

REPLY COMMENT

Statistical power and plausible alternate hypotheses of gametic recapture estimates from wintering grounds of humpback whales

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In Garrigue et al. (2004) we present multiple lines of evidence to suggest that humpback whales *Megaptera novaeangliae* from the winter grounds around New Caledonia (NC) form a small autonomous population unit that is *relatively* closed to demographic and reproductive interchange with other populations in the South Pacific. Our evidence included a 7 yr database of sighting–resighting records for both individual identification photographs (photo-identification) and microsatellite genotypes from small skin samples collected with a biopsy dart. From these we derived estimates and 95% confidence intervals (CI) of abundance for the non-calf population and for the sex-specific components of the population using standard closed-population, capture-recapture models (Fig. 1). The low coefficient of variation (CV) of these estimates, reflecting a high proportion of recapture for individuals across the 7 yr study, and the limited interchange documented with other breeding grounds (Garrigue et al. 2002) supported our conclusion that the population was small and closed demographically.

From the total sample of 133 non-calf males, we also inferred the paternity of 5 calves from a total sample of 16 calves (representing about 42% of all cow–calf pairs sighted in the small population over 7 yr). Following the logic of capture-recapture models, we used the proportion of inferred paternities as a male ‘gametic’ recapture estimate of abundance for comparison to the male ‘organismal’ recapture estimate. These 2 estimates were essentially identical (Fig. 1), suggesting that the population of males wintering near NC were likely to be the fathers of the calves. Formally stated, we were unable to reject the null hypothesis that the number of paternities inferred from the sample of

calves was greater or less than expected given the estimated number of males in the local population. This finding was unusual, as the success rate of paternity assignments in populations of marine mammals is generally below expectations, even when sampling of males is considerably more complete than in the case of the NC humpback population (e.g. Worthington-Wilmer et al. 1999, Gemmel et al. 2001, Krützen et al. 2004). We considered that the evidence of relative

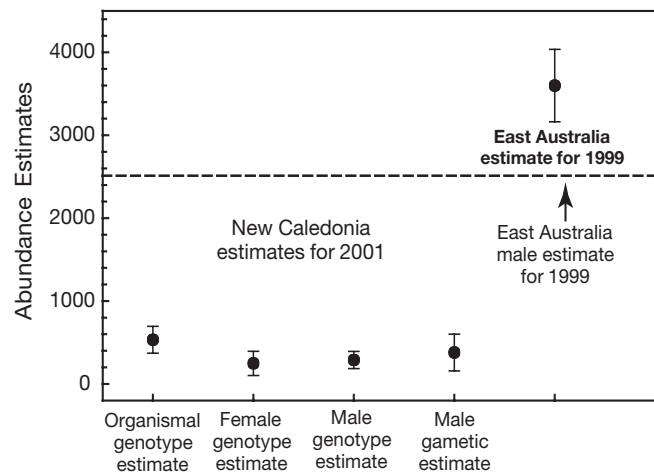


Fig. 1. *Megaptera novaeangliae*. Gametic and organismal recapture estimates (and 95% CI) for humpback whales on the New Caledonia wintering ground for 1996 to 2001 (Tables 4 & 6 in Garrigue et al. 2004), and shore-based estimate (and 95% CI) of the east Australia migratory corridor for 1999 (Paterson et al. 2001). The dashed line indicates the likely male-specific component of the shore-based estimate of east Australia, assuming a male:female ratio of 2.4:1, as reported from biopsy sampling in Brown et al. (1995)

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demographic and reproductive closure helps to explain the variable rates of recovery observed among humpback whales in the South Pacific and the potential vulnerability to exploitation of these and other subdivided populations of whales (Clapham et al. 1999).

In their Comment, Palsbøll et al. (2005, this volume) question the statistical certainty of our gametic recapture estimate and comment that we did not address the alternate possibility that some or many 'outside' males were mating with NC females. They use computer simulations to construct a 'closed' population of 330 mature males (representing NC), that is 'open' to temporary immigration by some number of additional males drawn as a proportion, ranging from 10 to 50%, of an outside population of 1250 males (representing eastern Australia). From the probability of obtaining the observed number of inferred paternities under these scenarios, they conclude that there is insufficient evidence from the gametic recapture estimate 'alone' to support our conclusion that the New Caledonia population is reproductively autonomous.

The rather complicated scenario developed by the Palsbøll et al. (2005) simulations belies a basic question of statistical power applicable to most capture–recapture estimates; in our case, how large (or small) could the true population of males be, and still yield the observed gametic recaptures of 5 fathers from the 16 calves? We addressed the question of statistical power in 2 ways.

(1) We reported the CV and 95% CI for both the gametic and organismal recapture estimates (Fig. 1). From these, it seems unlikely that either estimate was derived from a population of more than about 600 males. Not surprisingly, the results of the analytic approach of Palsbøll et al. (their Fig. 1A) do not differ greatly from the expectations of the upper tail of the 95% CI for our gametic estimate. However, it is important to note that their analytical approach and computer simulations make the artificial assumption that the abundance of NC males is known with certainty (i.e. fixed at $N_m = 330$) and that any additional males come from 'outside'. This ignores the fact that our comparison is between 2 *estimates*, one for male gametic abundance and one for male organismal abundance, each with accompanying sampling variance. The overlapping CIs of the 2 estimates suggest that the probability of the 5 paternities being drawn from a larger number of males is consistent with the probability that the true population of NC is larger than the point estimates.

(2) We also considered the statistical power of our gametic recapture estimate to reject an alternative, biologically plausible, null hypothesis: fathers of NC calves were drawn from a larger population that migrates past eastern Australia, as a result of mating

during migration. We rejected this hypothesis based on the 95% CI of our estimate and the estimate of the migratory population of east Australia made in 1992 (Paterson et al. 1994). Here, we update this comparison using the estimate of 3400 individuals (95% CI: 400) from the year 1999 (Paterson et al. 2001), a date closer to the midpoint of our gametic recapture estimate. Because the estimate of east Australian humpbacks is not sex-specific (and the variance of the male-specific component is unknown) we cannot calculate a test of difference between the 2 estimates. However, a graphical presentation of the 95% CI shows that this alternative hypothesis is highly unlikely (Fig. 1). Although we consider panmixis due to breeding during migration a plausible alternative hypothesis, we do not consider the scenario of temporary immigration in the Palsbøll et al. (2005) model to be consistent with other evidence. Such a scenario, if true, would result in larger (and more heterogeneous) organismal capture estimates over the 7 yr study.

Palsbøll et al. (2005, p. 306) ask 'how much data would be necessary for a gametic recapture inference to provide conclusive evidence that a population is reproductively autonomous?' Given their implied requirement of conclusive evidence, this is equivalent to asking, 'how large a sample would be necessary for an *exact* estimate of population abundance?' It is perhaps more instructive to accept that any capture–recapture estimate will have some sampling variance, and ask instead, 'to improve the power of gametic recapture, should greater effort be directed at increasing the sample size of males or calves?' Because the CV of capture–recapture estimates largely depends on the number of recaptures, doubling either the sample size of males or calves would presumably double the number of inferred paternities (i.e. recaptures). As calves are a conspicuous and less abundant component of the population, they are likely to require less effort to sample in the field (and less effort to genotype given the smaller number of samples). Males, because of the absence of obvious sexual dimorphism (other than the presumed sex-specific roles of singers and escorts), will be sampled in the field by chance along with females, and can only be identified later in the laboratory using a sex-specific marker.

Hypothesis testing using gametic recapture could also be improved by extending the geographic sampling to several breeding grounds. For 2 or more populations, the first step would be to construct a test of panmixis, perhaps using computer simulations such as those in Palsbøll et al. (2005). If the null hypothesis of panmixis cannot be rejected, the power of the test would need to be considered given some specified level of 'relative reproductive autonomy' (Taylor & Dizon 1996). If the null hypothesis of panmixis is

rejected, the next step would be to estimate the degree of reproductive autonomy relative to reproductive exchange, similar to indices of migratory return and migratory interchange based on photo-identification records (Baker et al. 1986, Calambokidis et al. 2001, Garrigue et al. 2002). The large number of geographically discrete breeding grounds in the South Pacific from eastern Australia to South America, and the parallel collection of biopsy samples and individual identification photographs (e.g. Andersen et al. 2001, Garrigue et al. 2002, C. Olavarría, C. S. Baker, C. Garrigue, M. Poole and 15 others unpubl.) present a compelling opportunity for such a study. Some of these breeding populations have not experienced the rapid increase in abundance observed in east Australia but may yet be threatened by expansions of scientific hunting or a return to commercial exploitation on the Antarctic feeding grounds (Gales et al. 2005).

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Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: May 24, 2005; Accepted: May 26, 2005
Proofs received from author(s): June 8, 2005