Whales Before Whaling in the North Atlantic

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It is well known that hunting dramatically reduced all baleen whale populations, yet reliable estimates of former whale abundances are elusive. Based on coalescent models for mitochondrial DNA sequence variation, the genetic diversity of North Atlantic whales suggests population sizes of approximately 240,000 humpback, 360,000 fin, and 265,000 minke whales. Estimates for fin and humpback whales are far greater than those previously calculated for prewhaling populations and 6 to 20 times higher than present-day population estimates. Such discrepancies suggest the need for a quantitative reevaluation of historical whale populations and a fundamental revision in our conception of the natural state of the oceans.

Approaching the New World in 1635, English minister Richard Mather rejoiced in the "multitude of great whales, which now was grown ordinary and usuall to behold" (*1*). Commercial whalers consumed this abundance in the centuries that followed. The northern right whale (*Eubalaena glacialis*), humpback whale (*Megaptera novaeangliae*), fin whale (*Balaenoptera physalus*), and minke whale (*Balaenoptera acutorostrata*) were intensively hunted, and all North Atlantic baleen whales are now protected because of low population levels (*2*). Despite the initial recovery of most species, restoration goals are difficult to establish. How many great whales were in the North Atlantic before commercial exploitation? Whaling logbooks provide clues, but may be incomplete, intentionally underreported, or fail to consider whales that were struck and lost (*3*).

Levels of neutral genetic variation can help track population trends across deep ecological time, because variation increases with population size (*4*–*6*). For maternally inherited mitochondrial DNA (mtDNA), the relation between θ, a measure of genetic diversity, and the long-term effective female population size [$N_{e(f)}$] is $\theta = 2N_{e(f)}\mu$, where μ is the substitution rate per generation. Migration, fluctuations in population size, selection, and population structure affect levels of genetic variation (*7*), but a recent maximum likelihood method simultaneously estimates θ and migration rates for multiple populations (*8*). We used the largest genetic data set available for whales, from mtDNA control region sequences, to calculate θ for North Atlantic humpback, fin, and minke whales. Analyses included global data sets when available, to account for gene flow between ocean basins (*9*) (Fig. 1).

Values of θ were surprisingly high for North Atlantic populations of all species, varying from 0.022 for humpback whales to 0.043 for fin whales. Gene flow estimates indicate that the North Atlantic is largely isolated, with fewer than one female migrant per generation between the Atlantic and the Southern Hemisphere for humpbacks. The lack of Southern Hemisphere data for fin whales makes interoceanic gene flow difficult to estimate, but migration was less than one female per five generations of fin whales between the North Pacific and Atlantic.

To estimate long-term population numbers from these data requires reliable estimates of μ. The humpback genus *Megaptera* is known from the late Miocene, ~6 million years ago (*10*), and the diversification of its parent genus, *Balaenoptera*, occurred by about 10 million years ago, so the origin of humpbacks is at least 6 to 10 million years old. Given a Tamura-Nei gamma-corrected distance of 0.211 between humpback and fin whales (range, 0.155 to 0.264), we estimate the mitochondrial substitution rate to be 1.1×10^{-8} bp^{-1} year^{-1} to 1.8×10^{-8} bp^{-1} year^{-1} (bp, base pair) (*9*). Pesole *et al*. calculated an average rate of 1.5×10^{-8} bp^{-1} year^{-1} for the 5′ end of the D loop, based on *Balaenoptera* divergence dates (*11*). Rooney *et al*. calculated 2.0×10^{-8} bp^{-1} year^{-1}, based on *Balaena-Eubalaena* diversification in the Pliocene (*12*). To reflect this range of rates, we employed estimates of 1.5×10^{-8} bp^{-1} year^{-1} to 2.0×10^{-8} bp^{-1} year^{-1}.

We used the average age of sexually mature females to estimate generation time, which is equivalent to the average age of mothers giving birth if fecundity remains constant with age (*9*). For Antarctic minke whales, the age of maturity is 8 years (*13*) and the average age of females is 17 years (*14*). For Atlantic fin whales in the late 20th century, respective ages were 11 years (*15*) and 25 years (*16*). Humpback maturity is at 5 to 6 years, and the average age of adult females in the Australian fishery was 12 years (*17*, *18*). From life-table data, the mean age of reproductive females in the Gulf of Maine was 24 years (*19*).

We determined N_C, total census size, from $N_{e(f)}$, based on three conversion factors. First, we converted $N_{e(f)}$ to total effective population size, N_e, by multiplying by two, because the sex ratio is 1:1 (*20*). Second, we converted N_e to the total number of breeding adults, N_T. The N_T:N_e ratio approaches 2.0 in most populations with a constant population size (*21*), although numerous genetic studies suggest that this is a very conservative estimate (*9*). Third, to account for the number of juveniles, we multiplied N_T by an estimate of (no. of adults + juveniles)/(no. of adults) derived from catch data and surveys. This ratio is 1.6 to 2.0 for humpbacks (*17*, *18*), 1.5 for gray whales (*22*), and 2.5 to 3.0 for bowhead whales (*23*). Considering these ranges, we used a multiplier of 1.5 to 2.0. Thus, we estimate total population size as six to eight times the number of breeding females. This is one of the most conservative values ever used in genetic estimates of large mammal demography, and it ignores fluctuations in population size, polygyny, and female fecundity, all of which would increase the ratio between census and effective population size (*21*, *24*). A Monte Carlo resampling scheme (*9*) was used to estimate mean values and 95% confidence limits for the number of breeding females and total census size (Table 1).

Genetic diversity in baleen whales suggests that historical population sizes were large, with long-term estimates of 240,000 humpback, 360,000 fin, and 265,000 minke whales in the North Atlantic. Although some studies suggest that North Atlantic whales are approaching present-day carrying capacity (*3*, *25*), the genetic data indicate that current populations (10,000 humpback, 56,000 fin, and 149,000 minke whales) (*9*, *26*, *27*) are a fraction of past numbers (Fig. 1). Genetic

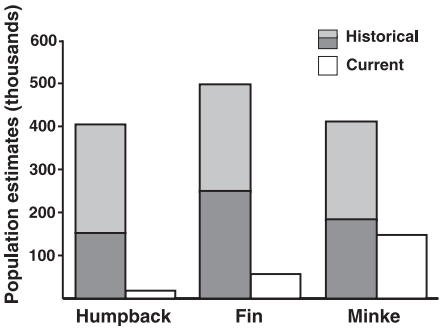

Fig. 1. Genetic estimates and current census sizes (*9*, *25*, *26*) for North Atlantic humpback, fin, and minke whales. The confidence intervals are in light gray.

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data for baleen whales support conclusions from archaeological and ecological research that the past abundance of large consumer species such as turtles, sharks, and pelagic fish was much greater than recent observations suggest (*28*–*30*).

Genetically based estimates are also far higher than estimates from whaling records of preexploitation populations of fin and humpback whales. Historical estimates indicate that widespread commercial exploitation began in the 19th century and that approximately 20,000 humpbacks and 30,000 to 50,000 fin whales existed in the North Atlantic before hunting began (*2*, *9*, *31*–*33*). If historical records are accurate, then the genetic data overestimate abundance by nearly an order of magnitude. Because genetic values are much higher than expected, we explored reasons why they might be inflated.

Genetic data yield estimates of long-term population numbers, not necessarily those that occurred at the time when whaling records were first collected. If whale populations were unusually low at the start of commercial whaling, genetic and historical estimates could both be true. Such a drop in numbers would have had to be brief, or genetic diversity would have declined. We know of no data that support or refute this hypothesis.

Population structure can increase values of θ, especially if lineage variation in fitness (*34*) is spatially variable (*9*). Several strongly differentiated populations, mistakenly analyzed together, can have a higher cumulative θ than if analyzed separately. However, for Atlantic humpback and fin whales, eastern and western populations have high gene flow; and analyzing subpopulations together, as we have done here, generates a lower population estimate than analyzing subpopulations separately [results were produced with the MIGRATE program (*35*)]. Mildly deleterious mutations, known to be common in mtDNA (*36*), can also delay fixation and enhance haplotype number. In our data sets, phylogenetic tests for selection were all nonsignificant (*9*).

Injection of genetic variation from outside populations can also increase θ. For minke whales, this is not possible because southern and northern populations are genetically distinct at the level of typical mammalian species, and North Atlantic mtDNA sequences are monophyletic (*37*). However, migration events are evident in humpback whales. The Atlantic haplotype pool is composed of two old clades that occur in other oceans (*38*). This could increase θ if both clades are maintained by immigration from the south. One clade [the IJ clade of (*38*)] shows a diversification of recent lineages in the North Atlantic but mostly basal lineages in other oceans, suggesting that it has been in the North Atlantic for a long time. We analyzed diversity patterns for worldwide humpback samples from the IJ clade and found θ values similar to those in Table 1, suggesting that the high values reported here are not artifacts of mixing divergent clades with different biogeographic histories.

In addition, our analysis of global humpback sequences suggests that the North Atlantic houses only a small fraction of the genetic diversity of this species. Worldwide values of θ sum to about 0.100 (implying that the global population was above 1 million), as compared to 0.022 in the North Atlantic. The reduction of diversity in this basin would not occur if Atlantic humpbacks were broadly connected to global populations. Could humpbacks have invaded the North Atlantic recently, bringing with them a great deal of genetic variation from the south, and then lost 80% of their original diversity? With a population size of 5000 females, such a loss would take thousands of generations and be unlikely to result in the phylogenetic structure evident between oceans (*9*).

One caution is that we have no samples from the South Atlantic, which could provide a genetic link to southern oceans. Inclusion of these data might lower our estimate of diversity native to the North Atlantic. However, South Atlantic humpbacks feed near the Antarctic and, like southern Pacific populations, may be genetically similar to whales sampled from the Antarctic Peninsula. If so, inclusion of this population would have little impact on our conclusions. A larger gap is the absence of southern fin whales, because we cannot exclude the possibility that the high θ value for the Atlantic is inflated by gene flow from the south. However, gene frequencies for two of three polymorphic allozyme loci are significantly different across the equator (*39*), suggesting that fin whales in the North Atlantic and southern oceans have had low historical gene flow. Only data from southern populations will resolve this issue.

Analyses of effective population size are far stronger when based on multiple loci,

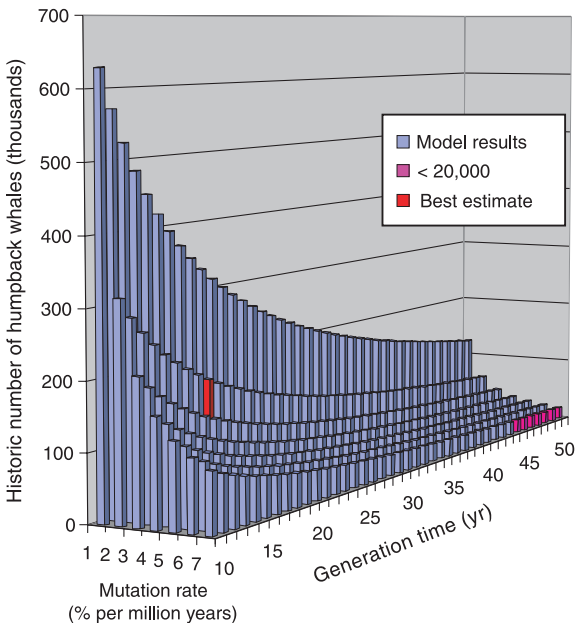

Fig. 2. The genetic diversity of humpback whales demands higher than expected values of historical population size. Genetic estimates of historical population size are based on the lower 95% confidence limit of θ (0.018). Only extreme values of both mutation rate ($\mu > 7 \times 10^{-8}$ bp^{-1} year^{-1}) and generation time (45 years) are consistent with estimates of historical population size (<20,000).

Table 1. Historical population estimates based on genetic diversity and generation time of baleen whales in the North Atlantic Ocean. *n* indicates number of individuals analyzed in the North Atlantic.

Species	*n*	θ mean (95% CI)	Generation time (years)	$N_{e(f)}$ (thousands) (95% CI)	Genetic population estimates (thousands) (95% CI)	Current estimates (thousands)
Humpback whale	188	0.0216 (0.0179–0.0274)	12–24	34 (23–57)	240 (156–401)	9.3–12.1
Fin whale	235	0.0430 (0.0346–0.0526)	25	51 (38–65)	360 (249–481)	56.0
Minke whale	87	0.0231 (0.0161–0.0324)	17	38 (26–57)	265 (176–415)	149.0
Total					865 (581–1297)	214–217

because a single locus could retain higher than expected levels of diversity. In particular, certain positions in the mammalian D loop appear hypermutable. In our humpback analysis, for example, some positions changed four to eight times. Because these positions contribute disproportionately to intraspecific diversity, they may inflate θ. Removing the 14 sites with more than three intraspecific changes reduces diversity by about 25 to 33%, suggesting that this may be a source of error. Given the idiosyncratic features of this single locus, data from more loci are required before a fully accurate estimate of historical populations is possible. Unfortunately, no comparable nuclear data sets are yet available (*9*). Yet even if we assume that diversity is reduced by 50%, and rely on the lowest 95% confidence limit, our estimate of humpback populations would be about 75,000. Populations would also be halved if generation time estimates were doubled, but errors of this magnitude are unlikely. To bring our results completely in line with historical humpback population sizes of approximately 20,000 requires generation times of more than 45 years plus a substitution rate nearly four times higher than estimated (Fig. 2).

The genetic diversity of humpback, minke, and fin whales is inconsistent with the low historical population sizes currently assumed (*9*). The discrepancy of these values represents a crucial challenge. To reconcile these results requires genetic analyses of additional loci; more information about South Atlantic populations; and reevaluation of the time period, severity, and demographic impacts of North Atlantic whaling.

Reconciling these numbers is crucial, because the possibility that vast cetacean populations existed across deep ecological time has fundamental implications not only for their management but also for our perception of the world's oceans. In its Revised Management Procedure, the International Whaling Commission (IWC) states, "catches should not be allowed on stocks below 54% of the estimated carrying capacity" (*27*). Genetic data cannot be used alone to define carrying capacity, because effective population sizes are often orders of magnitude lower than population censuses (*5*, *7*, *9*, *24*), but they can be useful in setting a lower limit to these values. In light of our findings, current populations of humpback or fin whales are far from harvestable. Minke whales are closer to genetically defined population limits, and hunting decisions regarding them must be based on other data.

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Supporting Online Material

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Materials and Methods
Fig. S1
References

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Cannibalism by Sporulating Bacteria

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Spore formation by the bacterium *Bacillus subtilis* is an elaborate developmental process that is triggered by nutrient limitation. Here we report that cells that have entered the pathway to sporulate produce and export a killing factor and a signaling protein that act cooperatively to block sister cells from sporulating and to cause them to lyse. The sporulating cells feed on the nutrients thereby released, which allows them to keep growing rather than to complete morphogenesis. We propose that sporulation is a stress-response pathway of last resort and that *B. subtilis* delays a commitment to spore formation by cannibalizing its siblings.

Some microorganisms respond to nutritional limitation by entering a resting state in which they remain inactive for an extended time. *Bacillus subtilis* produces a robust resting cell, the endospore, that can remain dormant for many years. Endospore formation is an elaborate and energy intensive process that requires several hours to complete (*1*–*4*). If during this period nutrients were once again to become plentiful, the sporulating cells would be at a disadvantage relative to cells able to resume growth rapidly. Thus, bacteria could be expected to delay spore formation until forced to do so by prolonged depletion of nutrients. Here we present evidence that cells that have entered the pathway to sporulate delay development by killing their siblings and feeding on the nutrients thereby released. Cannibalism is mediated by an extracellular killing factor and a novel intercellular signaling protein that act cooperatively to cause cell death and impede sporulation.

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