

A NEW BIRTH-INTERVAL APPROACH TO ESTIMATING DEMOGRAPHIC PARAMETERS OF HUMPBACK WHALES

JAY BARLOW¹ AND PHILLIP J. CLAPHAM²

¹Southwest Fisheries Science Center, National Marine Fisheries Service, P.O. Box 271, La Jolla, California 92038 USA

²Cetacean Research Program, Center for Coastal Studies, P.O. Box 1036, Provincetown, Massachusetts 02657 USA

Abstract. A demographic model is developed based on interbirth intervals and is applied to estimate the population growth rate of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine. Fecundity rates in this model are based on the probabilities of giving birth at time t after a previous birth and on the probabilities of giving birth first at age x . Maximum likelihood methods are used to estimate these probabilities using sighting data collected for individually identified whales. Female survival rates are estimated from these same sighting data using a modified Jolly–Seber method. The youngest age at first parturition is 5 yr, the estimated mean birth interval is 2.38 yr (SE = 0.10 yr), the estimated noncalf survival rate is 0.960 (SE = 0.008), and the estimated calf survival rate is 0.875 (SE = 0.047). The population growth rate (λ) is estimated to be 1.065; its standard error is estimated as 0.012 using a Monte Carlo approach, which simulated sampling from a hypothetical population of whales. The simulation is also used to investigate the bias in estimating birth intervals by previous methods. The approach developed here is applicable to studies of other populations for which individual interbirth intervals can be measured.

Key words: birth intervals; birth rate; demography; fecundity; growth rate; humpback whale; *Megaptera novaeangliae*; modelling; population; survival.

INTRODUCTION

Long-term studies that monitor the lives of identified individuals have greatly expanded the opportunities to collect demographic information on many wild populations of cetaceans, as well as other terrestrial and aquatic taxa. Examples of the former include several species of baleen whales (Hammond et al. 1990), bottlenose dolphins (*Tursiops truncatus*) (Wells and Scott 1990), and killer whales (*Orcinus orca*) (Bigg et al. 1990, Brault and Caswell 1993).

These and other studies have provided a wealth of information on reproduction. Unfortunately, however, most basic approaches to estimating birth rates from such data are biased. In estimating the rate of births to mature females, a birth event is usually the only evidence of maturity. Including the first birth event will result in an overestimate of birth rate and excluding it will result in an underestimate. Alternatively, mean birth rates can be estimated as the inverse of the mean birth interval, but this approach is also biased because: (1) the measurement of longer birth intervals is obviously constrained by the length of the study, and, therefore, mean birth intervals may be underestimated, and (2) if some animals are not seen every year, mean birth intervals will tend to be overestimated (Baker et al. 1987). The exclusive use of known-aged animals to estimate reproductive parameters eliminates some bias

problems but severely restricts sample size and reduces precision (Barlow 1990).

Recently, two approaches have been developed to produce unbiased estimates of reproductive rates from the reproductive histories of individual animals (Barlow 1990, Payne et al. 1990). Both methods are based on estimating the conditional probability of giving birth at time t after a prior birth using maximum likelihood methods. Both methods assume that the probability of birth to a female in a given year is dependent only on the time since her most recent prior birth. Barlow's method also assumes that the probability of seeing an individual in a given year is independent of reproductive status. The method in Payne et al. (1990) relaxes that assumption but requires that the probability of observing a birth event is independent of whether the prior birth event was observed. Barlow (1990) also developed a maximum likelihood approach to estimate maturation probabilities posed as the probability of giving birth at age x conditional on not giving birth prior to age x .

Taken together, the birth-interval probabilities and first-birth probabilities can be considered an alternative to the usual model of age-specific fecundities, and we will refer to this as a birth-interval model. A birth-interval model can be used to specify the age-specific fecundities of a Leslie matrix population model and, when combined with age-specific survival rates, can be used to estimate the intrinsic rate of growth of a population.

In this paper we estimate birth-interval probabilities

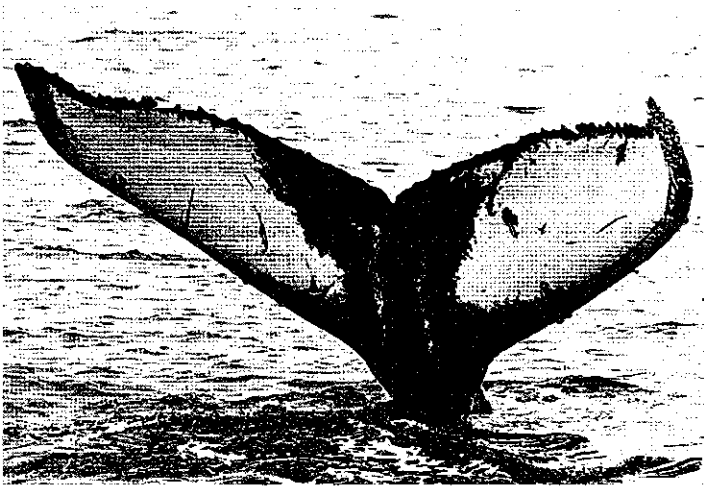


FIG. 1. Photograph of the ventral flukes of a humpback whale showing color patterns, notches, and serrations used to identify individuals. This whale (called Beltane, BE1 in Appendix A) is the first humpback whale in our sample to have been seen as a calf (in 1980) and then seen later with its own calf (in 1985). (Photo courtesy of Center for Coastal Studies).

and first-birth probabilities for a well-studied population of humpback whales (*Megaptera novaeangliae*) in the Gulf of Maine. The humpback whale is a large baleen whale with a cosmopolitan distribution. Humpbacks feed in high latitudes during spring, summer, and autumn, but migrate to tropical waters during the winter to mate and calve (Chittleborough 1965). Most humpback whales in the North Atlantic migrate each winter to the West Indies (Katona and Beard 1990). Calves are born there following a 1-yr gestation, and at the age of several weeks migrate with their mothers to their feeding areas, arriving in April or May. Weaning occurs between 6 and 10 mo after birth, and calves generally attain independence at the end of their natal year (Clapham and Mayo 1990).

Major oceanic populations of humpback whales are made up of relatively discrete feeding stocks, fidelity to which is determined matrilineally (Baker et al. 1990, Clapham and Mayo 1990). In the Gulf of Maine feeding area, humpback whales have been under continuous study since 1976 (Katona and Beard 1990). In this region, a combination of extensive survey effort and a high annual return rate has produced detailed sighting histories of individually identified whales. These data have been used to study various aspects of their biology and behavior (Clapham and Mayo 1990, Clapham 1993, Clapham et al. 1993, Wiley and Clapham 1993). We use these data to estimate reproductive and survival rates of whales that feed in the Gulf of Maine. We use the birth-interval and maturation parameterization of Barlow (1990) but develop new, more efficient likelihood estimators. We combine the estimated birth-interval and first-birth probabilities with estimates of survival rates to develop an age-structured model for this population and to estimate its asymptotic rate of growth. (The asymptotic growth rate is that which would be achieved given constant birth and death rates after a population has reached a stable age distribution. The realized growth rate of any population may differ

from the asymptotic rate due to effects of demographic stochasticity and nonstable age structure.)

METHODS

Field methods

Field studies were conducted between 1979 and 1991. Identification photographs were taken with 35 mm cameras either from 30-m commercial whale-watching vessels operating daily between April and October each year, or from a 14-m auxiliary ketch. The principal study area was Massachusetts Bay, with additional data collected from other areas in the Gulf of Maine. The amount of field effort varied each year, but generally increased during the study period. Humpback whales were individually identified from photographs of variable natural markings, notably the ventral fluke pigmentation pattern (Fig. 1) and the shape, size, and scarring of the dorsal fin (Katona and Whitehead 1981). Identification of individuals is unequivocal in all cases. Although fluke patterns have been shown to change in a small percentage of individuals in the first two years of life (Carlson et al. 1990), we know from experience which animals will exhibit these changes (those with hazy melanistic color patterns on their flukes), and matching of these individuals is accomplished using scars or patterns of serration on the posterior margin of the fluke. In addition, all individuals are double marked because, in this population, every animal is also recognizable by the shape, size, and scarring of the dorsal fin.

Where possible, the sex of individuals was determined from photographs of the genital area (Glockner 1983), or from molecular analyses of skin biopsies (Palsbøll et al. 1992). A recent study used blind cross-checks to confirm the reliability of both methods and to establish that the sex ratio in this population is at parity (Clapham et al. 1995).

A whale was considered to be a calf if it was esti-

mated to be <9 m in length and was observed in repeated close proximity to a much larger whale, assumed to be the mother. Birth to a female in a given year was assumed based on the presence of a calf. With very few exceptions, correct assignment of a calf to its mother is easy because such pairs typically maintain a tight association. In addition, in the great majority of cases, specific mother/calf pairs were observed together on more than one occasion, permitting further confirmation of the assignment. The resulting sighting and reproductive histories of female humpback whales (Appendix A) were used as the basis for fitting the birth-interval model.

Estimating birth-interval probabilities

Birth-interval probabilities, γ_t , represent the probability that a female will give birth at time t after a prior birth, conditional on her surviving and on her not giving birth at an earlier time after that birth. Because humpback whales are not available for study in the Gulf of Maine until calves have successfully completed their migration from the West Indies, a birth event will be considered a birth followed by survival to age 6 mo. There are 32 possible combinations of birth events in the 5 yr after an observed birth event (Table 1). The probability of each of these 5-yr combinations (${}_5\Gamma_z$ for $z = 1$ to 32) is fully specified by γ_1 through γ_5 :

$$\begin{aligned}
 {}_5\Gamma_1 &= (1 - \gamma_1)(1 - \gamma_2)(1 - \gamma_3)(1 - \gamma_4)(1 - \gamma_5), \\
 {}_5\Gamma_2 &= (1 - \gamma_1)(1 - \gamma_2)(1 - \gamma_3)(1 - \gamma_4)\gamma_5, \\
 {}_5\Gamma_3 &= (1 - \gamma_1)(1 - \gamma_2)(1 - \gamma_3)\gamma_4(1 - \gamma_1) \\
 &\vdots \\
 {}_5\Gamma_{32} &= (\gamma_1)(\gamma_1)(\gamma_1)(\gamma_1)(\gamma_1)
 \end{aligned}$$

(respectively for birth patterns given in Table 1). Many females are not seen every year following a birth event. An observed 5-yr sighting history following a birth event can therefore be defined as a five-element state vector (G) with three possible states for each element: seen with a calf (1), seen without a calf (0), or not seen (-). The probability of observing a particular sighting history that includes missing years [such as $\text{Pr}(0\ 1\ -\ 1\ 0)$] is the sum of the probabilities of the possible patterns [in this case, $\text{Pr}(0\ 1\ 0\ 1\ 0)$ plus $\text{Pr}(0\ 1\ 1\ 1\ 0)$, or ${}_5\Gamma_{11} + {}_5\Gamma_{15}$].

We used the Simplex algorithm (Press et al. 1988) to find the values of γ that maximize the joint probabilities [measured as log-likelihood, $\ln(L)$] of obtaining the observed sample (Appendix A) of n 5-yr sighting histories following a birth event for female humpback whales.

$$\ln(L) = \sum_{i=1}^n \ln[\text{Pr}(G_i | \gamma)]. \tag{1}$$

We limit ourselves to 5-yr sighting histories for computational simplicity and because the probability of a

TABLE 1. The 32 possible combinations of 5-yr birth histories following a birth or starting at the age of first parturition where "1" symbolizes a birth event in the given year and "0" symbolizes no birth. The probabilities of each birth pattern following a previous birth event (${}_5\Gamma_z$) are calculated from the estimated birth-interval probabilities γ . The probabilities of each birth pattern starting at the minimum age of first parturition (${}_5B_z$) are calculated from the estimated first-birth probabilities (β) and birth-interval probabilities (γ).

| z | Birth patterns | | | | | ${}_5\Gamma_z$ | ${}_5B_z$ |
|----|----------------|----------|----------|----------|--------------|----------------|-----------|
| | (1 5.5) | 2 6.5 | 3 7.5 | 4 8.5 | 5)† 9.5)‡ | | |
| 1 | 0 | 0 | 0 | 0 | 0 | 0.0163 | 0.0000 |
| 2 | 0 | 0 | 0 | 0 | 1 | 0.0138 | 0.0000 |
| 3 | 0 | 0 | 0 | 1 | 0 | 0.0451 | 0.1957 |
| 4 | 0 | 0 | 0 | 1 | 1 | 0.0020 | 0.0086 |
| 5 | 0 | 0 | 1 | 0 | 0 | 0.1235 | 0.0803 |
| 6 | 0 | 0 | 1 | 0 | 1 | 0.1780 | 0.1158 |
| 7 | 0 | 0 | 1 | 1 | 0 | 0.0128 | 0.0083 |
| 8 | 0 | 0 | 1 | 1 | 1 | 0.0005 | 0.0003 |
| 9 | 0 | 1 | 0 | 0 | 0 | 0.0437 | 0.0278 |
| 10 | 0 | 1 | 0 | 0 | 1 | 0.1780 | 0.1134 |
| 11 | 0 | 1 | 0 | 1 | 0 | 0.3059 | 0.1949 |
| 12 | 0 | 1 | 0 | 1 | 1 | 0.0135 | 0.0086 |
| 13 | 0 | 1 | 1 | 0 | 0 | 0.0094 | 0.0060 |
| 14 | 0 | 1 | 1 | 0 | 1 | 0.0135 | 0.0086 |
| 15 | 0 | 1 | 1 | 1 | 0 | 0.0009 | 0.0006 |
| 16 | 0 | 1 | 1 | 1 | 1 | 0.0000 | 0.0000 |
| 17 | 1 | 0 | 0 | 0 | 0 | 0.0012 | 0.0069 |
| 18 | 1 | 0 | 0 | 0 | 1 | 0.0020 | 0.0108 |
| 19 | 1 | 0 | 0 | 1 | 0 | 0.0128 | 0.0694 |
| 20 | 1 | 0 | 0 | 1 | 1 | 0.0005 | 0.0030 |
| 21 | 1 | 0 | 1 | 0 | 0 | 0.0094 | 0.0510 |
| 22 | 1 | 0 | 1 | 0 | 1 | 0.0135 | 0.0736 |
| 23 | 1 | 0 | 1 | 1 | 0 | 0.0009 | 0.0053 |
| 24 | 1 | 0 | 1 | 1 | 1 | 0.0000 | 0.0002 |
| 25 | 1 | 1 | 0 | 0 | 0 | 0.0001 | 0.0007 |
| 26 | 1 | 1 | 0 | 0 | 1 | 0.0005 | 0.0030 |
| 27 | 1 | 1 | 0 | 1 | 0 | 0.0009 | 0.0053 |
| 28 | 1 | 1 | 0 | 1 | 1 | 0.0000 | 0.0002 |
| 29 | 1 | 1 | 1 | 0 | 0 | 0.0000 | 0.0001 |
| 30 | 1 | 1 | 1 | 0 | 1 | 0.0000 | 0.0002 |
| 31 | 1 | 1 | 1 | 1 | 0 | 0.0000 | 0.0000 |
| 32 | 1 | 1 | 1 | 1 | 1 | 0.0000 | 0.0000 |

† Numbers refer to years 1-5 after previous birth.
‡ Numbers refer to age (yr).

birth interval >5 yr was found to be only 0.016. When additional births were observed >4 yr after an initial birth event, the 5-yr sighting histories after that event were treated as an independent sample [thus, for example, 5-yr postbirth sighting histories for individual EQ1 (Appendix A) would be (0 1 0 - 1) and (- 1 - 1 -)]. When sighting series were <5 yr long, the series were extended to 5 yr, and the added years were treated as missing observations (coded as "-" in Appendix A).

Estimating first-birth probabilities

First-birth probabilities, β_x , represent the probability that a female will give birth at age x , conditional on her survival to that age and on her not having given birth at a previous age. Again, for humpback whales a birth event will be considered as a birth followed by

survival of the calf for ≈ 6 mo. As noted above, 32 patterns of birth events (Table 1) represent all the possible patterns for the 5-yr sighting histories starting at age α (the first age class with observed births). The probability of each of these 5-yr combinations (${}_5B_z$ for $z = 1$ to 32) is fully specified by the vectors β and γ :

$${}_5B_1 = (1 - \beta_1)(1 - \beta_2)(1 - \beta_3)(1 - \beta_4)(1 - \beta_5)$$

$${}_5B_2 = (1 - \beta_1)(1 - \beta_2)(1 - \beta_3)(1 - \beta_4)\beta_5$$

$${}_5B_3 = (1 - \beta_1)(1 - \beta_2)(1 - \beta_3)\beta_4(1 - \gamma_1)$$

⋮

$${}_5B_{32} = (\beta_1)(\gamma_1)(\gamma_1)(\gamma_1)(\gamma_1)$$

(respectively for birth patterns given in Table 1). Again, an observed 5-yr sighting history starting with the minimum age of sexual maturity can be defined as a five-element state vector (\mathbf{H}) with three possible states for each element: seen with a calf, seen without a calf, or not seen. If an individual is not observed in all years, the probability of its sighting history is the sum of all possible patterns.

The Simplex algorithm was used to find the values of β that maximize the joint probability (measured as log-likelihood) of obtaining the observed sample of 5-yr observation histories (Appendix A) for the 19 known-aged females that are at least α years old.

$$\ln(L) = \sum_{i=1}^{19} \ln[\text{Pr}(H_i | \beta, \gamma)]. \quad (2)$$

Values for γ are taken from the maximum likelihood estimates as described above. For this population of humpback whales, the youngest known-aged female with a calf was 5.5 yr old.

Estimating survival rates

A modified Jolly-Seber mark-recapture model (Buckland 1980) was used to estimate the survival rate of noncalf females (females that are older than 1 yr) using the sighting data presented in Appendix A. The same program (RECAPCO) and similar protocols were previously used by Buckland (1990) to estimate the survival rate of this same humpback whale population. The overall survival rate was estimated as a weighted arithmetic mean of "age"-specific survival rates, where "age" in this context refers to time after the first observation of an individual. The first and last estimate were deleted to reduce bias (Buckland 1990). The model uses information about the verified death of individuals to improve precision, but no assumptions of death are made based on patterns of nonobservation. The only differences in protocol were that the present study included only females (males and females were pooled in the previous study) and more recent sightings were included in the present study (1979–1991) than in the previous study (1976–1986). The standard error

of the noncalf survival rate was estimated by a non-parametric bootstrap implemented in RECAPCO.

First-year (calf) mortality could not be estimated directly by the same methods, but we were able to delimit its likely range. A maximum likely calf survival rate can be estimated as the square of the adult survival rate based on Barlow and Boveng's (1991) argument that a cetacean calf is likely to experience a greater risk of mortality than its mother plus an added risk of mortality (assumed to be certain mortality) if the mother dies. A minimum likely survival rate can be estimated simply as the fraction of identified calves seen through 1990 that were subsequently seen in a later year. For this paper, calf mortality is estimated as the average of the above two methods. The standard error of this value is estimated as half the difference between the two estimates, implicitly defining the high and low estimates to be 66% confidence intervals.

Asymptotic rate of increase

The birth-interval probabilities (γ) and first-birth probabilities (β) were used to estimate age-specific fecundity rates (F_x) for a Leslie matrix using simple Markov probability chains (Barlow 1990). The Leslie matrix fecundities are for female births to females and were estimated by assuming the calf sex ratio is at parity (Clapham et al. 1995). The noncalf survival rate (estimated as described above) is a mean of all age classes, with defacto weighting by the age structure of the population. The Leslie matrix was constructed (with calves as age class 1) using the above age-specific fecundity rates, a constant noncalf survival rate, and a maximum age of 35. The asymptotic rate of increase (λ) for this population was estimated by solving the following characteristic equation:

$$1 = \sum_{x=1}^{35} \lambda^{-x} l_x F_x \quad (3)$$

where, l_x = survivorship to age class x , and F_x = fecundity of age class x . In this formulation, age class 1 represents whales that are ≈ 6 mo old, and the fecundity term includes components of survival for the mother (which must survive a year from one census to the next) and for the calf (which must survive 6 mo from birth to census). As estimated above, the fecundity rates already include the calf survival probabilities (if a calf does not survive to census, birth intervals are increased proportionately). The calf survival rate (estimated as described above) represents the probability of surviving from age 0.5 yr to age 1.5 yr.

Bias and precision estimation

The bias and precision of the above estimation procedures were determined using a Monte Carlo simulation that mimicked the dynamics and sighting histories of a hypothetical humpback whale population. Parameters were chosen to equal those estimated for

mated to be <9 m in length and was observed in repeated close proximity to a much larger whale, assumed to be the mother. Birth to a female in a given year was assumed based on the presence of a calf. With very few exceptions, correct assignment of a calf to its mother is easy because such pairs typically maintain a tight association. In addition, in the great majority of cases, specific mother/calf pairs were observed together on more than one occasion, permitting further confirmation of the assignment. The resulting sighting and reproductive histories of female humpback whales (Appendix A) were used as the basis for fitting the birth-interval model.

Estimating birth-interval probabilities

Birth-interval probabilities, γ_t , represent the probability that a female will give birth at time t after a prior birth, conditional on her surviving and on her not giving birth at an earlier time after that birth. Because humpback whales are not available for study in the Gulf of Maine until calves have successfully completed their migration from the West Indies, a birth event will be considered a birth followed by survival to age 6 mo. There are 32 possible combinations of birth events in the 5 yr after an observed birth event (Table 1). The probability of each of these 5-yr combinations (${}_5\Gamma_z$ for $z = 1$ to 32) is fully specified by γ_1 through γ_5 :

$$\begin{aligned}
 {}_5\Gamma_1 &= (1 - \gamma_1)(1 - \gamma_2)(1 - \gamma_3)(1 - \gamma_4)(1 - \gamma_5), \\
 {}_5\Gamma_2 &= (1 - \gamma_1)(1 - \gamma_2)(1 - \gamma_3)(1 - \gamma_4)\gamma_5, \\
 {}_5\Gamma_3 &= (1 - \gamma_1)(1 - \gamma_2)(1 - \gamma_3)\gamma_4(1 - \gamma_1) \\
 &\vdots \\
 {}_5\Gamma_{32} &= (\gamma_1)(\gamma_1)(\gamma_1)(\gamma_1)(\gamma_1)
 \end{aligned}$$

(respectively for birth patterns given in Table 1). Many females are not seen every year following a birth event. An observed 5-yr sighting history following a birth event can therefore be defined as a five-element state vector (\mathbf{G}) with three possible states for each element: seen with a calf (1), seen without a calf (0), or not seen (-). The probability of observing a particular sighting history that includes missing years [such as $\text{Pr}(0\ 1\ -\ 1\ 0)$] is the sum of the probabilities of the possible patterns [in this case, $\text{Pr}(0\ 1\ 0\ 1\ 0)$ plus $\text{Pr}(0\ 1\ 1\ 1\ 0)$, or ${}_5\Gamma_{11} + {}_5\Gamma_{15}$].

We used the Simplex algorithm (Press et al. 1988) to find the values of γ that maximize the joint probabilities [measured as log-likelihood, $\ln(L)$] of obtaining the observed sample (Appendix A) of n 5-yr sighting histories following a birth event for female humpback whales.

$$\ln(L) = \sum_{i=1}^n \ln[\text{Pr}(G_i | \gamma)]. \quad (1)$$

We limit ourselves to 5-yr sighting histories for computational simplicity and because the probability of a

TABLE 1. The 32 possible combinations of 5-yr birth histories following a birth or starting at the age of first parturition where '1' symbolizes a birth event in the given year and '0' symbolizes no birth. The probabilities of each birth pattern following a previous birth event (${}_5\Gamma_z$) are calculated from the estimated birth-interval probabilities γ . The probabilities of each birth pattern starting at the minimum age of first parturition (${}_5B_z$) are calculated from the estimated first-birth probabilities (β) and birth-interval probabilities (γ).

| z | Birth patterns | | | | | ${}_5\Gamma_z$ | ${}_5B_z$ |
|----|----------------|----------|----------|----------|--------------|----------------|-----------|
| | (1 5.5) | 2 6.5 | 3 7.5 | 4 8.5 | 5)† 9.5)‡ | | |
| 1 | 0 | 0 | 0 | 0 | 0 | 0.0163 | 0.0000 |
| 2 | 0 | 0 | 0 | 0 | 1 | 0.0138 | 0.0000 |
| 3 | 0 | 0 | 0 | 1 | 0 | 0.0451 | 0.1957 |
| 4 | 0 | 0 | 0 | 1 | 1 | 0.0020 | 0.0086 |
| 5 | 0 | 0 | 1 | 0 | 0 | 0.1235 | 0.0803 |
| 6 | 0 | 0 | 1 | 0 | 1 | 0.1780 | 0.1158 |
| 7 | 0 | 0 | 1 | 1 | 0 | 0.0128 | 0.0083 |
| 8 | 0 | 0 | 1 | 1 | 1 | 0.0005 | 0.0003 |
| 9 | 0 | 1 | 0 | 0 | 0 | 0.0437 | 0.0278 |
| 10 | 0 | 1 | 0 | 0 | 1 | 0.1780 | 0.1134 |
| 11 | 0 | 1 | 0 | 1 | 0 | 0.3059 | 0.1949 |
| 12 | 0 | 1 | 0 | 1 | 1 | 0.0135 | 0.0086 |
| 13 | 0 | 1 | 1 | 0 | 0 | 0.0094 | 0.0060 |
| 14 | 0 | 1 | 1 | 0 | 1 | 0.0135 | 0.0086 |
| 15 | 0 | 1 | 1 | 1 | 0 | 0.0009 | 0.0006 |
| 16 | 0 | 1 | 1 | 1 | 1 | 0.0000 | 0.0000 |
| 17 | 1 | 0 | 0 | 0 | 0 | 0.0012 | 0.0069 |
| 18 | 1 | 0 | 0 | 0 | 1 | 0.0020 | 0.0108 |
| 19 | 1 | 0 | 0 | 1 | 0 | 0.0128 | 0.0694 |
| 20 | 1 | 0 | 0 | 1 | 1 | 0.0005 | 0.0030 |
| 21 | 1 | 0 | 1 | 0 | 0 | 0.0094 | 0.0510 |
| 22 | 1 | 0 | 1 | 0 | 1 | 0.0135 | 0.0736 |
| 23 | 1 | 0 | 1 | 1 | 0 | 0.0009 | 0.0053 |
| 24 | 1 | 0 | 1 | 1 | 1 | 0.0000 | 0.0002 |
| 25 | 1 | 1 | 0 | 0 | 0 | 0.0001 | 0.0007 |
| 26 | 1 | 1 | 0 | 0 | 1 | 0.0005 | 0.0030 |
| 27 | 1 | 1 | 0 | 1 | 0 | 0.0009 | 0.0053 |
| 28 | 1 | 1 | 0 | 1 | 1 | 0.0000 | 0.0002 |
| 29 | 1 | 1 | 1 | 0 | 0 | 0.0000 | 0.0001 |
| 30 | 1 | 1 | 1 | 0 | 1 | 0.0000 | 0.0002 |
| 31 | 1 | 1 | 1 | 1 | 0 | 0.0000 | 0.0000 |
| 32 | 1 | 1 | 1 | 1 | 1 | 0.0000 | 0.0000 |

† Numbers refer to years 1-5 after previous birth.
‡ Numbers refer to age (yr).

birth interval >5 yr was found to be only 0.016. When additional births were observed >4 yr after an initial birth event, the 5-yr sighting histories after that event were treated as an independent sample [thus, for example, 5-yr postbirth sighting histories for individual EQ1 (Appendix A) would be (0 1 0 - 1) and (- 1 - 1 -)]. When sighting series were <5 yr long, the series were extended to 5 yr, and the added years were treated as missing observations (coded as "-" in Appendix A).

Estimating first-birth probabilities

First-birth probabilities, β_x , represent the probability that a female will give birth at age x , conditional on her survival to that age and on her not having given birth at a previous age. Again, for humpback whales a birth event will be considered as a birth followed by

survival of the calf for ≈ 6 mo. As noted above, 32 patterns of birth events (Table 1) represent all the possible patterns for the 5-yr sighting histories starting at age α (the first age class with observed births). The probability of each of these 5-yr combinations (${}_5B_z$ for $z = 1$ to 32) is fully specified by the vectors β and γ :

$${}_5B_1 = (1 - \beta_1)(1 - \beta_2)(1 - \beta_3)(1 - \beta_4)(1 - \beta_5)$$

$${}_5B_2 = (1 - \beta_1)(1 - \beta_2)(1 - \beta_3)(1 - \beta_4)\beta_5$$

$${}_5B_3 = (1 - \beta_1)(1 - \beta_2)(1 - \beta_3)\beta_4(1 - \gamma_1)$$

⋮

$${}_5B_{32} = (\beta_1)(\gamma_1)(\gamma_1)(\gamma_1)(\gamma_1)$$

(respectively for birth patterns given in Table 1). Again, an observed 5-yr sighting history starting with the minimum age of sexual maturity can be defined as a five-element state vector (\mathbf{H}) with three possible states for each element: seen with a calf, seen without a calf, or not seen. If an individual is not observed in all years, the probability of its sighting history is the sum of all possible patterns.

The Simplex algorithm was used to find the values of β that maximize the joint probability (measured as log-likelihood) of obtaining the observed sample of 5-yr observation histories (Appendix A) for the 19 known-aged females that are at least α years old.

$$\ln(L) = \sum_{i=1}^{19} \ln[\text{Pr}(H_i | \beta, \gamma)]. \quad (2)$$

Values for γ are taken from the maximum likelihood estimates as described above. For this population of humpback whales, the youngest known-aged female with a calf was 5.5 yr old.

Estimating survival rates

A modified Jolly-Seber mark-recapture model (Buckland 1980) was used to estimate the survival rate of noncalf females (females that are older than 1 yr) using the sighting data presented in Appendix A. The same program (RECAPCO) and similar protocols were previously used by Buckland (1990) to estimate the survival rate of this same humpback whale population. The overall survival rate was estimated as a weighted arithmetic mean of "age"-specific survival rates, where "age" in this context refers to time after the first observation of an individual. The first and last estimate were deleted to reduce bias (Buckland 1990). The model uses information about the verified death of individuals to improve precision, but no assumptions of death are made based on patterns of nonobservation. The only differences in protocol were that the present study included only females (males and females were pooled in the previous study) and more recent sightings were included in the present study (1979–1991) than in the previous study (1976–1986). The standard error

of the noncalf survival rate was estimated by a non-parametric bootstrap implemented in RECAPCO.

First-year (calf) mortality could not be estimated directly by the same methods, but we were able to delimit its likely range. A maximum likely calf survival rate can be estimated as the square of the adult survival rate based on Barlow and Boveng's (1991) argument that a cetacean calf is likely to experience a greater risk of mortality than its mother plus an added risk of mortality (assumed to be certain mortality) if the mother dies. A minimum likely survival rate can be estimated simply as the fraction of identified calves seen through 1990 that were subsequently seen in a later year. For this paper, calf mortality is estimated as the average of the above two methods. The standard error of this value is estimated as half the difference between the two estimates, implicitly defining the high and low estimates to be 66% confidence intervals.

Asymptotic rate of increase

The birth-interval probabilities (γ) and first-birth probabilities (β) were used to estimate age-specific fecundity rates (F_x) for a Leslie matrix using simple Markov probability chains (Barlow 1990). The Leslie matrix fecundities are for female births to females and were estimated by assuming the calf sex ratio is at parity (Clapham et al. 1995). The noncalf survival rate (estimated as described above) is a mean of all age classes, with defacto weighting by the age structure of the population. The Leslie matrix was constructed (with calves as age class 1) using the above age-specific fecundity rates, a constant noncalf survival rate, and a maximum age of 35. The asymptotic rate of increase (λ) for this population was estimated by solving the following characteristic equation:

$$1 = \sum_{x=1}^{35} \lambda^{-x} l_x F_x \quad (3)$$

where, l_x = survivorship to age class x , and F_x = fecundity of age class x . In this formulation, age class 1 represents whales that are ≈ 6 mo old, and the fecundity term includes components of survival for the mother (which must survive a year from one census to the next) and for the calf (which must survive 6 mo from birth to census). As estimated above, the fecundity rates already include the calf survival probabilities (if a calf does not survive to census, birth intervals are increased proportionately). The calf survival rate (estimated as described above) represents the probability of surviving from age 0.5 yr to age 1.5 yr.

Bias and precision estimation

The bias and precision of the above estimation procedures were determined using a Monte Carlo simulation that mimicked the dynamics and sighting histories of a hypothetical humpback whale population. Parameters were chosen to equal those estimated for

this population. Two additional parameters were used to tune the simulation to give the same sample sizes for birth-interval and first-birth probability estimation: the initial population size for the simulation ($n = 122$) was chosen to give the same number of 5-yr birth-interval patterns (mean = 104.2) as were observed in the actual data ($n = 105$) and the probability of photo-identifying a calf given that its mother was identified (0.57) was chosen to give the same number of known-aged females with calves (mean = 19.1) as were observed in the actual data ($n = 19$). The population was projected 12 yr from 1979 to 1991. The simulated population projection, sampling, and parameter estimation were repeated 1000 times to estimate the mean and standard error of the resulting values of asymptotic rates of increase.

The population dynamic model was individual based with full demographic stochasticity; random numbers determined whether each female died or gave birth in a given year. Birth probabilities were contingent upon age (for primiparous females) or time since previous birth, and births were distributed randomly as males or females. The probability of seeing a female in a specific year was estimated as the observed fraction seen that year of those known to be alive (see *Results*). The starting population was distributed randomly as males and females with an initial age distribution characteristic of a population growing at the rate estimated for Gulf of Maine humpback whales (as estimated from this study). Birth-interval and first-birth probabilities were estimated from the simulated sighting history of this population. For each of the 1000 iterations, the calf and noncalf survival rates were calculated as the mean estimate plus a random normal deviate with a mean of zero and a standard deviation equal to the standard error of the mean estimate. The realized rate of increase for each iteration (which differs from the asymptotic rate of increase due to stochastic variation in initial age distribution and the projection model) is defined as the constant, annual rate that would have resulted in the observed population growth from 1979 (N_{1979}) to 1991 (N_{1991})

$$N_{1991} = \lambda^{12} N_{1979}$$

and was estimated as

$$\lambda = (N_{1991} / N_{1979})^{1/12}.$$

RESULTS

Sighting probabilities

The probability of sighting an individual during a year is estimated as the overall fraction of females seen alive in one year that were also seen the previous year, or 0.823 (714/867). Sighting probabilities increased during the study period (0.71, 0.72, 0.81, 0.79, 0.70, 0.80, 0.87, 0.94, 0.78, 0.88, 0.88, and 0.86 for 1979–1990, respectively). The prior-year sighting probability

for females that were seen with a calf (0.805 = 186/231) is not significantly different from that for females without calves (0.830 = 528/636).

Birth-interval probabilities

Between 1979 and 1991, 107 female humpback whales were observed in association with calves. Of these, 79 were seen in subsequent years and provide some information on birth intervals. The maximum likelihood estimates of conditional birth-interval probabilities, γ (conditional on the animal not having calved at a shorter interval) are 0.043, 0.590, 0.803, 0.610, and 0.458 for birth intervals of 1 through 5 yr, respectively. The unconditional probabilities for birth intervals of 1 through 5 yr are 0.043, 0.565, 0.315, 0.047, and 0.014, respectively. Clearly, birth intervals of 2 yr are most common, followed closely by 3-yr intervals. The resulting probabilities of the 32 possible combinations of births in the 5 yr following a birth (Table 1) indicate that the probability of not giving birth for five consecutive years after a previous birth is only 0.016. Therefore, birth intervals >5 yr can be ignored.

First-birth probabilities

Between 1979 and 1990, 58 female calves were identified photographically in the Gulf of Maine population. Of these known-aged females, the youngest one observed with her own calf was 5.5 yr old. Nineteen of these females were observed at least once at age 5.5 or greater and therefore provide some information about first-birth probabilities. The maximum likelihood estimates of conditional first-birth probabilities (conditional on not having given birth at an earlier age), β , are 0.230, 0.468, 0.501 and 1.000 for first births at ages 5.5 through 8.5 yr, respectively. The resulting probabilities of birth patterns (Table 1) indicate that the highest probability of first births occurs at 6.5 yr, and approximately equal probabilities occur at 5.5, 7.5, and 8.5 yr. All known-aged females that were seen when >8 yr old had given birth previously.

Survival rate estimates

The modified Jolly–Seber estimate of noncalf survival rate is 0.960 (SE = 0.0083). The high estimate of 1st-yr survival is the square of this estimate, or 0.922. The low estimate of calf survival is the fraction of identified calves born prior to 1991 that were subsequently seen, or 0.828. The calf survival rate is estimated as the average of these: 0.875 (SE ≈ 0.047).

Asymptotic rate of increase

Based on the age-specific fecundities calculated from the above estimated birth-interval and first-birth probabilities (Table 2) and the estimated survival rates, the asymptotic rate of increase is 1.065, and its standard error from the Monte Carlo simulation is 0.012. The total number of parameters estimated for this asymptotic rate of increase was 12: five birth-interval prob-

TABLE 2. Age-specific survival rates (P_x) and fecundity rates (F_x) used in a Leslie matrix to calculate the population growth rate ($\lambda = 1.065$). Fecundity rates are calculated from maximum likelihood estimates of first-birth (β) and birth-interval (γ) probabilities.

| Age x (yr) | Age class | P_x | F_x |
|-----------------|-----------|-------|-------|
| 0.5 | 1 | 0.875 | 0.000 |
| 1.5 | 2 | 0.960 | 0.000 |
| 2.5 | 3 | 0.960 | 0.000 |
| 3.5 | 4 | 0.960 | 0.000 |
| 4.5 | 5 | 0.960 | 0.111 |
| 5.5 | 6 | 0.960 | 0.178 |
| 6.5 | 7 | 0.960 | 0.168 |
| 7.5 | 8 | 0.960 | 0.241 |
| 8.5 | 9 | 0.960 | 0.167 |
| 9.5 | 10 | 0.960 | 0.206 |
| 10.5 | 11 | 0.960 | 0.190 |
| 11.5 | 12 | 0.960 | 0.192 |
| 12.5 | 13 | 0.960 | 0.194 |
| 13.5 | 14 | 0.960 | 0.192 |
| 14.5 | 15 | 0.960 | 0.193 |
| 15.5 | 16 | 0.960 | 0.192 |
| 16.5 | 17 | 0.960 | 0.192 |
| 17.5 | 18 | 0.960 | 0.192 |
| 18.5 | 19 | 0.960 | 0.192 |
| 19.5 | 20 | 0.960 | 0.192 |
| 20.5 | 21 | 0.960 | 0.192 |
| 21.5 | 22 | 0.960 | 0.192 |
| 22.5 | 23 | 0.960 | 0.192 |
| 23.5 | 24 | 0.960 | 0.192 |
| 24.5 | 25 | 0.960 | 0.192 |
| 25.5 | 26 | 0.960 | 0.192 |
| 26.5 | 27 | 0.960 | 0.192 |
| 27.5 | 28 | 0.960 | 0.192 |
| 28.5 | 29 | 0.960 | 0.192 |
| 29.5 | 30 | 0.960 | 0.192 |
| 30.5 | 31 | 0.960 | 0.192 |
| 31.5 | 32 | 0.960 | 0.192 |
| 32.5 | 33 | 0.960 | 0.191 |
| 33.5 | 34 | 0.960 | 0.191 |
| 34.5 | 35 | 0.000 | 0.000 |

abilities, the age at first possible birth, four first-birth probabilities, and two survival rates. From the 1000 Monte Carlo simulations, the average realized rate of increase is 1.064 (SE = 0.009), and the average asymptotic rate of increase estimated by the birth-interval model is 1.063 (SE = 0.012).

DISCUSSION

Population growth rate

The population growth rate estimated here (1.065) is consistent with estimated growth rates of other severely depleted populations of humpback whales throughout the world (Best 1993). Our estimate is consistent with a previous estimate of $r = 0.094$ (95% CI = -0.12 to 0.30) (or $\lambda = 1.099$, SE = 0.105) for the same general area (western North Atlantic; Katona and Beard 1990) but is considerably more precise.

Despite small sample size, the population growth rate estimated above is one of the most precise that has been estimated for any baleen whale population (cf. Best 1993). The birth-interval model presented here

effectively uses birth rate information for individuals of unknown age. The simulations show that it does so without introducing bias. Methods, such as a Leslie matrix, which utilize information from only known-aged individuals produce less precise estimates of population growth rate (Barlow 1990). Also, the sample of known-aged individuals is strongly biased toward younger individuals, which means that a model dependent only on known-aged individuals will be biased if fecundity rates change with age. The standard error of the population growth rate estimated from the birth-interval approach is not much greater than the standard error of the realized rate of increase in the simulations. This indicates that the birth-interval model estimates the intrinsic rate of growth almost as precisely as the realized growth rate would if it were known without error. Our methods do not appear sensitive to violations of assumptions such as caused by nonstable age distributions or time-varying vital rates (Appendix B).

Birth intervals

Typically, reproductive data from individual identification studies of baleen whales have been reported as mean birth intervals. For humpback whales, Glockner-Ferrari and Ferrari (1990) report mean birth intervals of 1.2 yr (SE = 0.15, estimated from their data) in Hawaiian breeding areas, and Straley (1994) reports mean birth intervals of 2.26 yr (SE = 0.12, estimated from her data) in Alaska feeding areas. To reduce bias, these authors limit their sample to birth intervals that are complete (i.e., do not have unobserved years within them). This approach is still biased because longer birth intervals are less likely to be observed. In our study, the mean birth interval without interrupted observations (2.32 yr) does not differ very much from the mean birth interval from the maximum likelihood estimates of the birth-interval parameters (2.38 yr, SE = 0.10 from simulations), primarily because the probability of being seen in a given year was so high in this study.

In contrast to the above studies, Baker et al. (1987) estimated birth rates as the fraction of known-mature females seen in a given year that were accompanied by a calf. They estimated birth rates of 0.36 (95% CI = 0.27–0.45) for feeding areas in southeastern Alaska and 0.58 (95% CI = 0.41–0.75) for breeding areas near Hawaii, which correspond to birth intervals of 2.78 yr (95% CI = 2.2–3.7 yr) for Alaska and 1.72 yr (95% CI = 1.3–2.4 yr) for Hawaii. Our estimate lies within the 95% confidence intervals for both Alaska and Hawaii. Using the methods of Baker et al. (1987) the "apparent" birth rate in our study was 0.53 for all years combined (Table 3). The birth interval estimated as the inverse of this birth rate is 1.89 yr, which is considerably smaller than our maximum likelihood estimate of 2.38 yr. This bias is caused (at least partially) by Baker et al.'s method of using a birth event as evidence of maturity in females.

Our simulation model allows us to investigate how

TABLE 3. Apparent birth rates for females known to be mature (based on observation of at least one calf in close proximity to that female in the given year or prior year) for years 1979–1991. Data are tabulated from Appendix A. All estimates are likely to be biased high because births are used as evidence of maturity.

| Year | No. calves seen | No. mature females seen | Apparent birth rate |
|---------|-----------------|-------------------------|---------------------|
| 1979 | 5 | 5 | 1.00 |
| 1980 | 4 | 8 | 0.50 |
| 1981 | 4 | 10 | 0.40 |
| 1982 | 10 | 17 | 0.59 |
| 1983 | 14 | 22 | 0.64 |
| 1984 | 13 | 30 | 0.43 |
| 1985 | 20 | 35 | 0.57 |
| 1986 | 22 | 46 | 0.48 |
| 1987 | 25 | 45 | 0.55 |
| 1988 | 14 | 45 | 0.31 |
| 1989 | 41 | 59 | 0.69 |
| 1990 | 31 | 62 | 0.50 |
| 1991 | 34 | 60 | 0.56 |
| Overall | 237 | 444 | 0.53 |

the annual sighting probability affects the “apparent” mean birth interval if calculated as it has been in other studies. If the annual sighting rate had been 0.25, 0.50, or 0.99, the corresponding mean birth intervals with uninterrupted observations would have been 1.84 (SE = 0.001), 2.08 (SE = 0.001), or 2.36 (SE = 0.001), respectively. Obviously, the “apparent” birth interval based on sighting histories that contain many missing years (but some uninterrupted birth intervals) is seriously biased and should not be used to compare reproductive rates between populations.

Survival rates

The noncalf survival rate estimated for females in this study (0.960, SE = 0.008) is not appreciably different from the rate estimated by Buckland (1990) for females and males (0.951, SE = 0.010), but is more precise (a statistical test of this difference is not appropriate because the two estimates are based on some of the same data). If survival rates were estimated without error, the standard error in the estimated asymptotic rate of increase would decrease from 0.011 to 0.007. Given that population growth rate is very sensitive to noncalf survival rate (Brault and Caswell 1993) and given that uncertainty in this parameter contributes much of the uncertainty in estimating growth rate, we consider two possible sources of error: violation of mark–recapture and age–structure assumptions. Our survival estimate assumes a closed population. Permanent emigration cannot be distinguished from mortality in mark–recapture models, and if this occurs, survival rates and population growth rates would be underestimated. Similarly, our use of a single rate for noncalf survival assumes that either survival rates do not change with age or that our estimated rate is weighted by the stable age distribution of the population (Goodman 1984). The former assumption is not real-

istic because survival rates are expected to vary with age for marine mammals (Barlow and Boveng 1991); lower survival rates are expected for juveniles and for senescent individuals. However, our method of estimating noncalf mortality should implicitly weight by the current age distribution, which should be equivalent to the stable age distribution if large perturbations have not occurred recently. Nonstable age structure could bias our survival rate estimate in either direction.

Little credence should be placed in our estimates of calf survival rates. Ours was simply an attempt to bracket the likely range of values by choosing a “reasonable” guess and a high standard error. Population growth rate is not very sensitive to this parameter, and even if calf survival were estimated without error, the standard error of the population growth rate would decrease only from 0.011 to 0.010.

Application to other species

The birth-interval approach to estimating demographic parameters makes efficient use of the types of information being collected from many cetacean populations worldwide (Hammond et al. 1990). Similar data are being collected for some terrestrial vertebrate populations. The birth-interval model is most suitable for populations that are small enough such that resightings of the same individuals are common, but use of this model will add little to studies for which all individuals in a population are seen every year. It is also better suited to species in which interbirth interval is variable than to those which produce young every year. Simple modifications of this model could be made for litter sizes that are greater than one by multiplying the Leslie matrix fecundities (derived from birth-interval and first-birth probabilities) by the mean litter size; however, additional developments would be needed if litter size were a function of interbirth interval.

ACKNOWLEDGMENTS

We thank the staff of the Center for Coastal Studies for data collection, and the Cetacean Research Unit for provision of additional sighting data. Steve Buckland provided his FORTRAN program RECAPCO for our survival rate estimates. Partial funding to P. J. Clapham from the American-Scandinavian Foundation is gratefully acknowledged. This paper was improved by suggestions from Scott Baker, Bob Brownell, Steve Buckland, Jim Estes, Barb Taylor, and two anonymous reviewers.

LITERATURE CITED

- Baker, C. S., S. R. Palumbi, R. H. Lambertsen, M. T. Weinrich, J. Calambokidis, and S. J. O'Brien. 1990. Influence of seasonal migration on geographic distribution of mitochondrial DNA haplotypes in humpback whales. *Nature* 344:238–240.
- Baker, C. S., A. Perry, and L. M. Herman. 1987. Reproductive histories of female humpback whales *Megaptera novaeangliae* in the North Pacific. *Marine Ecology Progress Series* 41:103–114.
- Barlow, J. 1990. A birth-interval model for estimating cetacean reproductive rates from rc-sight data. Report of the International Whaling Commission Special Issue 12:155–160.

- Barlow, J., and P. Boveng. 1991. Modelling age-specific mortality for marine mammal populations. *Marine Mammal Science* 7:84-119.
- Best, P. B. 1993. Increase rates in severely depleted stocks of baleen whales. International Council on the Exploration of the Sea *Journal of Marine Science* 50:169-186.
- Bigg, M. A., P. F. Olesiuk, G. M. Ellis, J. K. B. Ford, and K. C. Balcomb III. 1990. Social organization and genealogy of resident killer whales (*Orcinus orca*) in the coastal waters of British Columbia and Washington State. Report of the International Whaling Commission Special Issue 12: 383-405.
- Brault, S., and H. Caswell. 1993. Pod-specific demography of individually identifiable whales. *Ecology* 74:1444-1454.
- Buckland, S. T. 1980. A modified analysis of the Jolly-Seber capture-recapture model. *Biometrics* 36:419-435.
- . 1990. Estimation of survival rates from sightings of individually identifiable whales. Report of the International Whaling Commission Special Issue 12:149-153.
- Carlson, C. A., C. A. Mayo, and H. Whitehead. 1990. Changes in the ventral fluke pattern of the humpback whale (*Megaptera novaeangliae*) and its effect on matching; evaluation of its significance to photo-identification research. Report of the International Whaling Commission Special Issue 12:105-111.
- Chittleborough, R. G. 1965. Dynamics of two populations of the humpback whale, *Megaptera novaeangliae* (Borowski). *Australian Journal Marine Freshwater Research* 16:33-128.
- Clapham, P. J. 1993. Social organization of humpback whales on a North Atlantic feeding ground. Symposium of the Zoological Society of London 66:131-145.
- Clapham, P. J., L. S. Baraff, C. A. Carlson, M. A. Christian, D. K. Mattila, C. A. Mayo, M. A. Murphy, and S. Pittman. 1993. Seasonal occurrence and annual return of humpback whales in the southern Gulf of Maine. *Canadian Journal of Zoology* 71:440-443.
- Clapham, P. J., M. Bérubé, and D. K. Mattila. 1995. Sex ratio of the Gulf of Maine humpback whale population. *Marine Mammal Science* 11:227-231.
- Clapham, P. J., and C. A. Mayo. 1990. Reproduction of humpback whales, *Megaptera novaeangliae*, observed in the Gulf of Maine. Report of the International Whaling Commission Special Issue 12:171-175.
- Geraci, J. R., D. M. Anderson, R. J. Timperi, D. J. St. Aubin, G. A. Early, J. H. Prescott, and C. A. Mayo. 1989. Humpback whale (*Megaptera novaeangliae*) fatally poisoned by dinoflagellate toxin. *Canadian Journal of Fisheries and Aquatic Sciences* 46:1895-1898.
- Glockner, D. A. 1983. Determining the sex of humpback whales (*Megaptera novaeangliae*) in their natural environment. Pages 447-464 in R. S. Payne, editor. Behavior and communication of whales. American Association for the Advancement of Science Selected Symposium Number 76. Westview Press, Boulder, Colorado, USA.
- Glockner-Ferrari, D. A., and M. J. Ferrari. 1990. Reproduction in the humpback whale (*Megaptera novaeangliae*) in Hawaiian waters, 1975-1988: the life history, reproductive rates, and behavior of known individuals identified through surface and underwater photography. Report of the International Whaling Commission Special Issue 12:161-169.
- Goodman, D. 1984. Statistics of reproductive rate estimates, and their implications for population projection. Report of the International Whaling Commission Special Issue 6: 161-173.
- Hammond, P. S., S. A. Mizroch, and G. P. Donovan, editors. 1990. Individual recognition of cetaceans: use of photo-identification and other techniques to estimate population parameters. Report of the International Whaling Commission Special Issue 12.
- Katona, S. K., and J. A. Beard. 1990. Population size, migrations and feeding aggregations of the humpback whale (*Megaptera novaeangliae*) in the western North Atlantic Ocean. Report of the International Whaling Commission Special Issue 12:295-305.
- Katona, S. K., and H. P. Whitehead. 1981. Identifying humpback whales using their natural markings. *Polar Record* 20: 439-444.
- Palsbøll, P. J., A. Vader, I. Bakke, and M. R. El-Gewely. 1992. Determination of gender in cetaceans by the polymerase chain reaction. *Canadian Journal of Zoology* 70:2166-2170.
- Payne, R., V. Rowntree, J. S. Perkins, J. G. Cooke, and K. Lankester. 1990. Population size, trends and reproductive parameters of right whales (*Eubalaena australis*) off Peninsula Valdes, Argentina. Report of the International Whaling Commission Special Issue 12:271-278.
- Press, W. H., B. P. Flannery, S. A. Teukolsky, and W. T. Vetterling. 1988. Numerical recipes: the art of scientific computing. Cambridge University Press, Cambridge, England.
- Straley, J. M. 1994. Seasonal characteristics of humpback whales (*Megaptera novaeangliae*) in southeast Alaska. Master's thesis. University of Alaska, Fairbanks, Alaska, USA.
- Wells, R. S., and M. D. Scott. 1990. Estimating bottlenose dolphin population parameters from individual identification and capture-recapture techniques. Report of the International Whaling Commission Special Issue 12:407-417.
- Wiley, D. N., and P. J. Clapham. 1993. Does maternal condition affect the sex ratio of offspring in humpback whales? *Animal Behaviour* 46:321-324.

APPENDIX A

Sighting and birth histories of individual females photographed between 1979 and 1991. Sighting history indicates whether a female was seen as a calf (C), was seen with a calf (1), was seen without a calf (0), was not seen (-), or was known to be dead (D). Death was established only when a fluke or dorsal fin photograph matched that from a recovered carcass.

| Identification no. | Year | | | | | | | | | | | | |
|--------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
| AB1 | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | - | 0 | 1 | - |
| AL1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | - | - | - | - |
| AN2 | | | | | | 0 | 0 | 0 | 1 | 0 | - | - | - |
| AN3 | | | | | | | 0 | 0 | 0 | 0 | 1 | 0 | - |
| AP1 | | | | 0 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | - |
| AR2 | | | 0 | 0 | - | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| AR5 | | | | | | 0 | 0 | 0 | - | 0 | 0 | 1 | 0 |
| AS1 | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| AS8 | | | | | | | | | | | 1 | - | - |
| BA1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | - | - | 0 | 0 | 1 | - |
| BA4 | | | | | | 0 | 0 | 0 | 0 | 0 | - | 0 | 1 |
| BE4 | | | | | | | | | | | | 1 | - |
| BI2 | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | - | - | - | - | - |
| BI4 | | | | | | | | | | 0 | 1 | 0 | 1 |
| BU2 | 0 | - | 0 | 0 | - | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| C10 | | | | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| C2A | | | | | | | 0 | - | 0 | 0 | 1 | 0 | 0 |
| CA4 | | | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| CA5 | | | | 1 | 0 | 1 | 0 | 0 | - | - | 0 | 1 | 0 |
| CH2 | | | | | | 0 | 0 | 0 | 0 | 0 | - | 0 | 1 |
| CI3 | | | 0 | 0 | - | 0 | - | 0 | - | 0 | 1 | 0 | - |
| CL5 | | | | | 0 | 0 | 0 | - | - | 0 | 0 | 0 | 1 |
| CO3 | | 0 | 0 | 0 | 0 | 1 | 0 | 0 | - | - | - | 1 | - |
| CO9 | | | | | 0 | 0 | 0 | 1 | 0 | - | - | - | - |
| DE4 | | | | | | | | | 0 | 1 | - | - | 1 |
| DO1 | | | 0 | 0 | - | - | 1 | - | - | 1 | D | D | D |
| DO3 | | | | | | | 0 | 0 | 0 | 0 | 1 | - | 1 |
| EB1 | | | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 0 | 0 | 1 | - |
| EI1 | | | | | 1 | 0 | - | - | - | - | - | - | - |
| EI2 | | | | | | | | 0 | - | 1 | 0 | 0 | - |
| EQ1 | 1 | 0 | 1 | 0 | - | 1 | - | 1 | - | 1 | - | 1 | - |
| FA1 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 |
| FE1 | 1 | 0 | 1 | 0 | | 0 | - | 0 | 0 | - | - | - | - |
| FE3 | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| FI2 | | | | | 1 | 0 | - | 1 | - | 0 | 1 | - | - |
| FL1 | | | 0 | 1 | - | - | 1 | 0 | 1 | 0 | - | - | - |
| FR1 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | - | 1 | 0 | 1 | 0 |
| GL2 | | | | | | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| HA2 | | 0 | 0 | 0 | | 0 | - | - | - | - | 1 | - | 1 |
| HA5 | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | - | - |
| HO1 | | | 0 | - | - | - | - | 0 | 1 | - | - | - | - |
| IS1 | 1 | 0 | 1 | 0 | - | 1 | - | 1 | 0 | 1 | 1 | - | 0 |
| IV1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| IV2 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |
| JA1 | | | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | - | - | - |
| LA2 | | 0 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 1 | 0 | - |
| LE1 | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| LI1 | 0 | 0 | 0 | 0 | - | 0 | 1 | - | - | 0 | 1 | 0 | 0 |
| LI3 | | | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| LO3 | | | | | | | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| LY1 | | | | 0 | - | - | - | 1 | 0 | 0 | 1 | 0 | 1 |
| MA1 | 0 | 0 | 0 | 1 | 0 | 1 | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| MA11 | | | | | | | | | | | 1 | - | - |
| MI2 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| MI5 | | | | | | | 0 | 0 | - | 0 | 1 | 0 | - |
| MO1 | | | | 0 | - | - | - | - | - | 0 | 1 | 0 | - |
| MO4 | | | | 0 | 0 | 0 | 0 | 1 | 0 | - | - | - | - |
| NE2 | | | | 0 | - | - | - | 1 | - | - | - | - | - |
| NI2 | | | | | | | 0 | - | 1 | 0 | 0 | 1 | 0 |
| NU1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | - | 1 | - | 1 |
| OL1 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 1 |
| ON1 | | 0 | 0 | 0 | - | 0 | 0 | 0 | 0 | 0 | - | 0 | 1 |
| OR1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| PA5 | | | | | | | | | | | | 1 | - |
| PE2 | 1 | - | 0 | 1 | 0 | 0 | 1 | 0 | 1 | - | 1 | 1 | D |

APPENDIX A. Continued.

| Iden- tifi- cation no. | Year | | | | | | | | | | | | |
|---------------------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
| PE3 | | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 | 0 |
| PE6 | | | | | | | | | | 1 | 1 | 1 | - |
| PH1 | | | | 0 | - | - | 0 | 1 | - | - | - | - | - |
| PH3 | | | | | | | | 0 | 0 | 0 | 0 | 0 | 1 |
| PO2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | D | D | D | D |
| QU3 | | | | | | | 0 | 0 | 0 | 0 | - | - | 1 |
| RA3 | | | 0 | - | - | 0 | 0 | 0 | 0 | 0 | - | 1 | - |
| RO2 | | | | | | 0 | - | - | - | - | - | 1 | 0 |
| RU1 | | 0 | 0 | 0 | 1 | 0 | 1 | 0 | - | 0 | 1 | 0 | - |
| SA1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| SA3 | | | | | | 0 | 1 | - | 1 | - | 1 | - | - |
| SC1 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | - | 1 | 0 |
| SE4 | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| SH2 | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| SI1 | 0 | - | 0 | 0 | 0 | 0 | 0 | 1 | - | 1 | - | - | - |
| SI2 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | 0 |
| SI3 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 | - | 1 | - |
| SO1 | 0 | 0 | 0 | 0 | 0 | - | 1 | 0 | 1 | 0 | 0 | 1 | 0 |
| SO2 | | | | | 1 | - | - | - | - | - | - | - | - |
| SP1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| SP4 | | 0 | - | - | - | - | 0 | - | - | 0 | 1 | 0 | 1 |
| ST2 | | | | 0 | 0 | - | 0 | 0 | 1 | 0 | 0 | 1 | 0 |
| ST6 | | | | | | 0 | - | 0 | 1 | 0 | 0 | 1 | - |
| TO5 | | | | | | | 0 | 0 | - | - | 0 | 1 | - |
| TR5 | | | | 1 | - | 1 | 0 | 1 | - | - | - | - | - |
| TU2 | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| VA1 | | | | | | | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| VE2 | | | | 0 | - | - | - | 0 | - | 0 | 1 | - | 0 |
| VE3 | | | | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 | 0 | 1 |
| WA1 | | | | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 1 | 0 | 1 |
| AM1 | | | | | | | | C | - | 0 | 0 | 0 | 0 |
| AM2 | | | | | | | | | C | 0 | - | - | - |
| AN1 | | | | | C | 0 | 0 | 0 | 0 | 0 | 0 | 1 | - |
| AP3 | | | | | | | C | 0 | 0 | 0 | 0 | - | 1 |
| AS3 | | | | | C | - | - | - | - | - | - | - | - |
| AU1 | | | | C | 0 | - | - | - | - | - | - | - | - |
| BA3 | | | | C | C | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| BE1 | | C | 0 | 0 | 0 | 0 | 1 | 0 | 0 | D | D | D | D |
| C40 | | | | | | | C | 0 | - | - | - | - | - |
| CA12 | | | | | | | | | C | 0 | 0 | 0 | 0 |
| CH10 | | | | | | | | C | 0 | 0 | 0 | 0 | 0 |
| CO7 | | | | | C | 0 | 0 | - | - | - | - | - | - |
| CU2 | | | | | | | | C | 0 | 0 | 0 | - | - |
| CU3 | | | | | | | | | | C | 0 | - | - |
| CU4 | | | | | | | | | C | - | - | - | - |
| DI2 | | | | | C | - | 0 | 0 | - | - | 0 | - | - |
| EP1 | | C | 0 | 0 | - | - | - | - | - | - | - | - | - |
| EX1 | | | | | | | C | 0 | 0 | 0 | - | - | - |
| FI6 | | | | | | | | C | 0 | 0 | 0 | 0 | 0 |
| FR5 | | | | | | | | C | 0 | 0 | 0 | 0 | 1 |
| HU1 | | | | | | | C | 0 | 0 | - | - | - | - |
| IB1 | C | 0 | 0 | 0 | 0 | 0 | 0 | 1 | - | - | - | - | - |
| IS3 | | | | | | | | C | 0 | 0 | 0 | 0 | - |
| KK1 | | | | | | | C | 0 | 0 | - | - | - | - |
| MA4 | | | | | | C | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| MU2 | | | | | | | | | C | 0 | - | - | - |
| OW1 | | | | | | | | C | 0 | - | 0 | 0 | 0 |
| PL1 | | | | | | | C | - | - | - | - | - | - |
| S1P | | | | | | C | 0 | 0 | 0 | 0 | 1 | 0 | 1 |
| SC2 | | | C | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 |
| SP12 | | | | | | | | | | C | 0 | - | - |
| TA2 | | | C | 0 | 0 | 0 | 0 | 0 | 1 | D | D | D | D |
| TA3 | | C | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 |
| TA4 | | | | | | | C | 0 | 0 | 0 | 0 | 0 | 1 |
| TE3 | | | | | | | | | C | 0 | 0 | 0 | 0 |
| TH5 | | | | | | | C | 0 | 0 | 0 | 0 | 0 | 0 |
| TO6 | | | | | | | | | | C | 0 | 0 | 0 |
| TR4 | | | | C | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 1 | 0 |

APPENDIX A. Continued.

| Identification no. | Year | | | | | | | | | | | | |
|-----------------------|------|------|------|------|------|------|------|------|------|------|------|------|------|
| | 1979 | 1980 | 1981 | 1982 | 1983 | 1984 | 1985 | 1986 | 1987 | 1988 | 1989 | 1990 | 1991 |
| WH3 | | | | | | | | | C | 0 | 0 | 0 | 0 |
| WI2 | | | | | | | | C | - | - | - | - | - |
| BR6 | | | | | | | | | | | | C | - |
| CL8 | | | | | | | | | | | | C | 0 |
| DA5 | | | | | | | | | | | C | 0 | 0 |
| F18 | | | | | | | | | | | C | 0 | 0 |
| ME4 | | | | | | | | | | | | C | 0 |
| NI4 | | | | | | | | | | | C | - | 0 |
| PA10 | | | | | | | | | | | C | - | 0 |
| RA9 | | | | | | | | | | | C | 0 | - |
| RA7 | | | | | | | | | | | C | - | - |
| RE4 | | | | | | | | | | | | C | 0 |
| RO5 | | | | | | | | | | | | C | 0 |
| SC11 | | | | | | | | | | | C | - | - |
| SC12 | | | | | | | | | | | C | - | 0 |
| SE8 | | | | | | | | | | | | C | - |
| SP13 | | | | | | | | | | | | C | 0 |
| ST15 | | | | | | | | | | | C | - | - |
| SU5 | | | | | | | | | | | | C | 0 |
| ZE2 | | | | | | | | | | | C | - | - |

APPENDIX B

SENSITIVITY TO STOCHASTIC DYNAMICS

The methods presented here for estimating birth-interval and first-birth probabilities were developed without explicit consideration for stochastic population dynamics. They are based on the customary assumptions that the population is in stable age distribution and that vital rates are constant through time. The simulation model used to estimate the variance of birth-interval parameters does include demographic stochasticity (rates for individuals are treated as stochastic probabilities) but does not include environmental stochasticity (time-varying rates). Insufficient information exists to accurately parameterize a population model for humpback whales that includes environmental stochasticity. Instead we will explore the sensitivity of our methods to violations in assumptions using a worst feasible scenario for time-varying vital rates and nonstable age structure based on our knowledge of humpback whale dynamics.

Within our time series, the only observed event that might have caused a major perturbation in the dynamics of the Gulf of Maine humpback whale population occurred in 1987/1988. In 1987, at least 14 whales of all age classes died in a mass mortality event that was apparently caused by dinoflagellate toxin concentrated in a noncustomary prey (Geraci et al. 1989), and in the subsequent year, 1988, the apparent pregnancy rate was the lowest of our time series (Table 3). For our sensitivity analysis we assumed that our estimated birth-interval and survival parameters are valid in most years, but that, on average, once every 10 yr the birth-interval and first-birth parameters would decrease by 50% and survival rates would decrease by 10%. In fact, this type of event has been observed only once in the 20 yr that this population has been intensively studied (1976–1995), and, therefore, we feel justified in calling our sensitivity study a worst feasible scenario.

We used the same simulation model for this sensitivity study as was used to estimate variance in parameter estimates. The birth-interval probabilities, the first-birth probabilities, and the calf and noncalf survival rates estimated for this population (*Results* section) were used as the nominal values in "normal years." "Bad years" were allowed to occur stochastically with probability of 0.1 each year. In a "bad year," the nominal values of each of the five birth-interval probabilities and the four first-birth probabilities were multiplied by 0.5. The nominal values for calf and noncalf survival rates were multiplied by 0.9 in "bad years." The population sim-

ulation was not started with a stable age distribution; rather, the stochastic population simulation was run for 38 yr prior to the 12 yr of simulated sampling (for a total of 50 yr). We ran 1000 iterations of the population simulation starting with an initial population of 40 individuals and calculated the mean estimated parameters for birth-interval probabilities, first-birth probabilities, and population growth rate estimated from the birth-interval model.

The expected values for the realized birth-interval probabilities and first-birth probabilities were calculated as the nominal values times the probability of a normal year (0.9) plus the "bad year" values times the probability of a bad year (0.1). The expected values for the population growth rate λ are taken as the mean of the realized population growth rates from 1000 iterations. For simplicity, we present only the first three birth-interval and first-birth parameters in Table B1. These results indicate that birth-interval and first-birth probabilities are estimated without appreciable bias; the standard errors in each case are greater than the apparent bias (the difference between expected and mean estimated values). In contrast, a small bias appears evident in estimates of population growth rate using the birth interval model. The realized population growth rate from 1000 simulations (1.047, SE = 0.0003) is significantly different from the mean estimated population growth rate (1.050, SE = 0.0003). Although the bias in estimating population growth rate is statistically significant, it is small relative to the standard deviation and is therefore small relative to the expected error from a single population projection. Nonetheless, it may be appropriate to apply a bootstrap bias correction to a population growth rate from this model if such a simulation were based on realistic estimates of time-varying vital rates rather than on a worst feasible scenario.

Although this sensitivity study shows that parameter estimation for humpback whales is not biased by likely violations of assumption regarding stable age distribution or time-varying rates, this conclusion might not be valid in applying the birth-interval model to other populations. It is difficult to conceive of a generalized sensitivity test for all possible deviations from stable age distribution or all possible patterns of time-varying rates. It is likely that a case-specific sensitivity study such as this one will be required for all applications of the birth-interval model.

TABLE B1. Expected values of birth-interval parameters (γ), first-birth parameters (β), and population growth rate (λ) for a population experiencing episodic "bad years" and observed values estimated from Monte Carlo simulation studies. Means, standard deviations, and standard errors are based on 1000 iterations. Only the first three birth-interval and first-birth parameters are presented.

| Expected/ estimated value | β_1 | β_2 | β_3 | γ_1 | γ_2 | γ_3 | λ |
|------------------------------|-----------|-----------|-----------|------------|------------|------------|-----------|
| Expected values | 0.040 | 0.561 | 0.763 | 0.219 | 0.445 | 0.476 | 1.047 |
| Mean estimated values | 0.040 | 0.560 | 0.765 | 0.219 | 0.444 | 0.479 | 1.050 |
| SD estimated values | 0.014 | 0.049 | 0.072 | 0.090 | 0.144 | 0.246 | 0.011 |
| SE estimated values | 0.0004 | 0.002 | 0.002 | 0.003 | 0.005 | 0.008 | 0.0003 |