

The Effect of Differential Reproductive Success on Population Genetic Structure: Correlations of Life History With Matrilines in Humpback Whales of the Gulf of Maine

H. C. Rosenbaum, M. T. Weinrich, S. A. Stoleson, J. P. Gibbs, C. S. Baker, and R. DeSalle

To examine whether demographic and life-history traits are correlated with genetic structure, we contrasted mtDNA lineages of individual humpback whales (*Megaptera novaeangliae*) with sighting and reproductive histories of female humpback whales between 1979 and 1995. Maternal lineage haplotypes were obtained for 323 whales, either from direct sequencing of the mtDNA control region ($n = 159$) or inferred from known relationships along matrilines from the sequenced sample of individuals ($n = 164$). Sequence variation in the 550 bp of the control region defined a total of 19 maternal lineage haplotypes that formed two main clades. Fecundity increased significantly over the study period among females of several lineages among the two clades. Individual maternal lineages and other clades were characterized by significant variation in fecundity. The detected heterogeneity of reproductive success has the potential to substantially affect the frequency and distribution of maternal lineages found in this population over time. There were significant yearly effects on adult resighting rates and calf survivorship based on examination of sighting histories with varying capture-recapture probability models. These results indicate that population structure can be influenced by interactions or associations between reproductive success, genetic structure, and environmental factors in a natural population of long-lived mammals.

Variation in reproductive success among individuals of either sex, as well as among groups or cohorts, is well known in some wild populations of animals (Clutton-Brock 1988, 1989). It has generally been accepted that heritability of life-history characteristics related to fitness, such as female fecundity, is low (Charlesworth 1994; Nunney 1995; Roff and Mousseau 1987). Differential mating success and fecundity has been more recently associated with individual variation in phenotype, age-structured effects, and short-term environmental change related to climate, population density, or habitat quality (Clutton-Brock 1988; Hewison 1997; Magrath 1989; Price and Grant 1984; Sinervo and Zamudio 2001; Stoleson and Beissinger 1997). While annual variation in reproductive success has been suggested to account for differences in observed heterozygosity and higher inbreeding coefficients (Scribner et al. 1993), there are few examples where heritability (genetic or cultural) is correlated with variable reproductive success (Austerlitz and Heyer 1998). Recent modeling suggests that

variation in reproductive success may affect the level of genetic diversity (Tiedemann and Milinkovitch 1999). More often, such correlations with life-history traits are attributed to environmental, or more broadly, stochastic differences.

It has long been an objective of population genetics to integrate life-history parameters into understanding changes in allele frequency (Wright 1951). However, the lack of resolution of molecular markers and a paucity of appropriately detailed demographic structure and life-history information have made this analysis difficult in nonhuman populations (Clutton-Brock 1988, 1989). Only recently have molecular markers permitted the direct study of the interaction between population genetic structure and mating systems in a broader evolutionary context beyond the individual level. Correlation of trends in fecundity, survivorship, and resighting for both genealogy and distinct genetic lineages within a natural population provides a new approach to a fundamental question of traditional population genetics. Here we examine

From the Molecular Systematics Laboratory, American Museum of Natural History, 79th Street and CPW, New York, NY 10024 (Rosenbaum and DeSalle); Wildlife Conservation Society, Science Resource Center 2300 Southern Blvd., Bronx, NY 10460 (Rosenbaum); Whale Center of New England, P.O. Box 159, Gloucester, MA 01931 (Weinrich); USDA Forest Service, Northeast Research Station, P.O. Box 267, Irvine, PA 16329 (Stoleson); State University of New York, College of Environmental Science and Forestry, 350 Illick Hall, Syracuse, NY 13210 (Gibbs); and Ecology and Evolution Group, School of Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand (Baker). We thank the Lerner-Gray Fund for Marine Research of the American Museum of Natural History for helping to fund this work. We thank Mark Schilling, Cindy Belt, Malcolm Martin, and David Morin for help in the field obtaining biopsy samples, and the staff and interns of the Whale Center of New England for help in collecting and compiling all of the photographic identification data for this study. We are also grateful to Meghan Avolio for her assistance with editing and proofreading. Comments provided by George Amato, Junhyong Kim, Ken Kidd, Jeffrey Powell, Mitch Levesque, and four reviewers significantly improved this manuscript. Address correspondence to H. C. Rosenbaum, Wildlife Conservation Society, Science Resource Center, 2300 Southern Blvd., Bronx, NY 10460, or e-mail: hrosenbaum@wcs.org.

© 2002 The American Genetic Association 93:389–399

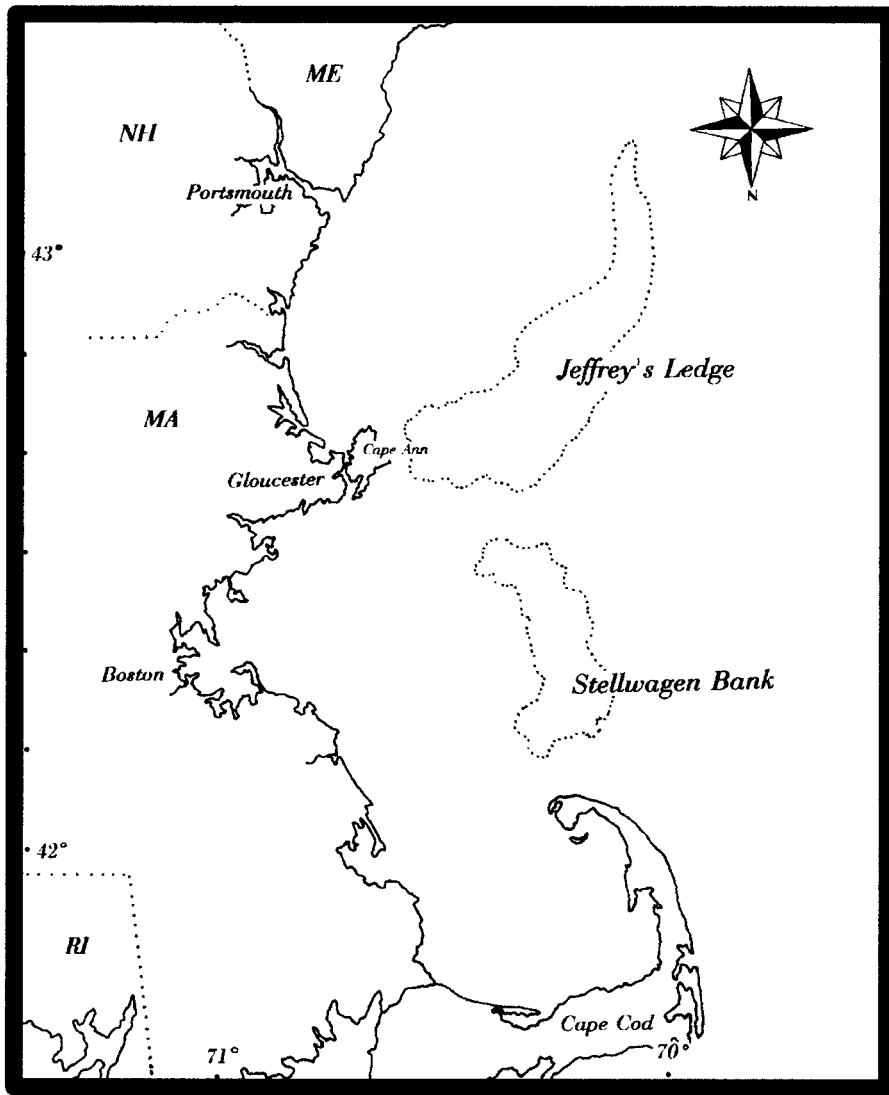


Figure 1. Survey areas of Jeffrey's Ledge and Stellwagen Bank for humpback whales in the Gulf of Maine between 1979 and 1995.

the interaction between genetic structure and fecundity in a long-lived nonhuman mammal and the consequences any association might have on maternal lineage distribution and viability in the study population.

The North Atlantic Ocean population of humpback whales consists of several relatively discrete feeding subpopulations (Katona and Beard 1990) with matrilineal fidelity (Clapham and Mayo 1987, 1990). One of these subpopulations is found in the Gulf of Maine during the months of April through December in the waters around Stellwagen Bank and Jeffrey's Ledge (Clapham et al. 1993; Weinrich et al. 1997) (Figure 1). This seasonally residential subpopulation of humpback whales has been studied extensively since the 1970s. Because individuals are identifiable by natural

markings on the ventral surface of their tail flukes and dorsal fins (Katona and Whitehead 1981), patterns of social organization and seasonal presence for Gulf of Maine humpback whales have been tracked from 1979 until the present (e.g., Clapham 1992; Clapham and Mayo 1987; Weinrich 1991, 1998; Weinrich and Kuhlberg 1991; Weinrich et al. 1997).

Mitochondrial DNA (mtDNA) as a maternal molecular marker has proven to be useful in identifying population structure and confirming consistent matrilineal recruitment of calves into the Gulf of Maine from a common breeding area (Baker et al. 1990; Clapham et al. 1993; Palsbøll et al. 1995). While population structure appears to be governed by maternal fidelity to a feeding area (Baker et al. 1990, 1994a; Palsbøll et al. 1995), the local distribution of whales throughout the Gulf of Maine

appears largely dependent on prey distribution and abundance (Payne et al. 1990; Weinrich et al. 1997) with minimal effects due to predators (Clapham 1996). It has been presumed that prey availability results in occasional disturbances rather than significant short-term changes in genetic variation or survivorship of animals within the Gulf of Maine.

Dramatic changes in frequency and age structure of individual maternal lineages across time have also been observed where substantial growth, redistribution, and local mass mortality have occurred over the last three decades (Baker et al. 1994b). The potential for combining molecular and ecological data to evaluate genetic consequences of natural events was demonstrated by Baker et al. (1994b). In that study, 8 of 10 victims of a natural mortality shared two of the less common maternal lineage haplotypes in this region, providing the first evidence for association between maternal lineage composition and demography.

In order to examine the potential interactive effects of population genetic structure with survival and reproductive success, we surveyed variations and correlations of life-history and demographic parameters with genetic structure using genealogical reconstruction of maternal lineages of humpback whales in the Gulf of Maine over a 16-year period (1979–1995). This approach was undertaken to determine if differential fecundity and reproductive success are correlated with the evolution of maternal genealogy or distinct matrilineal within this population. Pronounced variation in the distribution and frequency of maternal haplotypes within this population can arise from a relationship between maternal lineage variability and fecundity, raising questions about the process which potentially links the two and how genetic variation is interpreted for conservation and management of an endangered species.

Materials and Methods

Sighting Data and Capture-Recapture Histories

Extensive life-history data (spatial, temporal, social, reproductive, and behavioral) have been collected for the majority of the sampled individuals and their known relatives. Daily surveys were conducted (weather permitting) aboard commercial whale-watching boats and dedicated vessels primarily operating

from Gloucester, Massachusetts, from April 1 to November 1 in each year from 1979 to 1995. The study area included Stellwagen Bank and Jeffrey's Ledge, two underwater glacial deposits off the New England coastline (Figure 1). Humpback whales were photographically identified by pigment variation on the ventral surface of the tail flukes and scarring and shape of the dorsal fin (Katona and Whitehead 1981). Mother/offspring relationships were determined by accepted field techniques (Clapham and Mayo 1987, 1990; Weinrich et al. 1992). Further details on field methods can be found in Weinrich and Kuhlberg (1991) and Weinrich et al. (1991).

Skin samples for genetic analysis were collected using a biopsy darting procedure (Lambertsen 1987; Weinrich et al. 1991) from 159 individually identified free-ranging humpback whales in the southern Gulf of Maine between 1988 and 1993. Any other whales known to be part of the same matriline of a sampled whale through photographic identification studies (e.g., calves of a sampled female, a mother of a sampled calf, as well as the calf's half-siblings) were assigned the same mtDNA haplotype. As our photographic identification work includes a maximum of three generations within a matriline, we feel the assumption that there were no mutations in the mtDNA between direct descendants is justified for the study.

Molecular Studies

Total genomic DNA was isolated from the epidermal layer of tissue biopsies using standard proteinase K/phenol/chloroform procedures (Sambrook et al. 1989). A portion of the mtDNA control region, a noncoding region that is highly variable in many vertebrates (Vigilant et al. 1991), was amplified using polymerase chain reaction (PCR). Two oligonucleotide primers (Dlp 1.5 and Dlp 5) have been developed to amplify a 550 bp fragment within the mtDNA control region of humpback whales (Baker et al. 1993) and from other mammals (Kocher et al. 1989; Southern et al. 1988). This 550 bp region contains the majority of variable nucleotide positions in the mtDNA control region of the humpback whale (Baker and Medrano-Gonzalez, 2002; Baker et al. 1993). PCR products were purified using Bio 101 Gene Clean II (manual sequencing) or Centricon 100 columns (automated sequencing) according to the manufacturer's protocol.

Automated DNA sequencing of PCR products was done using cycle sequencing with fluorescently labeled dideoxy terminators and an Applied Biosystems 373A DNA sequencer. Determination or confirmation of gender (from field observations of presence or absence of a hemispherical lobe on the ventral surface posterior to the genital slit or by association with a calf) was accomplished using molecular methods. Gender was assigned by PCR amplification of a Y chromosome-specific sequence and amplification and subsequent *TaqI* digestion of homologous regions on the X and Y chromosomes (Palsbøll et al. 1992; Richard et al. 1994).

Data Analysis

DNA sequence variation patterns were characterized into existing haplotype definitions for this species according to the nomenclature of Baker et al. (1993). Sequences for this portion of the mtDNA control region were maintained for each individual in MacClade (version 3.01; Maddison and Maddison 1992). Alignment of DNA sequences from the mtDNA control region was performed using MALIGN (Wheeler and Gladstein 1992). The genealogy of Gulf of Maine mtDNA control region haplotypes was generated via parsimony using both the branch and bound and stepwise addition heuristic search options in PAUP (version 4.0; Swofford 1998) and rooted with homologous sequence from closely related intra- and interspecific outgroups (Baker et al. 1993). Strict consensus trees were constructed from all trees saved in the branch and bound search. Bootstrap values (Felsenstein 1985) were generated from 100 heuristic search replicates in PAUP (version 4.0; Swofford 1998). Bremer supports (Bremer 1994) were generated with AUTODECAY (Eriksson 1998) using five random-addition heuristic searches for each node.

Fecundity Among Maternal Lineages

Correlations among maternal lineage haplotypes and life history were tested using summary measures such as fecundity, annual survival, and recapture histories. Survival data and reproductive profiles were sorted by maternal lineage haplotype for known females over the 16-year study period. We calculated fecundity as the proportion of years in which a reproductively mature female was recorded with a calf during the study period. This enabled us to assess the

extent to which individual maternal lineages vary in reproductive success, while controlling for sampling effort and probability of recapture. Heterogeneity in fecundity was examined based on resolution in the genealogy at different levels (I–V) including two main lineages, individual lineages where sufficient data exist for statistical power, and other clades below the two primary clades where sufficient fecundity data and naturally resolved groupings in the genealogy exist (see Figure 3 for a graphical representation of these levels). These levels represent the various hierarchical nodes in the genealogy. The genealogical analysis offered independent justification to partition or pool rarer lineages based on levels of resolved nodes or branch support in order to test for correlations with life history. Testing for associations of fecundity with maternal lineage at different genealogical levels allowed us to consider the persistence of any detected relationship throughout the genealogy. Statistical significance of differences between reproductive success and lineage groupings (levels I–V) was determined by using a Kruskal-Wallis and a Fisher's exact test (two-tailed), owing to low (less than five) counts in certain cells of a contingency table analysis. Statistical testing of all individual maternal lineages (below level I) was not appropriate due to low numbers of females for certain lineages. To improve the power of the comparison, fecundity was classified into rates of less than 0.25 (low), 0.25–0.49 (medium), or 0.5–1.0 (high), and contrasted with the various levels throughout the genealogy with a Fisher's exact test (two-tailed).

Temporal trends in fecundity were examined throughout the 16-year (1979–1995) study period. Average fecundity was calculated among all females in aggregates of known reproductive age and regressed, using least squares linear regression, against year of observation. Trends were examined among females of the two main clades (BCD versus IJK, level V). Data were again too sparse to contrast individual maternal lineage haplotypes, but fecundity was calculated for each female and contrasted among four additional different maternal lineage combinations based on resolution in the genealogy and where sufficient data existed (level I: individual haplotypes C, D, I; level II: C, D1–D, I1–I2, K2–K3, and J–J1–J2–J3; level III: BCD, I1–I2, K1A–K2–K3–J–J1–J2–J3–J4; and level IV: C, D–D1, and I1–I2,

J-J1-J2-J3) for a finer resolution analysis (Figure 3). Multiple tests in this study were conducted in a nested fashion and were not repeated tests of the same hypothesis on exactly the same datasets. The latter is the typical situation where a correction for multiple comparisons is needed (Perneger 1998).

Because individual females were observed for variable durations (1–16 years), estimates of calving rates were potentially susceptible to sampling error based on the number of years a female was observed. For example, females with a higher number of resightings are likely to be observed with a calf more frequently than females with fewer resightings. In order to eliminate this bias, the probability of nonindependence between recapture and reproductive histories was investigated. Estimates of the coefficient of variation (CV) in reproductive rates became much more precise ($CV < 50\%$) after a threshold of 5 years of observation. For females observed for less than 5 years, coefficients of variation in their individual reproductive rates varied over time between 60% and 110%. In comparison, coefficients of variation varied between 18% and 38% for individuals observed over a longer period of time (i.e., 6–16 years). Therefore we included in the analysis only those 40 females (46% of a total of 87 individual females) observed for ≥ 6 years. This did not introduce further bias, because there was no difference in the proportion of individuals of different haplotypes and the number of years they were observed (likelihood ratio [LR] χ^2 ; $df = 36$; $\chi^2 = 40.64$; $P = .273$). There was also no significant relationship between the number of years a female was observed and her reproductive rate ($df = 86$; $r = 0.0355$; $P = .745$).

Reproductive Success and Annual Survival

Survival rates were based on resighting data of individually identified whales in the Gulf of Maine from 1979 through 1995. Because some individuals were not seen in some years, estimates of survival based on observations may confound survival with the likelihood of resighting (Clobert et al. 1987; Cooch et al. 1996). We therefore employed maximum likelihood techniques to obtain separate estimates of survival (ϕ) and resighting rates (p), using the software SURGE 4.2 (Cooch et al. 1996).

Capture-recapture models include three assumptions (1) ϕ and p are homogeneous within any subgroup, (2) marking is accurate and permanent, and (3) the resighting or death of any individual is independent of the fate of other individuals (Burnham et al. 1987). The recommended technique for testing assumption 1 is to use the goodness-of-fit tests (tests 2 and 3) of the program RELEASE (Burnham et al. 1987; Cooch et al. 1996). However, our data were too sparse for this analysis. Instead, we considered calves and adults separately, and used an overall goodness-of-fit chi-square test to compare observed frequencies with model predictions. For the second assumption above, individuals were identified by natural and permanent variations in ventral fluke pigmentation (Katona and Whitehead 1981); any variation in coloration of tail flukes after birth year did not dramatically affect annual sighting histories. Because whales travel in groups and occasionally form stable social affiliations, the probability of resighting individuals at any one time may not be independent (assumption 3 above; Weinrich 1991, 1998; Weinrich and Kuhlberg 1991). However, we considered resightings on an annual basis, so such dependence is likely to be reduced. Although the probability of resighting and possibility for calf mortality are linked to that of their mothers, the fact that we analyzed the two groups separately precludes any potential problems of nonindependence. Individuals were considered to be nonadults from birth until their fifth year of life (Clapham and Mayo 1990) or until they produced a calf.

Model selection followed the step-down methodology suggested by Lebreton et al. (1992), by modeling resighting probabilities first to retain as much power as possible for tests of survival parameters. We assessed the effects of year (y) and haplotype (h) on resighting rates to test for genetically based variation as well as to account for potential variation in observer effort from year to year. We also assessed the effects of haplotype (h), clade level V (c), year (y), and age (a) on survival for female calves. Age effects on resighting and survival were not considered for adults because we had no a priori criteria for delimiting meaningful age classes. The effects of year (and age) were modeled first to maintain power for tests by maternal lineage haplotype. The model structure

with the lowest Akaike Information Criterion (AIC) was selected as the most likely model (Lebreton et al. 1992). Formal tests of specific effects used LR tests between nested models. Model selection for calves used modified full capture histories that were coded as zero after 5 years (termed dummy variables). Subsequent analyses ignored effects based on ages greater than 5 years.

Projections of Genetic Variation

Fecundity and survivorship rates were used to construct a simple deterministic model to project likely population trajectories for individual haplotypes within the Gulf of Maine population. The model considered females only and was based on postbreeding censuses, as the actual data were collected this way. Two age classes, calf and adult, that differed in survival rates and fecundity were used. The model incorporated the fecundity and survival values determined for each haplotype from the analyses described above.

The model rests on six assumptions: (1) males do not affect the survival and reproduction of females, (2) rates of survival and fecundity are constant among individuals within an age class and among years, (3) breeding occurs in a single birth pulse, (4) the sex ratio of offspring is 50:50 and does not vary among haplotypes, (5) the population is near a stable age distribution, and (6) parameters are not density dependent. The second assumption in particular is unlikely to be true, as both fecundity and survival can vary among females and across years (see Results). Limited evidence also shows that maternal condition among some females may affect offspring sex ratio (Wiley and Clapham 1993). However, slight violations of these assumptions are unlikely to affect the qualitative results of the model (Noon and Sauer 1992). Populations were projected for 75 years from the present, beginning with an initial population of 100 individuals distributed in a stable age distribution. Numbers of individuals within each maternal lineage in the starting population approximated the overall proportion of adults known for each maternal lineage recorded during the study period.

Results

Genealogy

Maternal lineage haplotypes were determined for a total of 323 animals, either by

direct sequencing ($n = 159$) or by assignment based on known relationships along matriline ($n = 164$), including recent births and deceased individuals. A total of 23 variable and informative nucleotide sites defined 19 unique haplotypes within the population of known and sampled individuals from the Gulf of Maine (Figure 2). Haplotypes were consistent in type and number with Baker et al. (1993, 1994a) and Palsbøll et al. (1995). Direct sequencing of a larger portion of the mtDNA control region, as well as a more representative sample size presented here, reveals greater haplotype diversity than observed in earlier studies (Baker and Medrano-Gonzalez 2002) (Figure 2). Fifteen additional sites were found to be polymorphic with respect to a North Pacific humpback whale and/or the homologous fin whale sequence. Whales that possess the same haplotype have been grouped together by letter and numerical designation. Haplotypes are labeled so they may be connected by one or more mutational steps to the next haplotype.

The strict consensus genealogy of haplotypes is shown in Figure 3. Stepwise addition heuristic or branch and bound searches of haplotypes resulted in 15 equally parsimonious trees, each containing 37 steps (confidence interval = .622; RI = .860). Bootstrap values and decay indices provided support for the two principal clades containing BCD and IJK lineages. The topology for the mtDNA control region genealogy shown in Figure 3 is consistent with that of Baker et al. (1994a). The present and previous studies (Baker et al. 1994a; Palsbøll et al. 1995) do not test whether any of the maternal lineages are correlated with specific geographic areas within the Gulf of Maine.

Relationships of Fecundity With Genealogy

There was no significant difference in mean fecundity (number of calves per female accounting for heterogeneity of recapture probability over the study period) between the females found in the two clades (level V; Kruskal-Wallis test, $\chi^2 = 0.028$; $df = 1$; $P = .867$). The distribution of fecundity across low (0–0.25), medium (0.25–0.5), and high (greater than 0.5) categories also did not differ among the two principal clades (level V; Fisher's exact test, $P = .133$).

We tested individual maternal lineages and other clades for differential fecundity

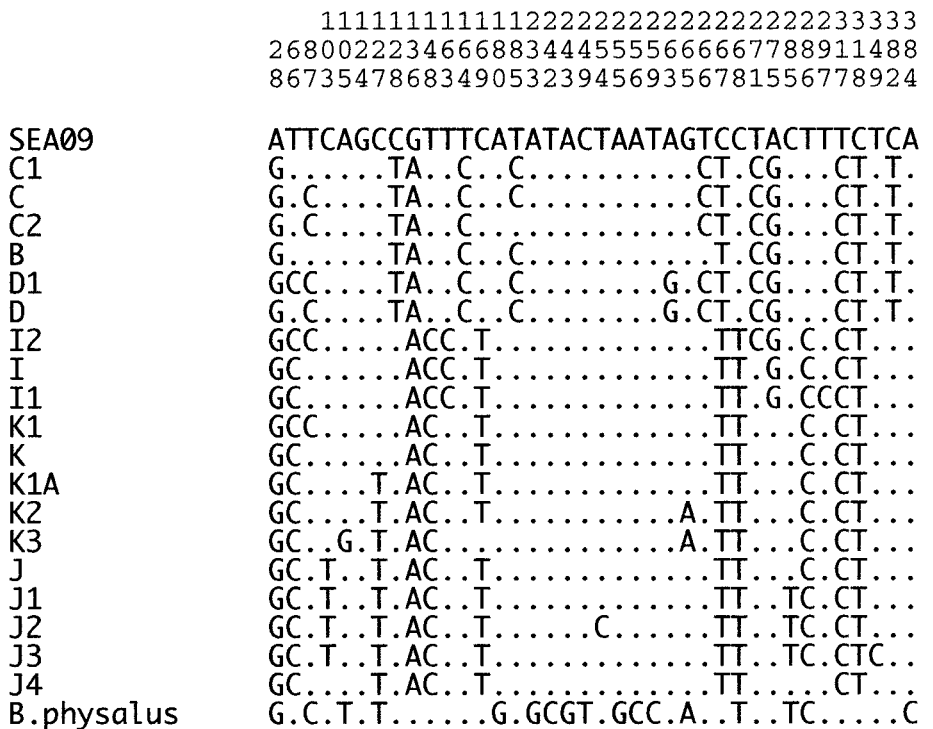


Figure 2. Haplotype designations for humpback whales in the Gulf of Maine. Sequences are aligned to both the homologous sequences for a North Pacific humpback whale, SEA 09, and the fin whale (*Balenoptera physalus*). This figure shows only the variable sites spanning the 550 bp amplified region of the mtDNA control region; other invariable sites are not included. Dots indicate matches with the reference sequence, SEA 09. The numbers above indicate the nucleotide position of the polymorphic sites in the control region *sensu* Baker et al. (1993).

over the study period. Based on fecundity, the proportion of individuals varied among the groupings of maternal lineages. There were no significant differences found among level I lineages (Fisher's exact test = 0.630) or level IV lineages within the BCD clade (Fisher's exact test = 0.300). Significant differences in fecundity were detected among females at level II (Fisher's exact test = 0.052), level III (0.019), and level IV lineages within the IJK clade (Fisher's exact test = 0.048).

Examination of level II lineage groupings revealed that females with the highest fecundity (probability of being observed with a calf > 0.5) were present in maternal lineage C (33%) and clade I-I1-I2 (24%). Clades D1-D, J-J1-J2-J3, and K2-K3 had no females that would be characterized with high reproductive rates. Individual females with the lowest fecundity (probability of being observed with a calf < 0.25) were most frequent in the K2-K3 (50%) and J-J1-J2-J3 (60%) clades, with lineage C and clade D1-D having no females with low reproductive rates. Thus fecundity could be characterized as generally high in lineage C and clade I-

I1-I2, intermediate in clade D1-D, and low in the K2-K3 and J-J1-J2-J3 clades.

Temporal Relationship of Reproductive Success and Genealogy

A significant difference in fecundity by year was detected from 1979 to 1995 for 887 sighting records of reproductive-age females (LR $\chi^2 = 28.01$; $df = 16$; $P = .032$). When a genetic component is included to test reproductive success by year for the two clades (BCD versus IJK), a strong and increasing temporal trend was observed in fecundity in reproducing females of the IJK clade ($F = 23.9$; $df = 1$; $P = .002$), growing steadily by a product of 1.022 each year (Figure 4). No trend was observed among females of the BCD clade ($F = 0.372$; $df = 1$; $P = .553$).

Patterns of Survival and Resighting History

For calf survival, the model with the best fit (as defined by the lowest AIC value) occurred where resighting probabilities for calves varied with age (Table 1; model 7). There was no significant effect of year by haplotype interaction on resighting or any effects associated with maternal

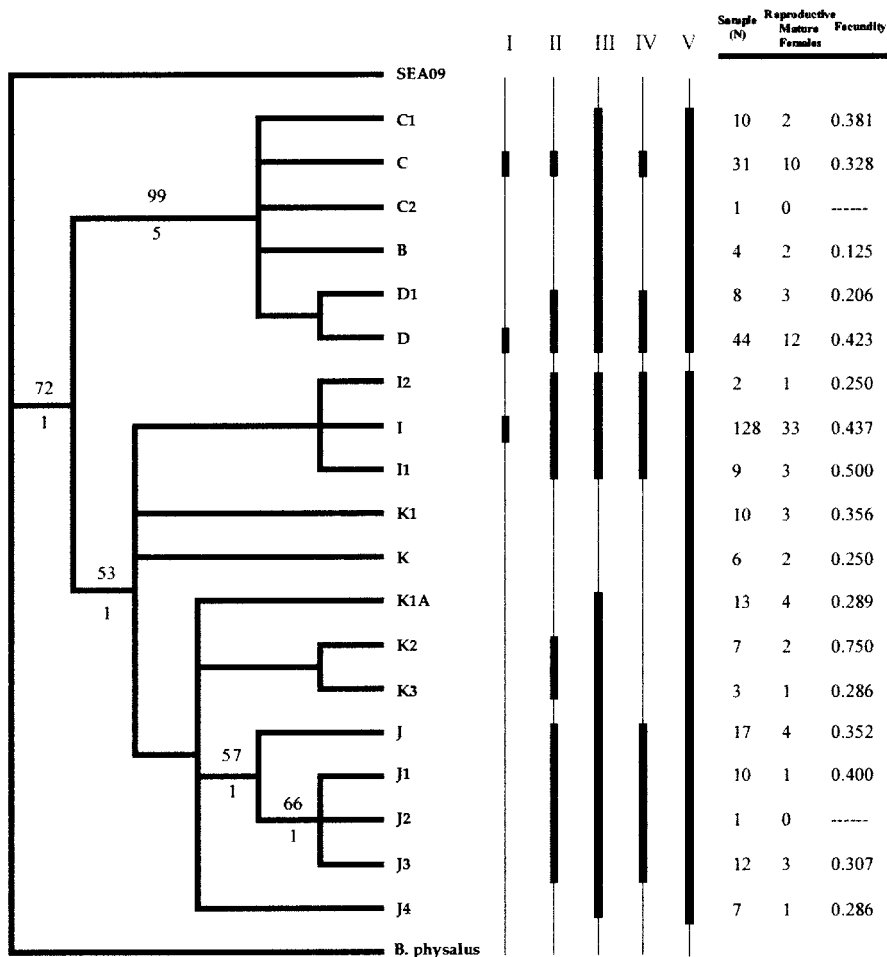


Figure 3. Genealogy of 19 unique haplotypes from Gulf of Maine humpback whales. This figure shows the consensus tree constructed via the parsimony method from a branch and bound search in PAUP version 4.0 using 100 random addition replicates (number of trees = 15, length of shortest tree = 37, CI = 0.622, RI = .860). Clade stability was evaluated using both bootstrap analysis and Bremer support analysis (decay indices). Bootstrap values (≥ 50) are shown above the branches. Bremer supports are shown below the branch. The set of bars to the right of the genealogy (I–V) illustrates the stepwise process of aggregating lineages based on resolution in the genealogy to test for differences in fecundity (i.e., the hierarchical levels in the genealogy which are used to test for such associations). Sample size (N) and reproductively mature females per haplotype (see text) are shown. Fecundity is summarized as a mean for each haplotype by the number of calves per sexually mature female normalized for total number of years sighted.

lineage on survival. Individuals were less likely to be seen during their first post-weaning year than between the ages of 2–5 years (Table 2). Calf survival varied among years, but was not significantly affected by age among the lineages analyzed (Table 1). The best model provided a good fit to the observed resighting data (goodness-of-fit test, $\chi^2 = 2.28$; $df = 16$; $P = .999$). Annual survival rate averaged 0.702 over 16 years, and ranged from 0.142 to 1.000 (Table 2). The lowest calf survival estimates occurred between 1993 and 1995.

The best-fitting model for adult female survival indicated that resighting varied significantly among years and survival was constant (Table 3, model 7). A model incorporating annual variation in resighting

rates provided a significantly better fit to the data than otherwise identical models with haplotype-dependent resighting (i.e., encountering certain lineages preferentially to others) or a constant rate of resighting (Table 3, models 1 and 2 versus 3). Models including variation in survival based on year, haplotype, and clade also failed to provide a significantly better fit than did a simpler model with a constant, common survival rate (Table 3, models 4, 5, and 6 versus 7). The estimated annual survival of adult female whales in the Gulf of Maine was high: 0.96. Based on the most likely model, survival and resighting rates for adult whales did not differ significantly between different haplotypes or among years (Table 4). The

best model for adult rates provided a good fit to the data based on a goodness-of-fit test ($\chi^2 = 5.27$; $df = 16$; $P = .994$).

Population Projection and Genetic Variation

The projections for Gulf of Maine humpback whales, based on the empirically determined survival, resighting, and reproductive rates suggest that the population will increase over the next 75 years. However, the fate of individual haplotypes varied due to the differential fecundity among haplotypes (Figure 5). The B lineage disappeared entirely from the population. The C, D1, J, J1, J3, J4, K, and K1A lineages persisted, but declined. In contrast, the D, I, I1, K2, and K3 lineages increased with time. After 75 years, the proportion of the female population comprising the BCD clade declined 11%, from 33% to 22% of the population, while the proportion of the population comprising the IJK clade increased 30%.

Discussion

For the most part, studies involving life history and genetic structure, particularly in cetaceans, have been conducted separately from one another. This study represents a detailed evaluation of the correlation of lifetime reproductive success with patterns of genetic variation in whales. Such associations at this specific level are typically detected in the context of controlled breeding experiments of organisms usually with shorter generation times or among isolated human populations with detailed demographic records (Austerlitz and Heyer 1998; Roff 1992). These experiments often measure the influence of selected quantitative traits on life history (Leroi et al. 1994a,b; Roff and Mousseau 1987). In related work, correlations between heritability of reproductive success among different sexes have also shown a manifestation of heterogeneity in phenotypic differences within a population (Sinervio and Zamudio 2001). Previous studies among whales have drawn links between life history and genetic diversity, but these have focused on the influence of migratory behavior over an entire population rather than on individual life-history traits (Baker et al. 1990; Palsbøll et al. 1995). Here we examine whether an association of fecundity occurred within

natural groupings of maternal lineages throughout the genealogy. These associations may be attributed to reproductive success having some underlying correlation with genetic or cultural maternal heritability, environment, or interaction between the two factors. Given neutral theory, direct selective effects associated with this mitochondrial marker are unlikely, but cannot be fully excluded. The possibility of genetic imprinting or maternal effects (noncultural) that produce differences in fecundity between the clades cannot be excluded as well. While a genetically or culturally inherited mechanism for differential reproductive success is not understood, maternal lineage variation and life-history characteristics appear to be correlated to varying degrees of evolutionary and ecological scales.

Association of Fecundity With Genealogy

Variation in the mtDNA control region allows for the designation of individuals as members of a particular maternal lineage. These maternal lineages are used to partition variation in life-history parameters. Furthermore, the genealogy of mtDNA lineages is used to guide the appropriate hierarchical levels of analysis for testing higher-level correlations with life history. Based on the genetic results and availability of demographic data, we felt that there were five major levels suitable for examination based on hierarchical levels within the genealogy. While no significant trends in fecundity were found at the lowest and highest levels (levels I and V), comparisons of fecundity based on resolved clades in the genealogy revealed that statistically sig-

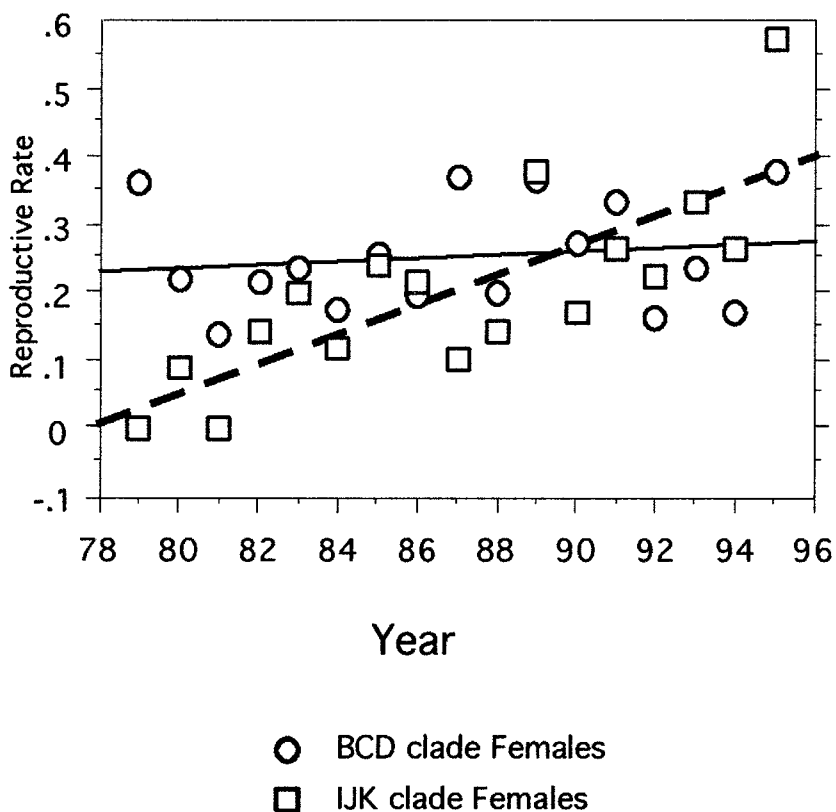


Figure 4. Regression of reproductive success among the two main clades by year. Females of the IJK clade show a significant increase in fecundity ($R^2_{IJK} = 0.615$) over the 16-year period (dashed line), while fecundity remains relatively constant ($R^2_{BCD} = 0.024$) among females of the BCD maternal lineages (solid line).

nificant differences do exist between natural groupings of these maternal lineages (levels II, III, and part of IV).

At the level of the two strongly supported clades (level V), a regression of fecundity by year reveals that the IJK clade shows a highly significant upward trend over time from 1979 to 1995, while the lineages within the BCD clade remain constant (Figure 4). Because fecundity of the IJK clade was low relative to the BCD

clade early in the study and high late in the study, comparisons of mean differences and distributions of fecundity values were not significantly different between clades. We would, however, expect them to become significant over time should the clade-related trends we observed in fecundity continue as shown in Figure 4. These results contradict a lack of significant findings in yearly reproductive success by Barlow and

Table 1. Resighting and survival of humpback whale calves in the Gulf of Maine

Model	NP	DEV	AIC	LR test between models	Source of variation tested by LR
Modeling resighting rates (p)					
(1) $\phi_y \times a, p_y \times a$	64	289.24	417.24	(1) vs. (5): $\chi^2_{31} = 32.07, P = .41$	NS effect of year \times age interaction on p
(2) $\phi_y \times a, p_y$	48	304.10	400.10	(2) vs. (5): $\chi^2_{15} = 17.21, P = .31$	No significant effect of year on p
(3) $\phi_y \times a, p_a$	35	312.60	382.60	(3) vs. (5): $\chi^2_2 = 8.71, P = .01$	Significant effect of age on p
(4) $\phi_y \times a, p_h$	39	310.22	388.22	(4) vs. (5): $\chi^2_6 = 11.09, P = .09$	No significant effect of haplotype on p
(5) $\phi_y \times a, p$	33	321.31	387.31		
Modeling survival rates (ϕ)					
(6) $\phi_y \times h, p_a$	99	273.75	471.75	(6) vs. (11): $\chi^2_{95} = 103.45, P = .26$	NS effect of year \times haplotype interaction on ϕ
(7) ϕ_y, p_a	19	336.30	354.30	(7) vs. (11): $\chi^2_{15} = 40.90, P < .0010$	Significant effect of year on ϕ
(8) ϕ_a, p_a	6	376.51	388.51	(8) vs. (11): $\chi^2_2 = 0.69, P = .71$	No significant effect of age on ϕ
(9) ϕ_h, p_a	9	376.99	394.99	(9) vs. (11): $\chi^2_5 = 0.21, P = .99$	No significant effect of haplotype on ϕ
(10) ϕ_c, p_a	5	377.06	387.06	(10) vs. (11): $\chi^2_1 = 0.14, P = .71$	No significant effect of clade on ϕ
(11) ϕ, p_a	4	377.20	385.20		

Models used to test for effects of age (a), year (y), haplotype (h), and clade (c) on rates of resighting (p) and survival (ϕ) of female humpback whale calves. Age effects were based on two age classes: 1 year old and 2–5 years old. We present the number of estimable parameters (NP), deviance (DEV), and Akaike Information Criterion (AIC) for each model, and likelihood ratio (LR) tests for specific effects between models. **Bold** type indicates the best model based on minimum AIC value. NS = no significant.

Table 2. Annual survival of humpback whale calves

Parameter	Estimate	95% CI	SD
Survival			
1979–1980	1.0000	1.0000, 0.0000	0.0000
1980–1981	0.8120	0.4359, 0.9602	0.1340
1981–1982	1.0000	0.0000, 1.0000	0.0000
1982–1983	0.7177	0.4667, 0.8807	0.1102
1983–1984	0.8328	0.6118, 0.9403	0.0818
1984–1985	0.9773	0.1415, 0.9999	0.0630
1985–1986	0.8052	0.6128, 0.9153	0.0768
1986–1987	0.6369	0.4577, 0.7847	0.0863
1987–1988	0.5987	0.4250, 0.7507	0.0861
1988–1989	0.7369	0.5281, 0.8751	0.0908
1989–1990	0.8082	0.6286, 0.9129	0.0721
1990–1991	0.7961	0.6279, 0.9003	0.0695
1991–1992	0.6505	0.4802, 0.7895	0.0813
1992–1993	0.4996	0.3347, 0.6645	0.0874
1993–1994	0.1712	0.0731, 0.3510	0.0697
1994–1995	0.1423	0.0220, 0.5499	0.1243
1995–1996	0.7516	0.0069, 0.9992	0.5792
Mean	0.7022		
Resighting			
1 year olds	0.6264	0.5304, 0.7134	0.0472
2–5 year olds	0.8256	0.7470, 0.8836	0.0347

Parameter estimates for calf survival and resighting rates based on the model with the lowest AIC value (Table 1, model 7).

Clapham (1997) based on apparent birth rate. Such trends in life-history characteristics become evident when consideration is given to correlations with genetic structure or other relevant variables.

Differences in reproductive success among individuals are a potential cause for change in gene frequencies over a short time period in humans (Austerlitz and Heyer 1998). This process appears to be similar to fecundity differences between reproducing females and their female offspring in Gulf of Maine humpback whales. Similar explanations have been invoked for explaining unequal distribution of mitochondrial haplotypes in a human population, as well as the increase in frequency of disease genes from lower initial frequencies (Murray-McIntosh et al. 1998; Risch et al. 1995). Scribner et al. (1993) suggested that a correlation between reproductive suc-

cess and genetic variation in a bog turtle may cause temporal changes in allele frequency. However, no clear trend in allele frequency over time was detected. Variation in reproductive success among a finite number of adults resulted in heterogeneity of maternal lineages of the Pacific oyster, which could not be attributed to geographic differences in spawning populations (Li and Hedgecock 1998). Similarly our results, showing an association between reproductive success and certain maternal lineages, cannot be attributed to geographic non-independence. This is demonstrated by a lack of significant findings of haplotype-dependent resighting models and a result of genealogical structure for our dataset consistent with those from other studies of this population (Baker et al. 1993; Palsbøll et al. 1995).

Variation in fecundity along maternal lineages has profound consequences for the frequency and distribution of maternal haplotypes within the Gulf of Maine, particularly when such effects are associated with one component of the population (Weir and Cockerham 1984). Barlow and Clapham (1997) reported an asymptotic rate of increase of 1.065 for this population based on estimated birth interval, first-birth probability, and survival rates. However, any rate of increase appears to be partitioned along maternal lineages, with one segment of the population increasing (JK) due to lineages with higher fecundity and the other remaining relatively constant (BCD) (Figure 4).

Population modeling shows that a redistribution of maternal lineages for this population is expected based on current parameters and the association of life history with genealogy. After 75 years, assuming current rates and trends, there is a decrease in maternal lineage frequencies, with the BCD clade showing re-

duced frequency in the population. Furthermore, several lineages (maternal lineages predominantly from the IJK clade) increase comparatively within the entire population because of the increased reproductive success experienced among females for some of these matrilineages. The projected shift of haplotype frequencies and potential reduction in genetic diversity in this population is only exposed by examination of differences in reproductive success among maternal lineages. The projection of lineage persistence and extinction is based on current rates and trends detected in our analyses. The modeling is not meant to be predictive, but is used to demonstrate how lineage viability might vary over time. Consideration of temporal changes in environmental conditions, stochastic effects, or other spurious events could obviously change maternal lineage projections.

Evaluating Population Effects Based on Fecundity/Genealogy Associations

Recent hypotheses suggest that a selective advantage associated with matrilineages, potentially at another locus in disequilibrium with certain maternal lineages, will drastically reduce a population's genetic variation (Whitehead 1998). Whitehead invoked differential fitness among matrilineages caused by matrilineally transmitted cultural traits to explain a reduction in genetic diversity. Our results directly demonstrate differential reproductive success among matrilineages, and empirically show its effects on mtDNA lineages in the populations. Furthermore, the presence of high diversity in humpback whales worldwide and at the oceanic level suggests that other mechanisms, such as mutational processes or large-scale migratory shifts due to climate change, must be considered to account for maintenance of

Table 3. Resighting and survival of reproductively mature female humpback whales in the Gulf of Maine

Model	NP	DEV	AIC	LR test between models	Source of variation tested by LR
Modeling resighting rates (p)					
(1) $\phi_y \times h, p_y$	112	605.38	829.38		
(2) $\phi_y \times h, p_h$	102	629.61	833.61	(2) vs. (3): $\chi^2_{15} = 10.10, P = .07$	No significant effect of haplotype on p
(3) $\phi_y \times h, p$	97	639.71	833.71	(1) vs. (3): $\chi^2_{15} = 34.33, P = .003$	Significant effect of year on p
Modeling survival rates (ϕ)					
(4) ϕ_y, p_y	32	646.46	710.46	(4) vs. (7): $\chi^2_{15} = 21.40, P = .12$	No significant effect of year on ϕ
(5) ϕ_h, p_y	22	663.53	707.53	(5) vs. (7): $\chi^2_{15} = 4.33, P = .50$	No significant effect of haplotype on ϕ
(6) ϕ_c, p_y	18	667.86	703.86	(6) vs. (7): $\chi^2_{15} < 0.01, P > .99$	No significant effect of clade on ϕ
(7) ϕ, p_y	17	667.86	701.86		

Models used to test for effects of year (y), haplotype (h), and clade (c) on rates of resighting (p) and survival (ϕ) of adult female humpback whales. We present the number of estimable parameters (NP), deviance (DEV), and Akaike Information Criterion (AIC) for each model, and likelihood ratio (LR) tests for specific effects between models. **Bold** type indicates the best model based on minimum AIC value.

Table 4. Annual survival of mature female humpback whales

Parameter	Estimate	95% CI	SD
Survival	0.9638	0.9463, 0.9758	0.0074
Resighting			
1979–1980	0.7500	0.2970, 0.9551	0.1875
1980–1981	0.8889	0.5293, 0.9827	0.0989
1981–1982	0.9000	0.5577, 0.9847	0.0902
1982–1983	0.8000	0.5163, 0.9375	0.1078
1983–1984	0.9656	0.7959, 0.9951	0.0335
1984–1985	0.8649	0.7134, 0.9427	0.0563
1985–1986	0.8537	0.7094, 0.9331	0.0555
1986–1987	0.8228	0.6685, 0.9144	0.0620
1987–1988	0.8887	0.7563, 0.9536	0.0477
1988–1989	0.7805	0.6451, 0.8743	0.0586
1989–1990	0.9597	0.8501, 0.9901	0.0283
1990–1991	0.8577	0.7336, 0.9295	0.0488
1991–1992	0.8937	0.7659, 0.9558	0.0458
1992–1993	0.6630	0.5244, 0.7782	0.0660
1993–1994	0.6028	0.4566, 0.7327	0.0722
1994–1995	0.5668	0.4180, 0.7327	0.0751

Parameter estimates for adult whale survival and resighting rates based on the model with the lowest AIC value (Table 3, model 7).

diversity despite changes predicted in this article based on variable reproductive success.

In one of the critiques of Whitehead's (1998) theory of selective heritability, Tiedemann and Milinkovitch (1999) have shown that sperm whales exhibit stochastic differences in reproduction through time and space, which increases the variance in reproductive success among haplotype matriline. The likelihood of such a phenomenon seemed plausible based on modeling (Whitehead 1999), but variability of fecundity between matriline had yet to be empirically demonstrated prior to the present study.

The effects of stochastic differences or environmental factors along matriline of humpback whales in this study are an equally viable alternative, but are difficult hypotheses to test. In the absence of highly significant geographic structuring of matriline of humpback whales on the feeding grounds, these stochastic events could be subtle environmental shifts that affect fecundity (discussed further below) or other nonspatial factors, such as disease, reflected by significant correlations between fecundity and matriline (Whitehead 1999). Furthermore, any stochastic influence (spatial or nonspatial) that causes variance in fecundity along matriline could occur along the migratory path or on the wintering grounds of this species.

With the potential for temporal or spatial heterogeneity, it is impossible to distinguish whether selection (genetics), stochasticity (environment), or an interaction between the two has caused heterogeneity in fecundity among mater-

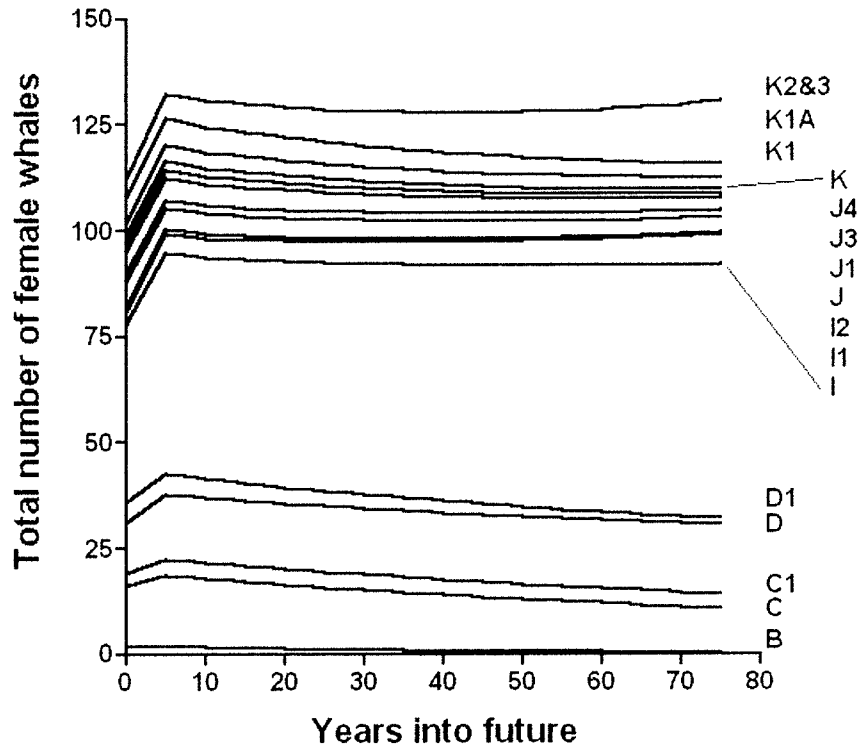


Figure 5. Projection of maternal lineage viability among Gulf of Maine humpback whales. The expected proportions of maternal lineages among humpback whales in the Gulf of Maine are projected out to 75 years using fecundity and survival rates determined from the analysis. The model uses an initial population size of 100 individuals in a stable age distribution and in the haplotype frequency proportions detected in the present study.

nal lineages of humpback whales. Direct genetic heritability of fecundity and its effects on N_e have been suggested in other species (Nei and Murata 1966), but is considered to be low (Charlesworth 1994; Nunney 1995; Roff and Mousseau 1987). The results of the present study suggest that a 2.2% change in fecundity per year could account for the differences in maternal lineage haplotype frequency. Based on our results over the 16-year period and projected trends, the predicted effects on amount and type of maternal lineage diversity persisting into future generations (shown in Figure 5) would be consistent with effects shown or discussed in Austerlitz and Heyer (1998) and Whitehead (1998).

Differences in cooperative feeding in areas of high prey, migratory behavior, disease, and environmental disturbances may have resulted in variance in fecundity among the different genealogical levels. The beneficial or detrimental effects conveyed from such occurrences may be due to spatial grouping of maternal relatives. Some form of genetic heritability coupled with parallel cultural inheritance of potentially adaptive feeding styles (Weinrich et al. 1992) and putative habitat stratification of different

age classes (Weinrich et al. 1997) could provide resource benefits among lineages that would be reflected in reproductive success. On larger geographical scales, previous studies have suggested female fidelity to feeding grounds. Differential conditions in certain areas within or between feeding grounds could have an effect on the differential reproductive success of matriline. Over a period of two decades, these possible ecological determinants or stochastic processes may account for the association of reproductive differences with maternal lineages among humpback whales in the Gulf of Maine.

Patterns of Resighting and Survival

There was no significant finding of heterogeneity in survival probabilities along maternal lineages for either adults or calves during the study period. While adult and calf survival do not appear to be influenced by maternal lineage structure, the overall trends in resighting and survival are similar to those estimated based on a model of interbirth intervals (Barlow and Clapham 1997). Any effects attributed to maternal lineage haplotype or clade do not appear to influence yearly resighting or survival. Potential

effects of haplotype or clade on within-year resighting probability are beyond the scope of the present study.

However, significant variation in terms of yearly effects on sighting and survival probabilities for calves and yearly effects on sighting probabilities for adults implies that other factors beyond maternal lineage influence the distribution and abundance of whales in this region. Shifts in prey abundance and location between 1992 and 1995 in the Gulf of Maine resulted in a temporary abandonment of Stellwagen Bank by humpback whales (Weinrich et al. 1997), as indicated by a decline in adult resightings in 1992–93 through 1994–95. Calf survival also declined moderately in 1992–93 and precipitously for the 2 years (1993–95) following the first detectable shifts in abundance and adult sightings. According to these models, calf survival between 1993 and 1995 dropped to a 16-year low mean value of 0.1568. However, it is difficult to discriminate between this hypothesis and preferential habitat use of Jeffrey's Ledge by adults rather than juveniles, thus confounding calf survival with sampling bias of calves (Weinrich 1998). In addition, lower probabilities for photographic identification of calves could affect interpretation of calf survival. One possible biological explanation is that prey type and distribution may have more of a significant effect on calf survival and adult resighting than simply causing a temporary relocation to another feeding area. The inability of adult females to meet energy requirements in this region could have resulted in the decline of resighting probability and possibly had even greater consequences for providing sufficient nutrition for offspring.

Environmental disturbances, such as documented shifts in prey abundance, may have also effected other trends in survival and resighting. The mortality event that occurred in 1987, in addition to having a nonrandom distribution among maternal lineages (Baker et al. 1994b), preceded the lowest apparent pregnancy rate for females the following year (Barlow and Clapham 1997). These types of environmental shifts may appear to occur more frequently than Barlow and Clapham (1997) suggest and can have complex ramifications for resighting rates and calf survival. Such effects are only identifiable when age class and year are considered as independent components of humpback whale survival.

Our results indicate that genetic variation can be correlated with ecological shifts, resighting rates, annual survival, and reproductive success. Crude changes in survival often lead to a search for underlying causative effects. Use of additional parameters in estimation models beyond yearly variation or age class may help increase accuracy and reduce sources of uncertainty in survival estimates. More structured models that include a genetic component can further illuminate trends in survival and growth rate, particularly in species whose social structure and organization are highly correlated with genealogy or phylogeny.

The approach described here can be applied to account for differences in reproductive success among a diverse group of long-lived species (Clutton-Brock 1988; Cooke and Rockwell 1988; Hamilton et al. 1998; LeBoeuf and Reiter 1988; Morin et al. 1994; Packer et al. 1988). The results have implications for conservation efforts by demonstrating that subtle differences in life-history traits among individuals can alter certain aspects of population genetic viability. The heterogeneity of life-history traits associated with population structure (i.e., maternal lineages) indicates that detecting trends in survival and resighting, as well as evaluating minimum and effective population sizes, requires in-depth analyses. In many instances where trends in survivorship, fecundity, and resighting are witnessed, the demographic models used to evaluate such trends have not considered the effects of genetic structure (i.e., Caswell et al. 1999). As demonstrated by our results, the evaluation of life-history parameters in the context of relevant genetic data offers a unique way to evaluate groups or cohorts of animals that share particular traits or may be exposed to different levels and types of stochastic effects. The ability to detect significant trends by evaluating and incorporating genetic and demographic data can provide enlightening information for conservation and management purposes. This is particularly important in evaluating the source of variation for observed and detected trends in the absence of obvious answers.

References

Austerlitz F and Heyer E, 1998. Social transmission of reproductive behavior increases frequency of inherited disorders in a young-expanding population. *Proc Natl Acad Sci USA* 95:15140–15144.

Baker CS and Medrano-Gonzalez L, 2002. World-wide distribution and diversity of humpback whale mitochondrial DNA lineages. In: *Molecular studies of marine mammals* (Pfeiffer C, ed). Melbourne: Krieger & Co.

Baker CS, Palumbi SR, Lambertsen RH, Weinrich MT, Calambokidis J, and O'Brien SJ, 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344:238–240.

Baker CS, Perry A, Bannister JL, Abernathy RB, Weinrich MT, Abernathy B, Calambokidis J, Lien J, Lambertsen R, Urban J, Clapham P, Ailing A, O'Brien SJ, and Palumbi SR, 1993. Abundant mitochondrial DNA variation and world-wide population structure in humpback whales. *Proc Natl Acad Sci USA* 90:8239–8243.

Baker CS, Slade RW, Bannister JL, Abernathy RB, Weinrich MT, Lien J, Urban J, Corkeron P, Calambokidis J, Vasquez O, and Palumbi SR, 1994a. Hierarchical structure of mitochondrial DNA gene flow among humpback whales. *Megaptera novaeangliae*, world-wide. *Mol Ecol* 3:313–327.

Baker CS, Weinrich MT, Early G, and Palumbi SR, 1994b. Genetic impact of an unusual group mortality among humpback whales. *J Hered* 85:52–54.

Barlow J and Clapham PJ, 1997. A new birth interval approach to estimating demographic parameters of humpback whales. *Ecology* 78:535–546.

Bremer K, 1994. Branch support and tree stability. *Cladistics* 10:295–304.

Burnham KP, Anderson GC, White C, Brownie C, and Pollock KH, 1987. Design and analysis methods for fish survival experiments based on release-recapture. *Am Fish Soc Monogr* 5.

Caswell H, Fujiwara M, and Brault S, 1999. Declining survival probability and its implications for the North Atlantic right whale. *Proc Natl Acad Sci USA* 96:3308–3313.

Charlesworth B, 1994. *Evolution in age-structured populations*. Cambridge: Cambridge University Press.

Clapham PJ, 1992. Age at attainment of sexual maturity in humpback whales. *Can J Zool* 70:1470–1472.

Clapham PJ, 1996. The social and reproductive biology of humpback whales: an ecological perspective. *Mamm Rev* 26:27–49.

Clapham PJ, Baraff LS, Carlson CA, Christian MA, Mattila DK, Mayo CA, Murphy MA, and Pittman S, 1993. Seasonal occurrence and annual return of humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Can J Zool* 71:440–443.

Clapham PJ and Mayo CA, 1987. Reproduction and recruitment in individually identified humpback whales (*Megaptera novaeangliae*) observed in Massachusetts Bay: 1979–1985. *Can J Zool* 65:2853–2863.

Clapham PJ and Mayo CA, 1990. Reproduction of humpback whales (*Megaptera novaeangliae*) observed in the Gulf of Maine. *Rep Int Whaling Comm Special Issue* 12:171–175.

Clobert J, Lebreton J-D, and Allain D, 1987. A general approach to survival rate estimation by recaptures or resightings of marked birds. *Ardea* 75:133–142.

Clutton-Brock TH, 1988. *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press.

Clutton-Brock TH, 1989. Mammalian mating systems. *Proc R Soc Lond B* 236:339–372.

Cooch EG, Pradel R, and Nur N, 1996. A practical guide to mark-recapture analysis using SURGE. Montpellier, France: Centre d'Ecologie Fonctionnelle et Evolutive—CNRS.

Cooke F and Rockwell RF, 1988. Reproductive success in a lesser snow goose population. In: *Reproductive success: studies of individual variation*

- in contrasting breeding systems (Clutton-Brock TH, ed). Chicago: University of Chicago Press; 403–418.
- Eriksson T, 1998. AutoDecay version 4.0 (program distributed by the author). Stockholm: Stockholm University.
- Felsenstein J, 1985. Confidence limits on phylogenies: an approach using the bootstrap. *Evolution* 39: 783–791.
- Hamilton PK, Knowlton AR, Marx MK, and Kraus SD, 1998. Age structure and longevity in North Atlantic right whales, *Eubalaena glacialis*, and their relation to reproduction. *Mar Ecol Prog Ser* 171:285–292.
- Hewison AJM, 1997. Evidence for a genetic component of female fecundity in British roe deer from studies of cranial morphometrics. *Funct Ecol* 11: 508–517.
- Katona SK and Beard JA, 1990. Population size, migration and substock structure of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. *Rep Int Whaling Commn Special Issue* 12:295–306.
- Katona SK and Whitehead HP, 1981. Identifying humpback whales using their natural markings. *Polar Record* 20:439–444.
- Kocher TD, Thomas WK, Meyer A, Edwards SV, Paabo S, Villablanca FX, and Wilson AC, 1989. Dynamics of mitochondrial DNA evolution in animals: amplification and sequencing with conserved primers. *Proc Natl Acad Sci USA* 86:6196–6200.
- Lambertsen RH, 1987. A biopsy system for large whales and its use for cytogenetics. *J Mammal* 68:443–445.
- LeBoeuf BJ and Reiter J, 1988. Lifetime reproductive success in northern elephant seals. In: *Reproductive success: studies of individual variation in contrasting breeding systems* (Clutton-Brock TH, ed). Chicago: University of Chicago Press; 403–418.
- Lebreton JD, Burnham K, Clobert J, and Anderson DR, 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67–118.
- Leroi AM, Chen WR, and Rose MR, 1994a. Long-term laboratory evolution of a genetic life-history trade-off in *Drosophila melanogaster* 2. Stability of genetic correlations. *Evolution* 48:1258–1268.
- Leroi AM, Chippendale AK, and Rose MR, 1994b. Long-term laboratory evolution of a genetic life-history trade-off in *Drosophila melanogaster* 1. The role of genotype-by-environment interaction. *Evolution* 48:1244–1257.
- Li G and Hedgecock D, 1998. Genetic heterogeneity, detected by PCR SSCP, among samples of larval Pacific oysters (*Crassostrea gigas*) supports the hypothesis of large variance in reproductive success. *Can J Aquat Sci* 55:1025–1033.
- Maddison WP and Maddison DR, 1992. MacClade: analysis of phylogeny and character evolution, version 3.0. Sunderland, MA: Sinauer.
- Magrath RD, 1989. Hatching asynchrony and reproductive success in the blackbird. *Nature* 339: 536–538.
- Morin PA, Moore JJ, Chakraborty R, Jin L, Goodall J, and Woodruff DS, 1994. Kin selection, social structure, gene flow, and the evolution of chimpanzees. *Science* 265:1193–1201.
- Murray-McIntosh RP, Scrimshaw BJ, Hatfield PJ, and Penny D, 1998. Testing migration patterns and estimating founding population size in Polynesia by using human mtDNA sequences. *Proc Natl Acad Sci USA* 95:9047–9052.
- Nei M and Murata M, 1966. Effective population size when fertility is inherited. *Genet Res Camb* 8:257–260.
- Noon BR and Sauer JR, 1992. Population models for passerine birds: structure, parameterization, and analysis. In: *Wildlife 2001: populations* (McCullough DR and Barrett RH, eds). London: Elsevier Applied Science; 441–464.
- Nunney L, 1995. The influence of variation in female fecundity on effective population size. *Biol J Linn Soc* 59:411–425.
- Packer C, Herbst L, Pusey AE, Bygott JD, Hanby JP, Cairns SJ, and Mulder MB, 1988. Reproductive success of lions. In: *Reproductive success: studies of individual variation in contrasting breeding systems* (Clutton-Brock TH, ed). Chicago: University of Chicago Press; 403–418.
- Palsbøll PJ, Clapham PJ, Mattila DK, Larsen F, Sears R, Siegmund HR, Sigurjonsson J, Vasquez O, and Arcander P, 1995. Distribution of mtDNA haplotypes in North Atlantic humpback whales: the influence of behavior on population structure. *Mar Ecol Prog Ser* 116:1–10.
- Palsbøll PJ, Vader A, Bakke I, and Raafat El-Gewely M, 1992. Determination of gender in cetaceans by the polymerase chain reaction. *Can J Zool* 70: 2166–2170.
- Payne PM, Wiley DN, Young SB, Pittman S, Clapham PJ, and Jossi JW, 1990. Recent fluctuations in the abundance of baleen whales in the southern Gulf of Maine in relation to changes in selected prey. *Fish Bull* 88:687–696.
- Perneger TV, 1998. What's wrong with Bonferroni adjustments. *BMJ* 316:1236–1238.
- Price TD and Grant PR, 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. *Evolution* 38:483–494.
- Richard KR, McCarrey SW, and Wright J, 1994. DNA sequence from the SRY gene of the sperm whale (*Physeter macrocephalus*) for use in molecular sexing. *Can J Zool* 72:873–877.
- Risch N, deLeon D, Ozelius L, Kramer P, Almasly L, Singer B, Fahn S, Brakefield X, and Bressman V, 1995. Genetic analysis of idiopathic torsion dystonia in Ashkenazi Jews and their recent descent from a small founder population. *Nat Genet* 9:152–159.
- Roff D, 1992. *The evolution of life histories*. New York: Chapman & Hall.
- Roff D and Mousseau TA, 1987. Quantitative genetics and fitness: lessons from *Drosophila*. *Heredity* 58: 103–118.
- Sambrook J, Fritsch EF, and Maniatis T, 1989. *Molecular cloning: a laboratory manual*, 2nd ed. Cold Spring Harbor, NY: Cold Spring Harbor Laboratory Press.
- Scribner KT, Congdon JD, Chesser RK, and Smith MH, 1993. Annual differences in female reproductive success affect spatial and cohort-specific genotypic heterogeneity in painted turtles. *Evolution* 47: 1360–1373.
- Sinervo B and Zamudio KR, 2001. The evolution of alternative reproductive strategies: fitness differential, heritability, and genetic correlation between sexes. *J Hered* 92:198–205.
- Southern SO, Southern PJ, and Dizon AE, 1988. Molecular characterization of a cloned dolphin mitochondrial genome. *J Mol Evol* 28:32–42.
- Stoleson SH and Beissinger SR, 1997. Hatching asynchrony, brood reduction, and food limitation in a Neotropical parrot. *Ecol Monogr* 67:131–154.
- Swofford DA, 1998. PAUP version 4.0. Sunderland, MA: Sinauer.
- Tiedemann R and Milinkovitch MC, 1999. Technical comment. *Science* 284:2056.
- Vigilant L, Stoneking M, Hawkes K, and Wilson AC, 1991. African populations and the evolution of human mitochondrial DNA. *Science* 253:1503–1507.
- Weinrich MT, 1991. Stable social associations among humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine. *Can J Zool* 69:3012–3019.
- Weinrich MT, 1998. Early experience in habitat choice in humpback whales (*Megaptera novaeangliae*). *J Mammal* 79:163–170.
- Weinrich MT and Kuhlberg A, 1991. Short-term association patterns of humpback whale (*Megaptera novaeangliae*) groups on their southern Gulf of Maine feeding grounds. *Can J Zool* 69:3005–3011.
- Weinrich MT, Lambertsen RH, Baker CS, Schilling MR, and Belt CR, 1991. Behavioural responses of humpback whales (*Megaptera novaeangliae*) in the southern Gulf of Maine to biopsy sampling. *Rep Int Whaling Commn Special Issue* 13:91–98.
- Weinrich MT, Martin M, Griffiths R, Bove J, and Schilling M, 1997. A shift in distribution of humpback whales (*Megaptera novaeangliae*) in response to prey in the southern Gulf of Maine. *Fish Bull* 95: 826–836.
- Weinrich MT, Schilling MR, and Belt CR, 1992. Evidence for acquisition of a novel feeding behavior: lobtailing feeding in humpback whales, *Megaptera novaeangliae*. *Anim Behav* 44:1059–1072.
- Weir BS and Cockerham CC, 1984. Estimating F-statistics for the analysis of population structure. *Evolution* 38:1358–1370.
- Wheeler W and Gladstein D, 1992. MALIGN version 1.2.
- Whitehead H, 1998. Cultural selection and genetic diversity in matrilineal whales. *Science* 282:1708–1711.
- Whitehead H, 1999. Technical comment. *Science* 284:2057–2058.
- Wiley DN and Clapham PJ, 1993. Does maternal condition affect the sex ratio of offspring in humpback whales? *Anim Behav* 46:321–324.
- Wright S, 1951. The genetical structure of populations. *Ann Eugen* 15:323–354.

Received December 18, 2001
Accepted September 30, 2002

Corresponding Editor: Stephen J. O'Brien