained by an atypical immigration event. Consequently, estimates for population growth at *MNPL*, the value of *MNPL* itself (as a fraction of K), carrying capacity, and hence the current population depletion level (percentage of carrying capacity) for the PCFG were influenced strongly by the prior distributions. For example, the upper prior limit for K for the PCFG was 500 for models A – D, and the posterior median estimates for K ranged from 265 – 293 with upper 95% estimates close to 500, whereas, the upper prior limit was 1000 for models E – M, and the posterior median estimates for K ranged up to 441 with upper 95% estimates close to 800 or higher for most of these models (Table 6). Thus, in all of these models, the right tail of the posterior distribution for K was truncated to some extent by the upper bound for the prior for K (Figure 2), implying non-trivial (and sometimes substantial) probability that carrying capacity could be as high as the specified upper bound (and thus substantial probability that current population size is below *MNPL*).

Constraining both *MSYR* and *MNPL* for the PCFG to equal those of the north group (thus drawing on north group data to estimate some PCFG growth parameters; models J through M) did not substantially improve inference. For models J and L, the probability of the PCFG being within OSP was 0.44 and 0.52, respectively (Table 6). Models K and M included the additional constraint of fixing annual bycatch at zero, and model M also assumed zero annual immigration. The posterior distribution for carrying capacity was reasonably unconstrained by the prior (Figure 2) and the carrying capacity estimates were ≤ 250 animals (Table 6) for these two models (and also for model I, where *MNPL* and bycatch, but not *MSYR*, were constrained). Even so, the estimated probability of the population being within OSP was not definitive in these cases (probability = 0.83 and 0.88), and the assumptions of zero bycatch (models I, K, M) or full population closure (model M) are not justified for the PCFG (Weller *et al*. 2013), so these models do not represent realistic scenarios anyway. However, the estimates for these models provided the insight that bycatch mortality and movement between the north group and PCFG makes it difficult to estimate other population parameters, given the nature of the time series of abundance estimates (since parameters were not estimated well for other models that did not include the same constraints). Specifically, the only way for the model to mimic population stability when the population is assumed to be closed to bycatch or emigration is for the population to be at or near K (when K is estimated to be small), but many possible levels of K can explain the data when the population is allowed to be open (with some population losses due to bycatch and emigration).

In summary, the apparent stability of the PCFG population size for the past decade has multiple possible explanations given the limited available information. One explanation is that the population is at or near its carrying capacity and thus above *MNPL* and within OSP. However, it is also possible that the PCFG area could support more whales and that current numbers are regulated by a combination of emigration and bycatch mortality that offsets immigration and internal production (recruitment of calves born to known PCFG females). The PCFG would be expected at most to grow at around 6% per year (if it were well below *MNPL* and had the same intrinsic growth potential as the north group; Punt and Wade [2012]). It would grow at a slower rate if it is close to *MNPL* or has a lower growth rate potential than the larger north group (e.g., feeding in a less productive environment). Considering its small population size (around 200 animals), the PCFG therefore has the potential to increase at most by approximately 12 animals per year from births minus deaths, and the increase could be much smaller (e.g., just several animals per year). The PCFG can additionally grow due to immigration from the larger north group, but as modeled, immigration is offset by emigration to an extent that depends on the estimated abundance levels of the two groups relative to their respective carrying capacities. For example, if both groups are currently at the same fraction of K, PCFG immigration and emigration would be estimated to be equal. As a result, small losses from emigration and bycatch are sufficient to offset population gains from birth and immigration, especially if the PCFG has a relatively low intrinsic growth rate compared to the north group (e.g., as in models E through I; see Table 6). Moreover, bycatch mortality estimates in the models are likely underestimates of true bycatch mortality (Weller *et al.* 2013). If higher bycatch mortality rates were included in the analyses, this would decrease the estimated likelihood of the PCFG being within OSP, but true bycatch mortality rates are unknown with no good way at present of being approximated (thus we used the same values as in IWC analyses; Table 2).

Obtaining better empirical estimates of bycatch mortality, net annual immigration rates, and reducing prior uncertainty in *MSYR* and *MNPL* could potentially improve inference about the likelihood of the PCFG being within OSP.

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Table 1
Historical catches of ENP gray whales (IWC, 2011).

Year	South			PCFG Jun-Nov			PCFG Dec-May			North			Total		
	M	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**	**M**	**F**	**Total**
1930	0	0	0	0	0	0	0	0	0	23	24	47	23	24	47
1931	0	0	0	0	0	0	0	0	0	5	5	10	5	5	10
1932	5	5	10	0	0	0	0	0	0	5	5	10	10	10	20
1933	30	30	60	0	0	0	0	0	0	8	7	15	38	37	75
1934	30	30	60	0	0	0	0	0	0	36	30	66	66	60	126
1935	55	55	110	0	0	0	0	0	0	16	28	44	71	83	154
1936	43	43	86	0	0	0	0	0	0	50	62	112	93	105	198
1937	0	0	0	0	0	0	0	0	0	12	12	24	12	12	24
1938	0	0	0	0	0	0	0	0	0	32	32	64	32	32	64
1939	0	0	0	0	0	0	0	0	0	19	20	39	19	20	39
1940	0	0	0	0	0	0	0	0	0	56	69	125	56	69	125
1941	0	0	0	0	0	0	0	0	0	38	39	77	38	39	77
1942	0	0	0	0	0	0	0	0	0	60	61	121	60	61	121
1943	0	0	0	0	0	0	0	0	0	59	60	119	59	60	119
1944	0	0	0	0	0	0	0	0	0	3	3	6	3	3	6
1945	0	0	0	0	0	0	0	0	0	25	33	58	25	33	58
1946	0	0	0	0	0	0	0	0	0	14	16	30	14	16	30
1947	0	0	0	0	0	0	0	0	0	11	20	31	11	20	31
1948	0	0	0	0	0	0	0	0	0	7	12	19	7	12	19
1949	0	0	0	0	0	0	0	0	0	10	16	26	10	16	26
1950	0	0	0	0	0	0	0	0	0	4	7	11	4	7	11
1951	0	0	0	0	0	0	1	0	1	5	8	13	6	8	14
1952	0	0	0	0	0	0	0	0	0	17	27	44	17	27	44
1953	0	0	0	0	0	0	6	4	10	15	23	38	21	27	48
1954	0	0	0	0	0	0	0	0	0	14	25	39	14	25	39
1955	0	0	0	0	0	0	0	0	0	22	37	59	22	37	59
1956	0	0	0	0	0	0	0	0	0	45	77	122	45	77	122
1957	0	0	0	0	0	0	0	0	0	36	60	96	36	60	96
1958	0	0	0	0	0	0	0	0	0	55	93	148	55	93	148
1959	1	1	2	0	0	0	0	0	0	73	121	194	74	122	196
1960	0	0	0	0	0	0	0	0	0	58	98	156	58	98	156
1961	0	0	0	0	0	0	0	0	0	77	131	208	77	131	208
1962	4	0	4	0	0	0	0	0	0	55	92	147	59	92	151
1963	0	0	0	0	0	0	0	0	0	68	112	180	68	112	180
1964	15	5	20	0	0	0	0	0	0	75	124	199	90	129	219
1965	0	0	0	0	0	0	0	0	0	71	110	181	71	110	181
1966	15	11	26	0	0	0	0	0	0	80	114	194	95	125	220
1967	52	73	125	0	0	0	0	0	0	109	140	249	161	213	374
1968	41	25	66	0	0	0	0	0	0	48	87	135	89	112	201
1969	39	35	74	0	0	0	0	0	0	50	90	140	89	125	214
1970	0	0	0	0	0	0	0	0	0	71	80	151	71	80	151
1971	0	0	0	0	0	0	0	0	0	57	96	153	57	96	153
1972	0	0	0	0	0	0	0	0	0	61	121	182	61	121	182
1973	0	0	0	0	0	0	0	0	0	97	81	178	97	81	178
1974	0	0	0	0	0	0	0	0	0	94	90	184	94	90	184
1975	0	0	0	0	0	0	0	0	0	58	113	171	58	113	171
1976	0	0	0	0	0	0	0	0	0	69	96	165	69	96	165
1977	0	0	0	0	0	0	0	0	0	87	100	187	87	100	187
1978	0	0	0	0	0	0	0	0	0	94	90	184	94	90	184
1979	0	0	0	0	0	0	0	0	0	58	125	183	58	125	183
1980	0	0	0	0	0	0	0	0	0	53	129	182	53	129	182
1981	0	0	0	0	0	0	0	0	0	36	100	136	36	100	136
1982	0	0	0	0	0	0	0	0	0	57	111	168	57	111	168
1983	0	0	0	0	0	0	0	0	0	46	125	171	46	125	171
1984	0	0	0	0	0	0	0	0	0	59	110	169	59	110	169
1985	0	0	0	0	0	0	0	0	0	54	116	170	54	116	170
1986	0	0	0	0	0	0	0	0	0	46	125	171	46	125	171
1987	0	0	0	0	0	0	0	0	0	48	111	159	48	111	159
1988	0	0	0	0	0	0	0	0	0	43	108	151	43	108	151
1989	0	0	0	0	0	0	0	0	0	61	119	180	61	119	180
1990	0	0	0	0	0	0	0	0	0	67	95	162	67	95	162

Year	South			PCFG Jun-Nov			PCFG Dec-May			North			Total		
	M	F	Total	M	F	Total	M	F	Total	M	F	Total	M	F	Total
1991	0	0	0	0	0	0	0	0	0	67	102	169	67	102	169
1992	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1993	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
1994	0	0	0	0	0	0	0	0	0	21	23	44	21	23	44
1995	0	0	0	0	0	0	0	0	0	48	44	92	48	44	92
1996	0	0	0	0	0	0	0	0	0	18	25	43	18	25	43
1997	0	0	0	0	0	0	0	0	0	48	31	79	48	31	79
1998	0	0	0	0	0	0	0	0	0	64	61	125	64	61	125
1999	0	0	0	0	0	0	0	1	1	69	54	123	69	55	124
2000	0	0	0	0	0	0	0	0	0	63	52	115	63	52	115
2001	0	0	0	0	0	0	0	0	0	62	50	112	62	50	112
2002	0	0	0	0	0	0	0	0	0	80	51	131	80	51	131
2003	0	0	0	0	0	0	0	0	0	71	57	128	71	57	128
2004	0	0	0	0	0	0	0	0	0	43	68	111	43	68	111
2005	0	0	0	0	0	0	0	0	0	49	75	124	49	75	124
2006	0	0	0	0	0	0	0	0	0	57	77	134	57	77	134
2007	0	0	0	0	1	1	0	0	0	50	81	131	50	82	132
2008	0	0	0	0	0	0	0	0	0	64	66	130	64	66	130
2009	0	0	0	0	0	0	0	0	0	59	57	116	59	57	116
2010	0	0	0	0	0	0	0	0	0	57	61	118	57	61	118

Table 2
Average estimated historical bycatches

Stratum	Average bycatch estimates
North	0[1]
PCFG [Dec – May]	2
PCFG [Jun – Nov]	1.4[2]
South	3.4

1 – obviously not actually zero, but will be small relative to population size
2 – includes southern whales during June – November as these whales are almost certainly PCFG animals

Table 3. The prior distributions for the ENP stock of gray whales, for the reference case scenario (case B in Table 5).

Parameter	**Prior distribution**
Maximum Sustainable Yield Rate, $MSYR_{1+}^{north}$	U[0.01,0.06]
$MSYR_{1+}^{PCFG}$	U[0.01,0.06]
Maximum Net Productivity Level, $\mathrm{MNPL}^{\mathrm{north}}$ (same as $MSYL_{1+}^{s}$)	0.6
$\mathrm{MNPL}^{\mathrm{PCFG}}$	0.6
Non-calf survival rate, S_{1+}	U[0.95, 0.99]
Age-at-maturity, a_{m}	U[6, 12]
K_{1+}^{north}	U[16,000, 70,000]
K_{1+}^{PCFG}	U[100, 500]
Maximum pregnancy rate, $f_{\max}$	U[0.3, 0.6]
$CV_{add}^{\mathrm{north}}$	U[0.1, 0.3]
CV_{add}^{PCFG}	U[0.05, 0.3]
1968 abundance, $P_{1968}^{\mathrm{north}}$	U[8,000, 16,000]
1968 abundance, P_{1968}^{PCFG}	U[50, 300]
Catastrophic mortality, $\tilde{S}$	U[0.5,1.0]
Annual Immigration, $\bar{I}$	U[0,4]
Pulse Immigration, $I_{1999,2000}$	U[10, 50]

Table 4a Estimates of absolute abundance (with associated standard errors of the logs) for the ENP stock of gray whales based on shore counts (source: Laake *et al*. 2012).

Year	**Estimate**	**CV**	**Year**	**Estimate**	**CV**
1967/68	13426	0.094	1979/80	19763	0.083
1968/69	14548	0.080	1984/85	23499	0.089
1969/70	14553	0.083	1985/86	22921	0.081
1970/71	12771	0.081	1987/88	26916	0.058
1971/72	11079	0.092	1992/93	15762	0.067
1972/73	17365	0.079	1993/94	20103	0.055
1973/74	17375	0.082	1995/96	20944	0.061
1974/75	15290	0.084	1997/98	21135	0.068
1975/76	17564	0.086	2000/01	16369	0.061
1976/77	18377	0.080	2001/02	16033	0.069
1977/78	19538	0.088	2006/07	19126	0.071
1978/79	15384	0.080			

Table 4b Estimates of absolute abundance (with associated CVs) for gray whales in the PCFG area, 41^0-52^0N (source: Laake, 2013).

Year	**Estimate**	**CV**	**Year**	**Estimate**	**CV**
1998	101	0.062	2005	206	0.109
1999	135	0.089	2006	190	0.099
2000	141	0.093	2007	183	0.126
2001	172	0.073	2008	191	0.084
2002	189	0.048	2009	185	0.125
2003	200	0.082	2010	186	0.100
2004	206	0.072			

Table 5. Specifications for the scenarios

Case	Difference from case B
A	No Annual Immigration
B	Reference case (see Table 3)
C	$MSYL^s_{1+} \sim U[0.4, 0.8]$; no annual immigration $(\bar{I} = 0)$
D	$MSYL^s_{1+} \sim U[0.4, 0.8]$
E	$MSYL^s_{1+} \sim U[0.5, 0.85]$; $K^{\mathrm{PCFG}}_{1+} \sim U[100, 1000]$; $\bar{I} \sim U[0, 6]$; $I_{1999,2000} \sim U[0, 60]$
F	$MSYL^s_{1+} \sim U[0.5, 0.85]$; $K^{\mathrm{PCFG}}_{1+} \sim U[100, 1000]$; no annual immigration; $I_{1999,2000} \sim U[0, 60]$
G	As for F except that MSYL for the two stocks constrained to be equal and $\bar{I} \sim U[0, 6]$
H	As for F except that MSYL for the two stocks constrained to be equal
I	As for E, except MSYL for the two stocks constrained to be equal, there are no historical bycatches and no additional variance for PCFG abundance estimates
J	As for E except MSYL and MSYR for the two stocks constrained to be equal
K	As for J, but there are no historical bycatches
L	As for J, but there is no additional variance for PCFG abundance estimates
M	As for J, but there are no historical bycatches and no annual immigration

Table 6. Summaries of the posterior distributions for selected parameters from all model scenarios (Table 5). P(N>MNPL) is probability that the 1+ population size is above the Max Net Productivity Level and thus the population is within OSP (for the north group and the PCFG). For other parameters, the posterior median and 95% credible intervals are presented. MSYR is the population growth rate at MNPL, which is estimated in terms of a proportion of abundance at MNPL.

Run	P(N>MNPL)	P(N>MNPL)		MSYR	MSYR	MNPL	MNPL	K	K
	North	PCFG		North	PCFG	North	PCFG	North	PCFG
A	0.771	0.7016	5%	0.019	0.011	0.6	0.6	20895	179
			50%	0.038	0.022	0.6	0.6	25384	265
			95%	0.055	0.045	0.6	0.6	57578	465
B	0.753	0.6418	5%	0.019	0.011	0.6	0.6	20997	194
			50%	0.037	0.022	0.6	0.6	25676	292
			95%	0.056	0.043	0.6	0.6	58693	472
C	0.847	0.659	5%	0.021	0.011	0.531	0.467	19514	183
			50%	0.042	0.021	0.702	0.612	22714	285
			95%	0.056	0.045	0.791	0.778	54866	475
D	0.836	0.643	5%	0.02	0.011	0.53	0.458	19596	191
			50%	0.042	0.02	0.701	0.612	22652	293
			95%	0.056	0.042	0.792	0.775	55224	476
E	0.8184	0.3962	5%	0.021	0.011	0.545	0.515	19447	196
			50%	0.041	0.017	0.704	0.651	22596	376
			95%	0.056	0.039	0.809	0.795	57869	920
F	0.849	0.3546	5%	0.021	0.011	0.554	0.517	19451	188
			50%	0.042	0.019	0.716	0.653	22502	439
			95%	0.056	0.039	0.811	0.8	52813	940
G	0.7988	0.3474	5%	0.02	0.011	0.543	0.543	19544	195
			50%	0.041	0.018	0.687	0.687	23164	398
			95%	0.056	0.039	0.791	0.791	58187	923
H	0.839	0.4178	5%	0.02	0.011	0.549	0.549	19622	188
			50%	0.042	0.018	0.7	0.7	22674	441
			95%	0.056	0.041	0.797	0.797	54808	927
I	0.756	0.6634	5%	0.02	0.01	0.532	0.532	19732	168
			50%	0.039	0.015	0.672	0.672	23466	250
			95%	0.056	0.033	0.778	0.778	61570	805
J	0.3386	0.4354	5%	0.017	0.017	0.515	0.515	21315	191
			50%	0.024	0.024	0.63	0.63	40607	346
			95%	0.043	0.043	0.771	0.771	47154	839
K	0.3594	0.8798	5%	0.016	0.016	0.515	0.515	20912	132
			50%	0.023	0.023	0.631	0.631	42624	241
			95%	0.049	0.049	0.762	0.762	67563	643
L	0.399	0.5168	5%	0.017	0.017	0.517	0.517	20760	193
			50%	0.025	0.025	0.647	0.647	37928	312
			95%	0.046	0.046	0.787	0.787	66508	791
M	0.5958	0.8262	5%	0.017	0.017	0.519	0.519	20112	122
			50%	0.03	0.03	0.651	0.651	27641	195
			95%	0.051	0.051	0.771	0.771	64866	772

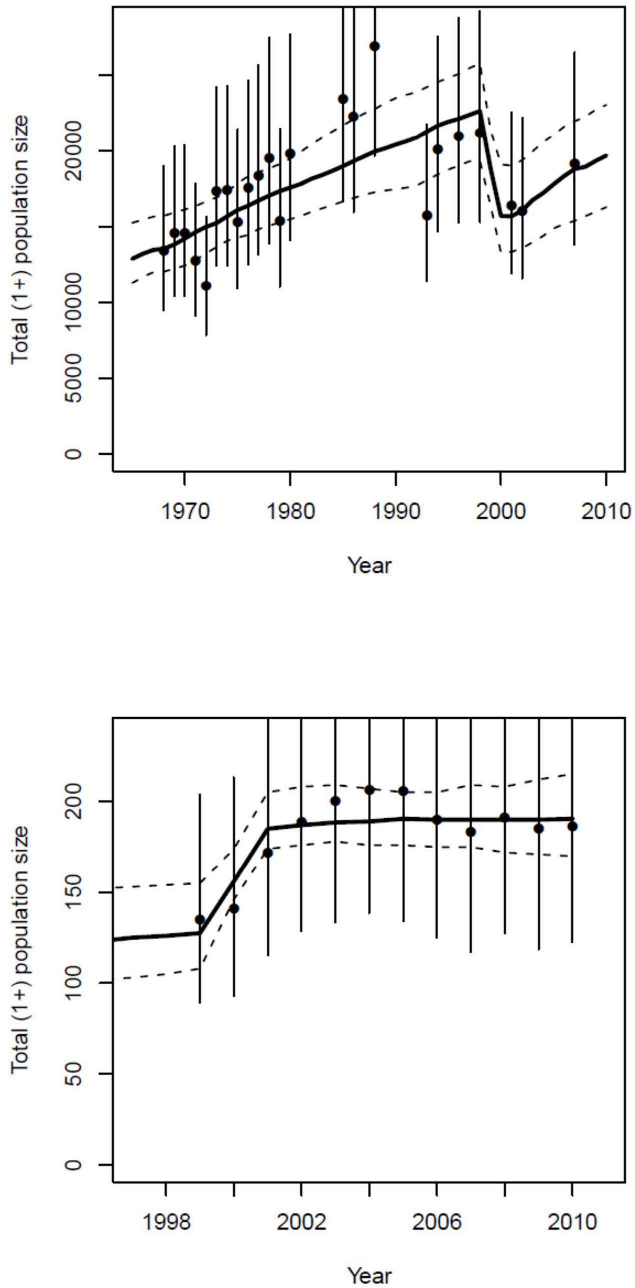

Figure 1. Abundance estimates for the north group (top) and PCFG (bottom) from the reference model (model B). Points and error bars represent actual estimates (Calambokidis *et al*, 2012). Solid line represents posterior median estimates (dotted lines represent 90% credible intervals). Estimates from all models (A – M) are similar.

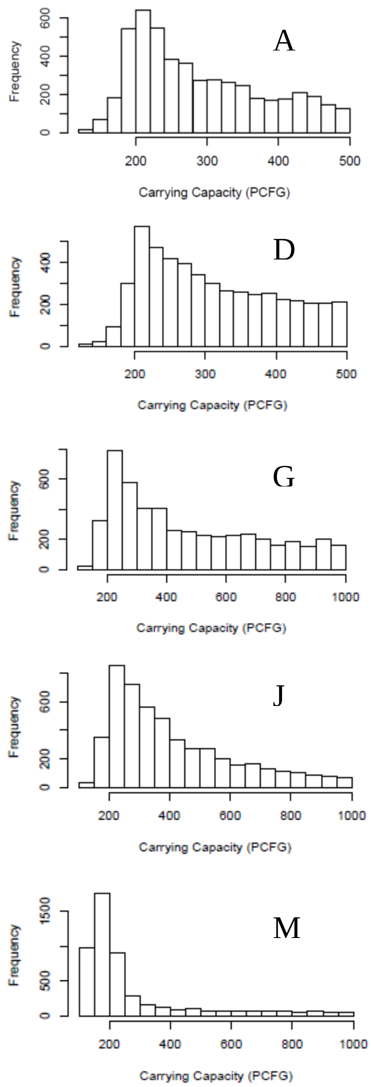

Figure 2. Posterior distributions for carrying capacity for the PCFG, for model scenarios A through M.

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