Can gray whale management units be assessed using mitochondrial DNA?

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ABSTRACT

Although most eastern North Pacific gray whales (*Eschrichtius robustus*) feed in Alaskan waters north of the Aleutian peninsula, some have been reported as long-term feeding residents in more southern waters ranging from northern California to southeast Alaska. The population history of this smaller putative southern feeding population is unknown. Recently, native Americans of the Makah tribe attained permits to harvest up to five whales per year in Washington State waters. Managers need to know whether southern summer residents could be potentially depleted through low-level harvesting. This paper investigates the feasibility of using genetic data to assess the plausibility of two possible population histories for the southern feeding group: panmixia with the northern feeding group and a single colonisation event less that a century ago. We find that a genetic study would most probably result in an unambiguous answer to the question of whether the southern feeding group is a separate population founded by a single colonisation event. Simulations show that a single founding event in the last century would result in genetic differentiation 97.8% of the time ($\alpha = 0.05$) between the two feeding groups. Further, sensitivity analyses of uncertain parameters used in the model show that the results do not depend on the values of growth rate, mitochondrial allele frequency distribution or population size of the eastern North Pacific gray whale after commercial harvest.

KEYWORDS: GENETICS; MODELLING; STOCK IDENTITY; GRAY WHALES

INTRODUCTION

The North Pacific gray whale is classified into two management stocks by the International Whaling Commission, the western North Pacific and the eastern North Pacific stock. The western North Pacific stock is highly endangered, and numbers less than a few hundred individuals (Weller *et al.*, 1999). Although the eastern North Pacific stock was hunted extensively, survey data have indicated a strong recovery (IWC, 1999), which recently resulted in downlisting from the USA Endangered Species Act.

Eastern North Pacific gray whales migrate along the coast of North America to breed in the lagoons of Baja California (Rice and Wolman, 1971). Most whales feed north of the Aleutian peninsula during the summer. However, some whales remain in more southern waters between California and southeast Alaska (Darling, 1977; Calambokidis *et al.*, 1991). In this paper these whales are termed the southern feeding group.

Although the southern and northern feeding groups are part of the same eastern North Pacific breeding pool, the population history of the southern feeding group is not known. The populations in British Columbia and Washington have been studied since the 1970s (Darling, 1977; Calambokidis *et al.*, 1991). Photographic identification data show that there are three types of whales in the southern feeding group: adult whales that are sighted over multiple years; adult whales sighted only once; and juveniles sighted for one or two years only (Steeves, 1998). Some adults gradually move up the coast during the summer (Steeves, 1998). IWC (2001) noted that:

> The number of Pacific-coast-summering whales is unknown, but may be in the low- to mid-hundreds. Photographic evidence, available from a limited number of Pacific coast sites, show that some of the whales return every year to specific areas along the Pacific coast, with some of these whales ranging between a number of sites within a season and others staying at the same site.

Shore-based total population counts of gray whales migrating past California started in 1967. Most whales migrate within 2.7km of the coast, making them easy to survey (Reilly *et al.*, 1983). Abundance estimates were combined with harvest estimates to calculate historical population sizes of gray whales. Early attempts by Ohsumi (1976), Cooke (1986) and Lankester and Beddington (1986) using standard models of density-dependence were largely unsuccessful at reconciling the catch history with both the current abundance and the recent rate of increase. Butterworth *et al.* (2001) proposed a series of models that better fit the current population size and estimates of growth rate. One of these models assumed pre-commercial aboriginal catch, and that historical catch was probably underestimated by 67% (estimated at 6.5% MSYR, 95% CI = 6.3, 6.8). The model also predicted that at the conclusion of commercial whaling (1900), the gray whale population was reduced to 13% (95% CI = 13%, 14%) of its carrying capacity, which translates to a population size of 3,236. In this paper, the eastern North Pacific gray whale population is modelled from 1900 to 2000 using this estimate of population size.

Aboriginal peoples have harvested the gray whale population since at least the 16th century (Mitchell and Reeves, 2001). Commercial whaling by European whalers began in 1824 and caused the population to decline sharply, making it unprofitable by the turn of the century (Reilly, 1992). Commercial whaling of gray whales has been prohibited by international treaty since 1937. However, the IWC has allowed limited aboriginal subsistence whaling on the eastern North Pacific management stock. This has almost exclusively been carried out off the coast of Chukotka (Russian Federation) with occasional catches being taken off Alaska (USA). Recently subsistence whaling by the Makah tribe in Washington State has been resumed. The Makah harvested one whale in 1999 and have permits to harvest up to five whales per year. Given this, it is important to

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investigate whether the northern and southern feeding groups should be managed as a single stock or separately.

One objective of the USA Marine Mammal Protection act is to maintain populations as functioning elements of their ecosystems, which has been interpreted as the need to strive to preserve the range of a population (Taylor, 1997). Humpback whales, another coastal species, have strong matrilineal site fidelity to feeding areas (e.g. Palsbøll *et al.*, 1995). If the southern feeding group differs matrilineally from the northern feeding group, and if site fidelity follows the pattern known for humpback whales, subsistence hunting off Washington has the potential to deplete the southern feeding range, and therefore, it should be managed separately. Given that matrilineal differentiation is a key issue relevant to management, maternally inherited mitochondrial DNA (mtDNA) is used as the most appropriate genetic marker.

Assuming that the southern feeding group represents a distinct entity, it could be a result of three different population historic hypotheses. The panmictic hypothesis assumes the southern feeding group to be panmictic with the northern feeding group. The separation hypothesis assumes that the southern feeding group is either a remnant or resulted from a single founding event. In either case of the separation hypothesis, this group is separate from the northern group and experiences no significant gene flow. Finally, the limited dispersal hypothesis assumes limited but continuous dispersal between the feeding groups. Simulation modelling is used here to assess whether a genetic study could be used to distinguish between the two most different hypotheses: panmixia and separation. The model simulates the population dynamics and genetics of both feeding groups assuming the southern area was colonised in a single founding event in the last century. In this paper, the elimination of one of these hypotheses is considered to be a successful genetic study. Although samples for genetic analysis have been collected from different regions, the individual identities (whether they are 'residents' or not) of these animals is uncertain, and further sampling would be necessary before undertaking a genetic study.

As there is considerable uncertainty regarding the various parameters used in the model, the paper investigates the sensitivity of the results to the assumed population growth rate, current population size of the southern feeding group, the population size of the entire eastern North Pacific gray whale population at the turn of the century and the initial haplotypic distribution.

METHODS

The following assumptions are made: the current abundance of the southern population is 150; the effective population size is the number of adult females (approximately 1/3 for N_{ef} = 50); and the growth rate for the southern population is the same as for the total population (2.5%). The model does not incorporate age structure. Founding events are assumed to be in intervals of twenty years, starting in 1900. Different colonisation times correspond to different minimal founder population sizes. The model simulates colonisation of the southern feeding area by the northern feeding group (assuming no further gene flow into the area), allows population growth to the year 2000 and then evaluates whether population structure can be distinguished from panmixia using a χ^2 permutation test (Roff and Bentzen, 1989). Mutation can be ignored as the model simulates a short time period. Because the data being simulated correspond to the mitochondrial *D* loop, which is considered neutral, selection can be ignored. Dispersal into the northern feeding group is also ignored because the only other population of gray whales in the western North Pacific numbers around 100 animals (Weller *et al.*, 1999) and appears isolated. As mentioned earlier, this paper only investigates the two most extreme historic scenarios for the southern feeding group: panmixia and separation. Therefore, dispersal between the northern and southern feeding group after the founding event is ignored.

Simulation model

The model simulates the following sequence of events.

(1) *Reduce the eastern North Pacific gray whale population size to the 1900 level (Butterworth et al., 2001) from historic levels*

The initial haplotype distribution is taken from simulations of a population of total abundance of 25,500 (Taylor and Chivers, 2000), which is the same as the historical estimate for gray whales of 24,895 (Butterworth *et al.*, 2001). The observed haplotypic diversity of the simulated allele frequency distribution (0.95) is comparable to the observed haplotypic diversity in eastern North Pacific gray whales (0.94 from P. Rosel, unpublished data). Simulations of large baleen whale demography typically estimate the proportion of adult females at 1/3 of total abundance. Thus, historical N_{ef} = 8,298. Given an estimated reduction to 13% of historical numbers, the number of adult females in 1900 was 1,080. In the model, this corresponds to randomly sampling 1,080 haplotypes from the initial genetic distribution.

(2) *Allow adult female population to grow in a density-dependent manner at a maximum growth rate of 2.5% per year (Butterworth et al., 2001)*

A birth and death Monte-Carlo process was used to decide whether an individual survives and/or reproduces. When a female reproduces, her offspring inherit her haplotype. Density-dependence is imposed through the birth rate according to the function:

$$b = d - (r/K_{ef})*N_{ef} \quad (1)$$

Where b is the birth rate, r is the annual growth rate per year ($r = b–d = 0.025$), d is the death rate ($d = 0.05$) (Reilly, 1992), K_{ef} is the carrying capacity (in terms of adult females) of the northern feeding group (K_{ef} = 8,298 (1/3 of K)) and N_{ef} is the effective number of females in a given year.

(3) *Found a southern resident feeding group from the northern feeding group*

The model investigates five possible founding events: 1900, 1920, 1940, 1960 and 1980. The founding population is determined by sampling the haplotypic distribution of the northern population without replacement for f haplotypes, where f is the number of founders. The number of founders can be calculated using the formula:

$$f = N_{2000}/e^{rt}$$

Where t is the time in years and N_{2000} is the estimate used for the effective number of females in the southern feeding group (150/3 = 50). Once founded, the southern feeding group is assumed to be genetically isolated from the northern feeding group. The founder population is allowed to grow from the time of the founding event to the present (2000) assuming $r = 0.025$ and using a similar birth and death model. The model for the southern feeding group differs by assuming a lower carrying capacity of 150 individuals in the southern feeding group.

(4) *Sample 30 individuals each ($n_1 = n_2 = 30$) from both feeding groups in the year 2000*

(5) *Compare the two samples using a permutation χ^2 procedure (Roff and Bentzen, 1989) using 1,000 permutations*
For each simulation, the number of haplotypes remaining in the southern feeding group and the χ^2 *p*-value were saved.

(6) *Repeat steps one to five 1,000 times to get the distribution of possible p-values given the stochastic properties of the simulation together with the sampling error associated with $n_1 = n_2 = 30$.*

Sensitivity analysis
As mentioned previously, difficulties in fitting models to both the catch and abundance data make the population size at its lowest point in history uncertain. Historical whaling records suggest that commercial whaling ceased at the end of the 19th century either because it was uneconomical, or because surviving whales avoided the breeding lagoons (Henderson, 1984). To investigate whether the results were sensitive to the number of whales surviving at the end of the 19th century, simulations are run at the lowest possible abundance. Using historical catch records and current population size, Reilly (1981) predicted a population trajectory where in 1875 the population size was 1,300. This value was used as a lower limit on lowest historical abundance. Whaling records suggest that commercial harvest targeted mainly adult females (Henderson, 1984). To investigate the lowest plausible number of surviving females, it was assumed that all adult females were hunted from the population. If it is assumed that the population prior to exploitation consisted of roughly 1/3 adult females, 1/3 adult males and 1/3 juveniles, then the post exploitation population would be approximately 1/2 adult males and 1/2 juveniles. Thus, the post-exploitation proportion of juvenile females is 1/4. The number of juvenile females was assumed to be the effective number of females (N_{ef} = N/4 = 1,300/4 = 325).

Wade and DeMaster (1996) suggested that in the absence of Russian harvest, the growth rate of gray whale populations is 3.4% (95% CI = 2.5-4.2%) per year. Since the southern group was not harvested, it is possible that it grew at this higher rate. To investigate the sensitivity of the results to growth rate in the southern feeding group, the above simulations are repeated with *r* for the southern population set at 3.4%.

Although scientists in various summering regions are collaborating to determine abundance using photographic data, the size of the southern feeding group is unknown. The sensitivity of the results to the population size of the southern residents is investigated by repeating the above simulations at a higher population size of 500.

Finally, the sensitivity of the results to the assumed initial distribution of haplotypes was investigated. The standard simulations use a distribution derived from evolutionary simulations that made a number of assumptions about both population dynamics and genetic factors, such as dispersal rates. In the sensitivity analysis, an empirical distribution sampled from North Pacific minke whales ($n = 188$; Goto and Pastene, 1999) is used. The estimates of current abundance for this area are 25,049 (95% CI = 13,689-45,835; IWC, 1992). Further, because these whales were never heavily exploited, their genetic composition should be roughly similar to the historic haplotypic distribution of eastern North Pacific gray whales.

RESULTS

The number of haplotypes in the southern feeding group was greatly reduced in all the simulations. The initial haplotypic distribution derived from evolutionary simulations had 191 haplotypes. At the lowest post-exploitation abundance, 100 haplotypes remained on average. Fig. 1 shows the number of haplotypes remaining in the southern feeding group after the founding event and growth to the year 2000.

As the founding event becomes more recent, the proportion of *p*-values < 0.05 decreases (Fig. 2). When $T \geq 40$, nearly all *p*-values are less than 0.05. The cumulative

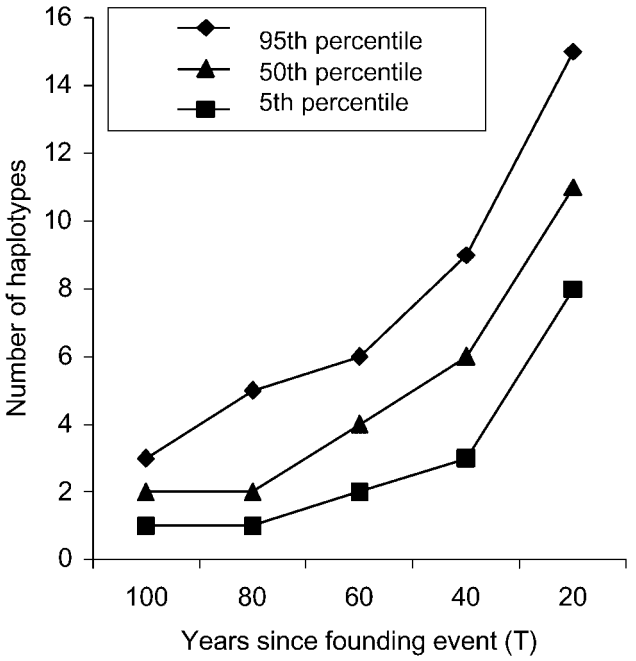

Fig. 1. The 95th, 50th and 5th percentile of the number of haplotypes remaining in simulations of the southern feeding group. Model assumes founding event occurred 20, 40, 60, 80 and 100 years ago.

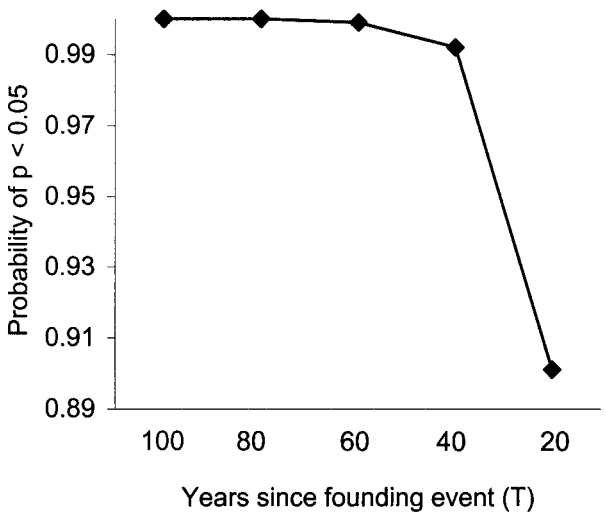

Fig. 2. The proportion of simulations resulting in a *p*-value < 0.05 if the southern feeding group was founded between 20 and 100 years ago.

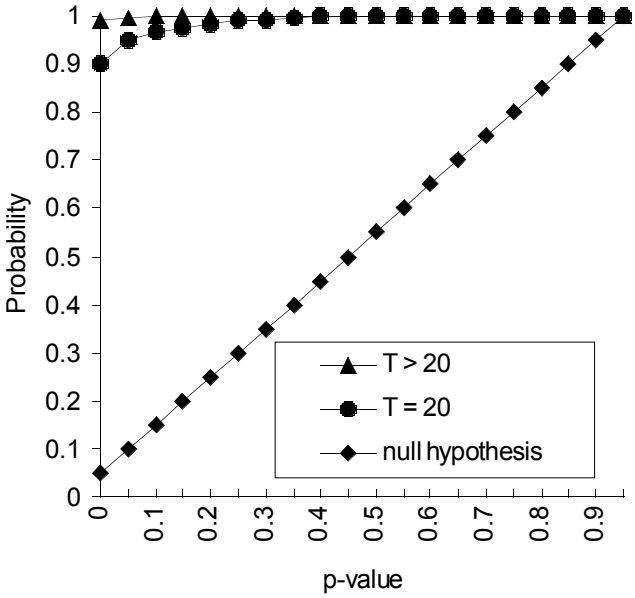

Fig. 3. Cumulative probability distribution of *p*-values when founding occurred more than 20 years ago ($T > 20$), 20 years ago ($T = 20$) and for the null hypothesis.

probability distribution of *p*-values demonstrates the ability to distinguish between colonisation hypotheses and the null hypothesis (H_0: northern = panmixia) over the range of possible *p*-values (Fig. 3). For $T \geq 40$, the cumulative probability is at the maximal value of one by $p = 0.05$. Thus, if the founding event took place 40 or more years ago, a genetic test will unequivocally distinguish between the northern and the southern feeding groups.

Another way to consider the results is to quantify the probability of making errors. A type I error, with probability alpha (α), is the probability of incorrectly rejecting the null hypothesis, which would incorrectly split the feeding groups and therefore result in overprotecting the southern feeding area. A type II error, with probability beta (β), is the probability of incorrectly accepting a false null hypothesis, which would incorrectly lump the feeding groups and result in under-protecting the southern feeding group. Trade-off curves (Fig. 4) give the error trade-off for all α values. For example, for $T = 20$, when $\alpha = 0.05$, $\beta = 0.099$. If a colonisation event 20 years ago is used as a criterion by which one should manage populations separately, then by choosing $\alpha = 0.05$, a manager would be 1.98 times as willing (0.099/0.05) to commit an under rather than an over-protection error. The $\alpha = \beta$ line shows one possible decision criterion where the errors are equalised. For $T \geq 40$, β is almost zero at a = 0.05, implying that the power (1-β) at $\alpha = 0.05$ is almost one. This is because at these values of *T*, almost all the observed *p*-values are less than 0.05.

Table 1

The proportion of trials (out of 1,000) that resulted in *p*-values less than the value specified in column headings, for all values of *T* and for the null hypothesis. The table also compares all four founding hypotheses with the null hypothesis.

Time since founding (years)	$p<0.05$	$0.05<p<0.1$	$p>0.1$
20	0.901	0.05	0.049
40	0.992	0.005	0.003
60	0.999	0.001	0
80	1.0	0	0
100	1.0	0	0
All five hypotheses	0.978	0.011	0.010
H_0	0.05	0.05	0.9

The summarised results (Table 1) show the proportion of simulations where $p < 0.05$, $0.05 < p < 0.1$ and $p > 0.1$, for $T = 20$ to 100 and H_0. If simulations from all the different founding events are pooled and each of the five separation hypotheses is assumed to be equally likely: 97.8% have $p < 0.05$ compared to 5% for H_0; 1.1% have $0.05 < p < 0.1$ compared to 5% for H_0; and only 1% have $p > 0.1$ compared to 90% for H_0. Thus, there is high contrast between the separation hypothesis and the null hypothesis of panmixia for all *p*-values except those lying between 0.05 and 0.1.

Results are not sensitive to a lower historical bottleneck size, increased growth rate, or the initial haplotypic distribution. Simulations assuming a higher population size (500) of the southern feeding group result in a lower proportion of *p*-values < 0.05 at $T = 20$ due to a higher number of founders. Table 2 shows the proportion of *p*-values < 0.05 for two values of *T*, chosen to demonstrate the greatest contrast between the different conditions.

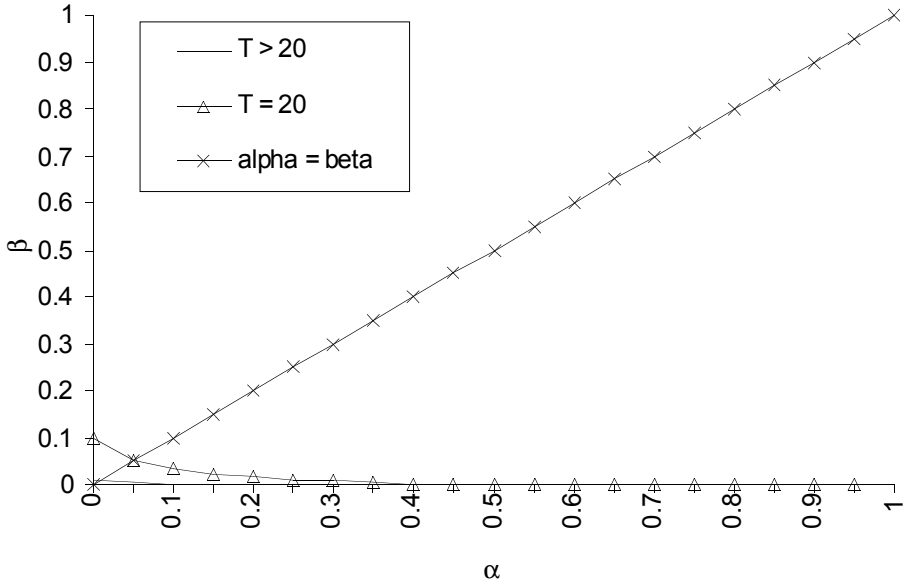

Fig. 4. Trade-off curve shows the Type II error (β) associated with various levels of significance (α) for the different founding hypotheses. The decision criterion $\alpha = \beta$ is also shown.

Table 2

The proportion of *p*-values less than 0.05 for $T = 20$ and $T = 40$ under different model conditions. The standard model corresponds to $N_{ef} = 1{,}083$, $r = 0.025$, population size = 150 and haplotypic distribution = simulated.

Model	$T = 20$	$T = 40$
Standard	0.901	0.992
$N_{ef} = 325$	0.866	0.992
$r = 0.034$	0.935	0.998
Population size = 500	0.404	0.790
Haplotypic distribution = empirical	0.899	0.994

DISCUSSION

The increase in the number of remaining haplotypes with respect to increasing founder size *f*, is not linear (Fig. 1). That is, even at larger founder sizes, few haplotypes make it through the founding event. Founding events that occurred between 40 and 100 years ago are characterised by small founder sizes, and as a result have only a few haplotypes, resulting in statistically significant genetic differentiation between the populations. The founder size is so small for $T = 80$ and 100 that it causes the southern population to go extinct in 9% and 20% of the simulations respectively. Even when the founder number increases to 30 ($T = 20$), there is a very high probability of getting a *p*-value of less then 0.05. Both the simulated and empirical haplotypic distributions are characterised by many rare haplotypes and a few common haplotypes. As a result, when the southern feeding group is founded by the separation hypothesis, it harbours a low number of haplotypes, which in turn causes rapid genetic differentiation.

The trade-off curve (Fig. 4) can be used to determine management implications for a specific *p*-value. For a manager to obtain an equal chance of overprotecting or underprotecting the population ($\alpha = \beta$) using the criterion of separate management based on a single founding event that occurred at least 20 years ago, the critical a level would be 0.1. However, if the single founding event was 40 or more years ago, then using $\alpha = 0.05$ is sufficient to reject the null hypothesis. Uncertainties concerning population size, growth rate and initial haplotypic distribution do not substantially influence the results (Table 2). It is possible that growth rates were higher than those used in the base-case because trends in abundance were measured only since 1967, after growth may have slowed due to density-dependence. The sensitivity analysis shows that increasing the growth rate increases the chance of detecting genetic differences because back calculation would result in a smaller number of founders. Thus, the conclusions are robust to the potential of higher growth.

Genetic distinctions between the southern and the northern feeding groups therefore arise because of the low number of southern founders required to yield the present number of residents through internal recruitment. As mentioned earlier, the simulations do not consider the genetic consequences of the limited dispersal hypothesis, which could potentially result in lower levels of genetic differentiation as new haplotypes could be added to the population through dispersal every year.

As mentioned earlier, 18 samples have been collected from the Clayoquot Sound (Britsh Columbia) area, of which only 50% of the individuals sampled are potentially residents, and 50% of the potential residents are young animals (Steeves, 1998). Steeves showed that the total sample of 18 animals had a haplotypic diversity of 0.94 (SD = 0.17) which is comparable to the haplotypic diversity of the northern feeding group in the simulations here. Steeves results could indicate that either the two feeding groups are panmictic or that the sample size of resident adult whales is too small to reject the separation hypothesis, indicating the need to further sample the southern feeding group for identified resident individuals.

Once genetic data have been collected, model choice based on a decision analysis framework could be used to best interpret the data. Such an analysis would compare three different historical scenarios mentioned earlier (the different hypotheses) that could have resulted in the southern feeding group. This study investigated the separation hypothesis, where founding occurred at discrete points in time. Biologically there is no need for this assumption. Founding could have occurred in any given winter migration. The models used in this study could be generalised to test a uniform distribution of years since founding. Models could be set up to examine the genetic consequences of the third hypothesis, the limited dispersal hypothesis. Models for these two hypotheses could investigate the effects of founding time, and dispersal rates on genetic differentiation between the northern and the southern feeding group. Comparison of model results to empirical results could then identify the most plausible hypothesis and the best-fit model.

In conclusion, given the founder hypothesis, this feasibility analysis indicates that carrying out a genetic study would probably be useful, because the results would be used to eliminate the hypothesis that the southern feeding group is entirely separate and would therefore require separate management. Thus, a relatively easy and inexpensive study could provide data to support separation. However, if this study finds *p*-values greater than 0.05, then additional research would be needed to further assess the remaining hypotheses, which include scenarios requiring separate management (continued by low dispersal) and scenarios where pooling is acceptable (panmixia or insufficient dispersal). We therefore recommend that a genetic study be carried out to address population structure for eastern North Pacific gray whales.

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