

Declining survival probability threatens the North Atlantic right whale

HAL CASWELL^{*†}, MASAMI FUJIWARA^{*}, AND SOLANGE BRAULT[‡]

^{*}Biology Department MS 34, Woods Hole Oceanographic Institution, Woods Hole, MA 02543; and [‡]Biology Department, University of Massachusetts, 100 Morrissy Boulevard, Boston, MA 02125

Communicated by Joel E. Cohen, The Rockefeller University, New York, NY, December 17, 1998 (received for review October 14, 1998)

ABSTRACT The North Atlantic northern right whale (*Eubalaena glacialis*) is considered the most endangered large whale species. Its population has recovered only slowly since the cessation of commercial whaling and numbers about 300 individuals. We applied mark-recapture statistics to a catalog of photographically identified individuals to obtain the first statistically rigorous estimates of survival probability for this population. Crude survival decreased from about 0.99 per year in 1980 to about 0.94 in 1994. We combined this survival trend with a reported decrease in reproductive rate into a branching process model to compute population growth rate and extinction probability. Population growth rate declined from about 1.053 in 1980 to about 0.976 in 1994. Under current conditions the population is doomed to extinction; an upper bound on the expected time to extinction is 191 years. The most effective way to improve the prospects of the population is to reduce mortality. The right whale is at risk from entanglement in fishing gear and from collisions with ships. Reducing this human-caused mortality is essential to the viability of this population.

The North Atlantic northern right whale (*Eubalaena glacialis*) is considered the most endangered of any population of large whales. The preferred target of commercial whalers during the 18th and 19th century, it was reduced to near extinction by 1900 (1, 2). It has recovered only slowly since the elimination of commercial whaling. There are now about 300 individuals in the western Atlantic; the eastern Atlantic population is considered extinct (2, 3). Right whales are found along the eastern coast of North America from Florida to the Bay of Fundy and are at risk of mortality from entanglement with fishing gear, collisions with ships, and pollution (2, 4–6).

We report here the first statistically rigorous estimates of survival for *E. glacialis*. We also develop a stochastic model from which we estimate population growth rates and extinction probabilities. Our results are a first step toward models that can be used to choose targets for management interventions (for example, see refs. 7–10).

1. METHODS

Individual right whales can be recognized by markings, scars, and callosity patterns. Since 1980 the New England Aquarium (NEA) has maintained a catalog of photographically identified whales (11, 12). These data, supplied to us by NEA in July 1997, contained sightings from 1980 through 1996.

We used mark-recapture statistics (13, 14) to estimate survival and sighting probabilities from these data. An individual is “marked” when first identified and “recaptured” when sighted in a subsequent year. We treat years as a sampling unit, but most observations occur in August and September.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked “advertisement” in accordance with 18 U.S.C. §1734 solely to indicate this fact.

PNAS is available online at www.pnas.org.

In all years except one, at least 50%, and usually more than 70%, of the individuals sighted are seen in those months.

We define the probabilities

$$p_i = P[\text{survival from year } i \text{ to } i + 1] \quad [1]$$

$$s_i = P[\text{sighting in year } i]. \quad [2]$$

Each individual has a sighting history, the probability of which can be written in terms of the p_i and s_i , by using methods in refs. 14 or 15. The survival probability p is what demographers call a “crude” rate (16, 17). The term is not an epithet; it indicates that the probability is averaged over the whole population rather than calculated separately for age classes, sexes, or other categories.

1.1. Model Fitting and Model Selection

We fitted 10 models to the data, each representing a different hypothesis about the p_i and s_i (Table 1). The likelihood of a model is proportional to the product of the probabilities of the individual sighting histories. We used the MATLAB routine `fminu` to find parameter values maximizing the likelihood and the profile likelihood from ref. 14 to generate 95% confidence intervals or regions.

In models M_1 – M_4 , survival and sighting probability are either fixed at constant values or allowed to vary freely from year to year. Model M_4 , in which both p_i and s_i are free to vary from year to year, is known as the Cormack–Jolly–Seber (CJS) model (18–20).

Models M_5 and M_6 parameterize survival probability as a logistic function (21) of time

$$P_t = \frac{e^{a+bt}}{1 + e^{a+bt}} \quad [3]$$

with sighting probability either constant (M_5) or variable (M_6). The parameter b gives the magnitude and direction of any trend in survival probability, increasing if $b > 0$ and declining if $b < 0$.

After 1990, two offshore sites (Great South Channel and the Nova Scotian Shelf) were no longer regularly sampled. This change might artificially reduce survival probability if certain individuals had a tendency to favor those sites. Sightings of such individuals would become less likely in the 1990s, and this might be misinterpreted as a reduction in survival.

To address this possibility, we developed an individual covariate to measure the tendency of each whale to be seen exclusively in the offshore region. This “offshore index,” f_j , is the proportion of years in which whale j was observed in which it was seen only in the offshore sites:

$$f_j = \frac{\text{years seen only offshore}}{\text{years seen}}. \quad [4]$$

Abbreviations: NEA, New England Aquarium; CJS, Cormack–Jolly–Seber; AIC, Akaike Information Criterion.

[†]To whom reprint requests should be addressed. e-mail: hcaswell@whoi.edu.

Table 1. The models fitted to the photographic catalog data, with the log likelihood (L), number of parameters (n) and the AIC measured relative to that of the best model (ΔAIC)

Model	Survival	Sighting	log L	n	ΔAIC
M_1	Constant	Constant	-2421.8	2	372.4
M_2	Constant	Variable	-2282.5	17	123.8
M_3	Variable	Constant	-2397.5	17	353.8
M_4	Variable	Variable	-2257.2	31	101.2
M_5	Logistic	Constant	-2420.2	3	371.2
M_6	Logistic	Variable	-2271.9	18	104.6
M_7	Logistic	Variable*	-2170.1	— [†]	— [†]
M_8	Variable	Variable [‡]	-2192.7	47	4.2
M_9	Logistic	Variable [‡]	-2203.6	34	0.0
M_{10}	Constant	Variable [‡]	-2211.14	33	13.1

*Strictly offshore whales excluded.

[†]Degrees of freedom and AIC not comparable with other models.

[‡]Sighting probability depends on offshore index.

If $f_j = 0$, elimination of offshore sampling has no effect on the data obtained from whale j , because we require only a single sighting to know that a whale is alive in a given year. If $f_j = 1$, whale j is a "strictly offshore" animal; data on such animals will be most affected by the change in sampling. The data set contains 21 strictly offshore whales.

Model M_7 removes the 21 strictly offshore whales from the data set and repeats the analysis of M_6 . Models M_8 and M_9 parameterize the sighting probability of individual j in year t by the logistic function

$$s_j(t) = \frac{e^{c_i+d_i f_j}}{1 + e^{c_i+d_i f_j}} \quad [5]$$

If $d_i < 0$, individuals with higher offshore index are less likely to be seen in year t . If the change in sampling affected sighting probability, d_i should become more negative after 1990.

We used likelihood ratio tests and the Akaike Information Criterion (AIC ; refs. 14, 22, 23) to compare models. If M_i with n_i parameters and likelihood L_i is a special case of M_j with n_j parameters, the log likelihood ratio is $G^2 = -2(\log L_i - \log L_j)$. G^2 is compared to a χ^2 distribution with $n_j - n_i$ degrees of freedom. If it is significantly large, the null hypothesis M_i is rejected in favor of M_j . AIC is

$$AIC_i = -2 \log L_i + 2n_i \quad [6]$$

The model that minimizes AIC has the best balance of goodness of fit and parsimony.

2. RESULTS: SIGHTING AND SURVIVAL PROBABILITIES

2.1. Sighting Probability

Time-invariant sighting probability estimates are $\hat{s} = 0.656$ from M_1 , $\hat{s} = 0.654$ from M_3 , and $\hat{s} = 0.654$ from M_5 . The null hypothesis of time-invariant sighting probability is, however, overwhelmingly rejected (Table 2).

Fig. 1a shows the sighting probability from model M_4 (the CJS model). The estimates from models M_2 , M_6 , and M_7 are nearly identical. Thus the pattern of sighting probability is robust to assumptions about survival. Sighting probability is correlated with sampling effort ($r = 0.77$, $P < 0.0005$; Fig. 1b), measured as the total number of sampling days.

2.2. Survival Probability

Time-invariant estimates of survival probability are $\hat{p} = 0.965$ from M_1 and $\hat{p} = 0.959$ (95% confidence interval [0.951, 0.965]) from M_2 . The null hypothesis of constant survival is rejected (Table 2). Fig. 2a shows estimates of survival probability from M_4 (the CJS model).

Table 2. Likelihood ratio tests of temporal variation in sighting probability, temporal variation in survival probability, and the logistic trend in survival probability

Test	G^2	df	Probability
Variation in sighting probability			
M_2 vs. M_1	278.6	14	$P \ll 10^{-14}$
M_4 vs. M_3	280.6	14	$P \ll 10^{-14}$
M_6 vs. M_5	296.6	15	$P \ll 10^{-14}$
Variation in survival probability			
M_3 vs. M_1	48.6	15	$P = 2.0 \times 10^{-5}$
M_4 vs. M_2	50.6	14	$P = 4.9 \times 10^{-6}$
Logistic trend in survival			
M_6 vs. M_2	21.2	1	$P = 4.1 \times 10^{-6}$
M_9 vs. M_{10}	15.1	1	$P = 7.0 \times 10^{-5}$

2.3. Trend in Survival Probability

Fig. 2 shows the estimated logistic trend in survival from M_6 . (The curve is fit directly to individual histories, not to the points in the figure.) The null hypothesis of no trend ($b = 0$) is rejected (Table 2).

The estimates of b are negative in all three models (M_6 , M_7 , and M_9) that include variable sighting probability, implying a declining trend in survival (Table 3). The 95% confidence regions for \hat{a} and \hat{b} exclude $\hat{b} = 0$ (Fig. 4).

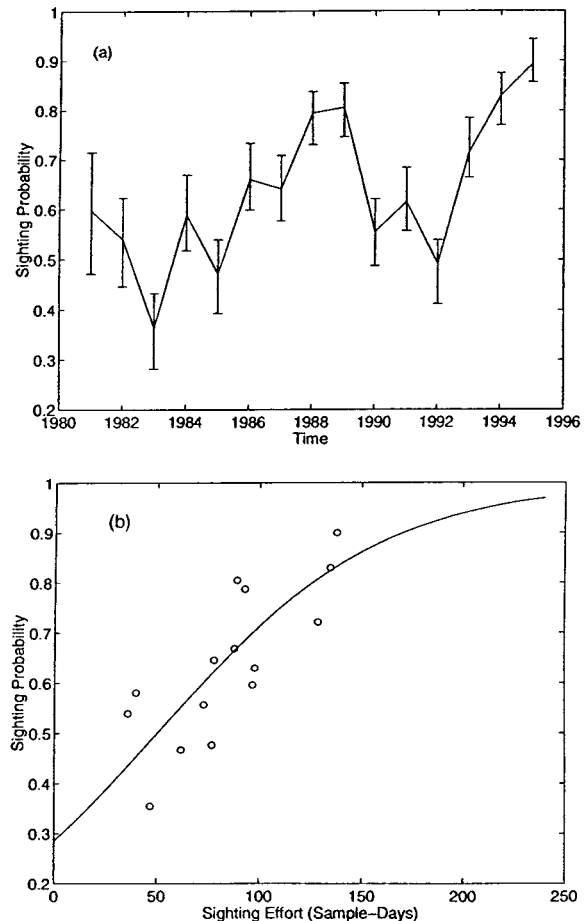


FIG. 1. (a) The sighting probability and 95% profile likelihood confidence intervals from model M_4 , the CJS model. (b) Sighting probability from M_4 as a function of sampling effort. The curve is a logistic regression fitted by least squares.

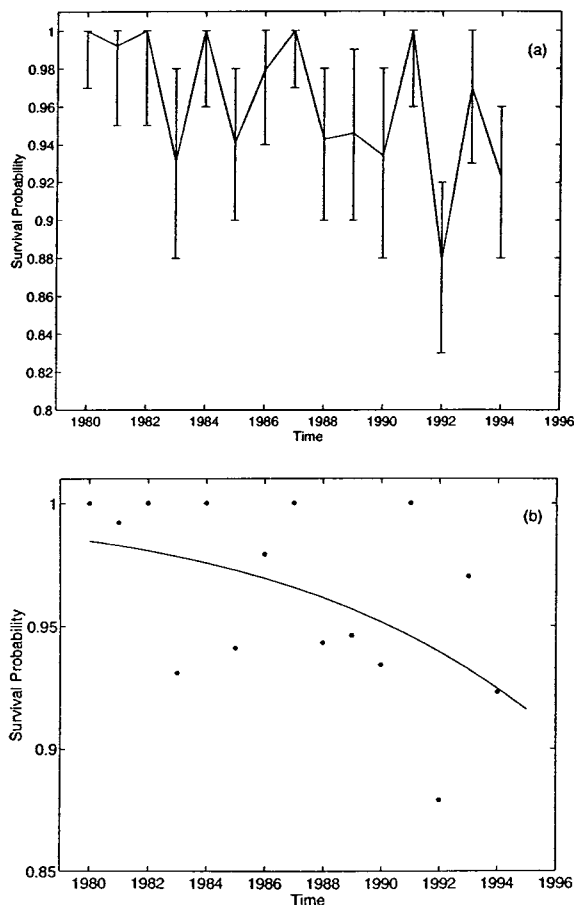


FIG. 2. (a) Survival probability from model M_4 , with pointwise 95% profile likelihood confidence intervals. (b) The logistic trend in survival probability from model M_6 . Points are estimates from the CJS model (M_4), included for comparison.

2.3.1. Changes in Sampling Protocol. As predicted, the offshore index has an increasingly negative effect on sighting after 1990 (Fig. 3). The 95% confidence intervals for the slope parameters include zero for most of the years before 1990, but not after 1990.

However, the trend parameter b is, if anything, slightly more negative in M_7 , which eliminates strictly offshore whales, and M_9 , in which sighting probability is a function of the offshore index, than in M_6 (Table 3).

Survival estimates from models M_4 (the CJS model) and M_8 (variable survival, with the offshore index) are very similar (Fig. 4). When the offshore index is included, the null hypothesis of constant survival is rejected (Table 2). The survival trends projected by models M_6 , M_7 , and M_9 are also very similar (Fig. 4). There is thus no evidence for the hypothesis that the trend in survival is an artifact of the change in sampling.

As yet another check on the results, we used the method of ref. 24 to correct for extra-binomial variation in the data, which may result from heterogeneity or lack of independence. The survival trend is still significant when tests are adjusted with a variance inflation factor, and the modified AIC (QAIC; refs. 14 and 23) still picks M_9 as the best model.

Table 3. The logistic trend parameters a and b

Model	a	b
M_6	4.28	-0.118
M_7	4.60	-0.133
M_9	4.46	-0.125

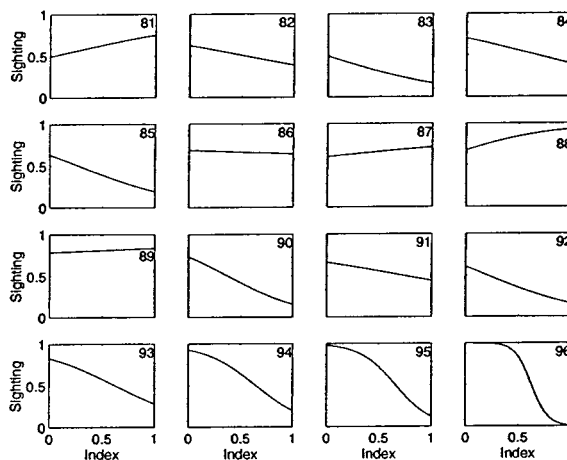


FIG. 3. Estimated sighting probability from 1980 to 1996 as a function of the offshore index, from model M_8 .

2.3.2. Model Selection. Model M_9 (a logistic trend in survival probability, with sighting a function of the offshore index) has the smallest AIC , and is thus the best of the models considered here. We use it for our analyses of population viability in the next section.

3. IMPLICATIONS FOR POPULATION VIABILITY

According to model M_9 , crude survival probability has declined from about 0.99 to about 0.94 in 15 years, a more than 5-fold increase in mortality rate in less than a generation. To explore the implications for population viability, we use a branching process model (25) that includes demographic stochasticity and allows us to predict population growth rate and extinction probability.

An individual at time t may produce 0, 1, 2, ... individuals at time $t + 1$. These individuals are customarily called “offspring,” but may include survival of the original individual as well as the production of new individuals. The model is specified by the probability distribution of offspring number.

A female right whale may produce 0, 1, or 2 females the following year. We assume that the death of a parent results in the death of a calf in its first year. Thus a female at t produces 0 offspring if it dies before $t + 1$, 1 offspring (itself) if it survives without reproducing, and 2 offspring (itself and its calf) if it survives and reproduces. Let p be the survival probability and let m be the probability of producing a female calf. The probabilities $P[i]$ of producing i offspring are then

$$\begin{aligned}
 P[0] &= (1 - p)(1 - m) + (1 - p)m \\
 P[1] &= p(1 - m) \\
 P[2] &= pm.
 \end{aligned}
 \tag{7}$$

We calculate m as

$$m = \frac{c}{2T},
 \tag{8}$$

where T is the mean inter-birth interval, c is the fraction of females that are reproductively active, and we assume a 1:1 sex ratio at birth (26). The mean inter-birth interval between 1980 and 1992 was 3.7 years (5). Recent analyses (S. D. Kraus, personal communication) find a significant linear increase in T , from $T \approx 3$ in 1980 to $T \approx 5$ in the late 1990s. The proportion of reproductively active females is $c \approx 0.38$ (26). Thus $m = 0.063$ when $T = 3$ years, $m = 0.051$ when $T = 3.7$, and $m = 0.038$ when $T = 5$. The latter figure is very close to that obtained by dividing the mean number of calves produced per year (approximately 11; ref. 5) by the number of females (approximately 150), and dividing by 2, which gives $m = 0.037$.

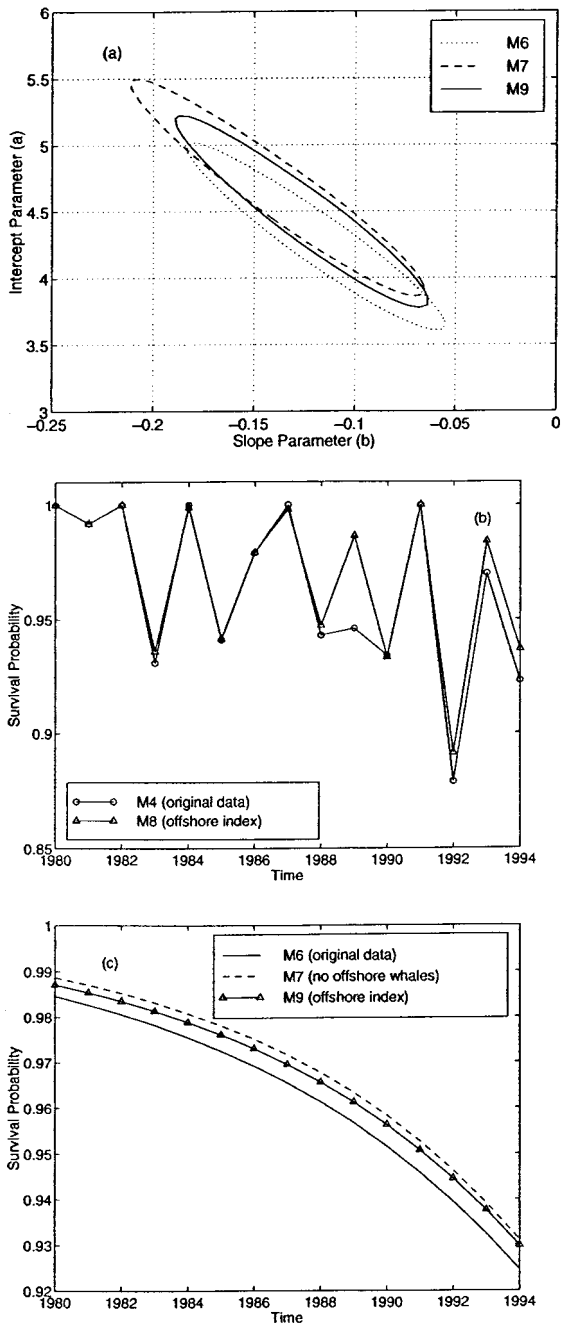


FIG. 4. (a) Joint 95% profile likelihood confidence regions for the logistic parameters a and b from models M_6 , M_7 , and M_9 . (b) Survival probability estimates from model M_4 (the CJS model) and M_8 (sighting a function of the offshore index). (c) Trends in survival probability from models M_6 , M_7 (strictly offshore whales excluded), and M_9 (with sighting dependent on offshore index).

3.1. Population Growth Rate

The probability generating function of the offspring distribution, g , is

$$g(s) = P[0]s^0 + P[1]s^1 + P[2]s^2 \quad [9]$$

$$= [1 - p] + p[1 - m]s + pms^2, \quad [10]$$

where s is a dummy variable, $|s| < 1$. The population growth rate is

$$\lambda = \left. \frac{dg(s)}{ds} \right|_{s=1} = p + pm, \quad [11]$$

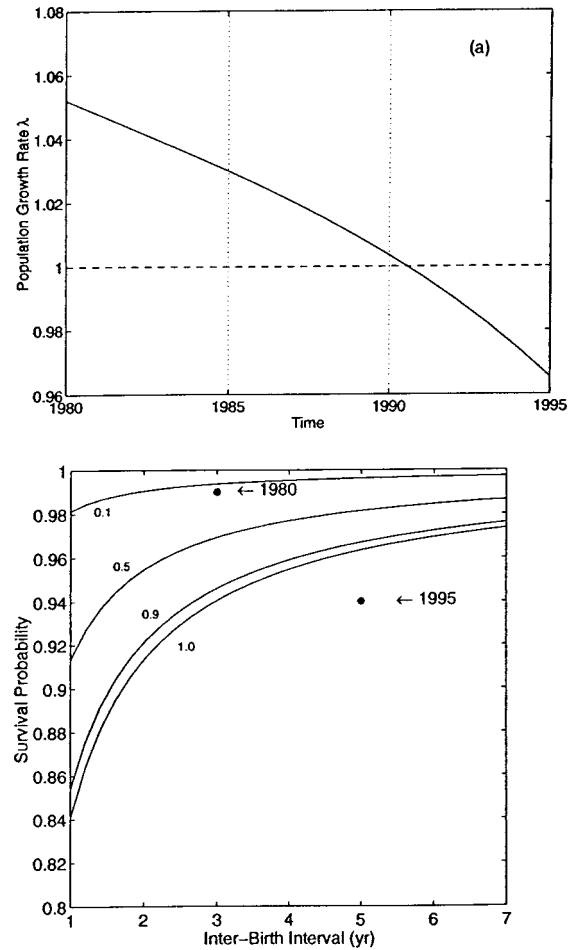


FIG. 5. (a) Population growth rate λ from **11**, obtained by combining the trends in survival (from M_9) and inter-birth interval. (b) Contours of extinction probability for the lineage of an individual as a function of inter-birth interval T and survival probability p . Points corresponding to 1980 and 1995 are indicated.

which is the familiar sum of the survival probability and the birth rate. If $\lambda < 1$, the population is decreasing. If $\lambda \leq 1$, extinction is certain. If $\lambda > 1$, the mean population increases, but extinction may still occur due to demographic stochasticity. Combining estimates of p and T , we find the following:

p	T			[12]
	3	3.7	5	
0.99	$\hat{\lambda} = 1.053$	$\hat{\lambda} = 1.040$	$\hat{\lambda} = 1.028$	
0.94	$\hat{\lambda} = 0.999$	$\hat{\lambda} = 0.988$	$\hat{\lambda} = 0.976$	

The combination of declining p and increasing T has moved the population well below the critical value for persistence. The result is $\hat{\lambda} = 0.976$, a 2.4% decrease per year. By using the survival trend from M_9 and the inter-birth interval trend, we find that $\hat{\lambda}$ reached the critical value $\lambda = 1$ circa 1990 (Fig. 5). Even with T fixed at its mean value (3.7), $\hat{\lambda}$ has declined to 0.988. The population cannot persist under the best estimates of current conditions.

3.2. Extinction Probability

The probability q of extinction of the lineage formed by an individual is the smallest positive solution of the equation

$$q = g(q) \quad [13]$$

$$= (1 - p) + p(1 - m)q + pmq^2, \quad [14]$$

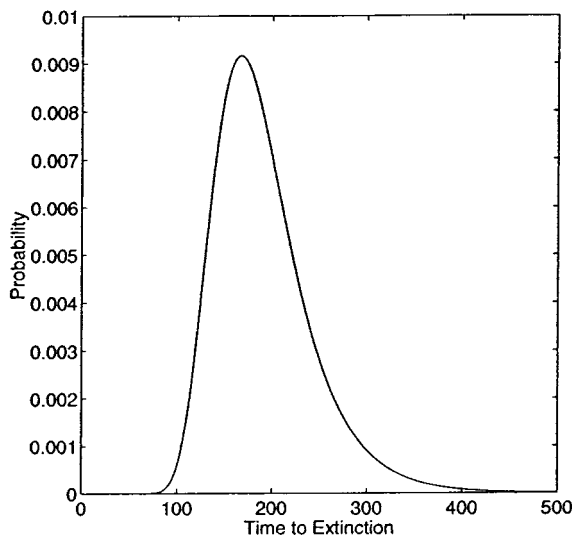


FIG. 6. The probability distribution of extinction time for a population of 150 females, with constant survival probability $p = 0.94$ and inter-birth interval $T = 5$ years.

where $g(\cdot)$ is the probability generating function (25). In 1980, with $p = 0.99$ and $T \approx 3$, the probability of extinction was $q = 0.160$. By 1995, extinction had become certain, since $\hat{\lambda} < 1$ (Fig. 5).

The probability of extinction of N independent individuals is q^N . The North Atlantic right whale population contains $N \approx 150$ females. Thus population extinction due to demographic stochasticity is highly unlikely as long as $\lambda > 1$. However, under current conditions, $\lambda < 1$ and eventual extinction is certain. If the vital rates were fixed at their current values, the distribution of time to extinction is shown in Fig. 6. The mean extinction time is 191 years, the median is 182 years, and extinction is almost certain by 400 years.

These calculations assume constant vital rates; they do not include continued trends in survival or fertility. They also assume that females survive and reproduce independently, and that there are always enough males to fertilize females. If the population continues to decline, it will eventually reach a point where breakdowns in social structure or failure to find mates will reduce reproduction and hasten extinction.

4. CONCLUSIONS AND DISCUSSION

Crude survival probability has declined since 1980 from about 0.99 to about 0.94. The decline is statistically significant, and is not an artifact of changes in the sampling program during the study. The decline in survival and the increase in inter-birth interval have reduced estimated population growth rate from $\hat{\lambda} = 1.053$ to $\hat{\lambda} = 0.976$.

The null hypothesis of constant survival is rejected with a very small probability of Type I error ($P = 7.0 \times 10^{-5}$). Refusal to reject the null hypothesis in face of such evidence dramatically increases the probability of a Type II error. In the case of an critically endangered species like the right whale, a Type II error, which leads to maintenance of the management status quo, is more to be feared than Type I error (27).

4.1. Causes of Mortality

The causes of the decline in survival are unknown. Human interactions are a significant source of mortality for this species. Of 40 known right whale deaths between 1970 and 1997, 35% were due to ship collisions and 5% to entanglement in fishing gear (4, 6, 28). As many as 70% of the individuals in the population show scars from entanglement. The National Marine Fisheries Service estimates an average of 2.6 deaths per

year due to human causes over the period 1990–1994 (2). The U.S. National Oceanic and Atmospheric Administration has recently restricted fishing operations in areas frequented by right whales to reduce mortality caused by entanglement (29).

The birth rate of this population is lower than that of the South Atlantic population, perhaps because of inbreeding depression, competition, or pollution (5). Increasing reproduction would increase λ and reduce extinction probability. However, both λ and extinction probability are more sensitive to changes in survival probability than to changes in fertility. The elasticities (proportional sensitivities, ref. 30) of λ to changes in p and m are, from 11:

$$e_p = \frac{p}{\lambda} \frac{\partial \lambda}{\partial p} = 1 \quad [15]$$

$$e_m = \frac{m}{\lambda} \frac{\partial \lambda}{\partial m} = \frac{m}{1+m}. \quad [16]$$

Unlike eigenvalue elasticities, these do not sum to 1 (30). Depending on the value of m , e_p is from 17 to 27 times greater than e_m . Proportional increases in survival will have larger impacts than the same proportional increases in fertility. Fig. 5 shows that extinction probability is also more sensitive to p than to m .

We conclude that reducing human-caused mortality is the most effective way of improving population performance.

4.2. Comparison with Other Estimates

Here we show that our model successfully predicts previous estimates (5, 31) of right whale survival and population growth rate during the 1980s and early 1990s. These studies did not look for trends in survival.

By using known and presumed deaths (a missing whale was assumed alive if missing for fewer than 6 years and dead if missing for 6 or more years), Knowlton *et al.* (5) reported a mean mortality rate of 0.021 for the period 1987–1992. Model M_0 yields a mean mortality rate of 0.033 over the same period. Although not strictly appropriate, a t test finds no significant difference ($P = 0.175$) between the two means.

Population growth rate was computed by back-calculating population size from 1992, adding estimated deaths and subtracting reproduction each year (5). The mean annual growth rate from 1987 to 1992 was 2.5% (i.e., $\lambda = 1.025$). To compare our results with this value, we constructed an individual-based stochastic simulation of the female population, with survival probability declining as in M_0 and inter-birth interval increasing (S. D. Kraus, personal communication); see Fig. 7. The

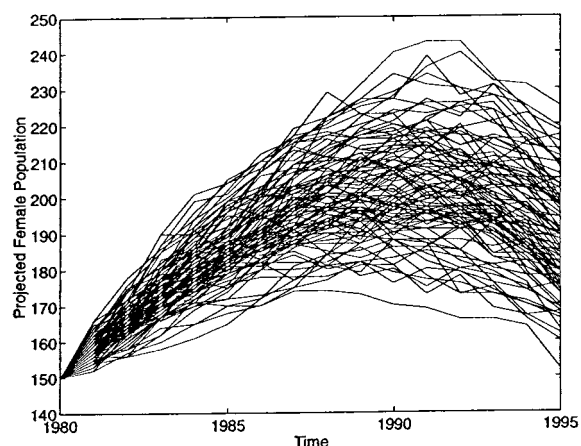


FIG. 7. Replicates (100) of a stochastic simulation for the female population, including trends in survival probability and inter-birth interval.

mean annual growth rate from 1987 to 1992, computed from 1000 realizations, was 1.44%, with a 95% confidence interval of [−0.27%, 3.12%]. The growth rate of 2.5% per year in ref. 5 falls within the 95% confidence interval of the values predicted by our model.

Although the methods in ref. 5 suffer from statistical weaknesses (not accounting for sighting probability, relying on assumptions about presumed mortality, and propagating errors during the back-calculation process), the results are valuable, and frequently cited. It is important that our analysis is able to predict them.

Kenney *et al.* (31) estimated population growth rate from 1979 to 1989 from aerial sightings of whales in the Great South Channel. They regressed the log of sighting rate (number of whales seen per unit distance flown, a proxy for population size) against time and found a mean annual growth rate of 3.8%. Applying the same regression approach to our stochastic simulations, we found a mean annual growth rate from 1980–1990 of 3.28%, with a 95% confidence interval of [1.88%, 4.53%].

Thus our estimated trend in survival probability, combined with the most recent estimates of the trend in inter-birth interval, projects population dynamics fully compatible with previous published estimates of survival and population growth rate during the 1980s and early 1990s.

4.3. Prediction of Survival Probability

Our model can explain previous observations, but can it predict future ones? The NEA catalog data for 1997 have recently become available; this permits us to estimate survival probability for 1995, and to compare it with the prediction for 1995 calculated from M_0 , which is independent of the new data. M_0 predicts a survival probability of 0.93 for 1995. The observed value, estimated by applying the CJS model to the 1997 data set, is 0.92, with 95% profile likelihood confidence interval [0.85, 0.95]. Thus model M_0 successfully predicts the next year's survival estimate.

4.4. Caveats

Like other analyses of this population (e.g., refs. 5 and 31), our calculations are based on crude, rather than stage-structured, rates. We are now developing stage structured models, similar to those in ref. 32, which will provide a more detailed picture of population performance.

The possibility that a trend in the vital rates is an artifact of a change in population composition can never be eliminated (33). For the trend we document here to be such an artifact, however, would require a truly dramatic change in population composition, which is unlikely since fully 40% of the individuals occur in both the first five and the last 5 years of the study. Our structured population models will disaggregate the rates by stage, but we do not expect that to change the trends in crude survival.

We thank S. Kraus and the NEA for the data, and S. Kraus, A. Knowlton, and P. Hamilton for advice. We thank J. Nichols, J. E. Cohen, and anonymous reviewers for comments on the manuscript. This article is Woods Hole Oceanographic Institution Contribution 9852. This research supported by National Marine Fisheries Service Grant 46EANF600004, Office of Naval Research Grant URIP N00014-92-J-1527, and a grant from the Reinhart Coastal Research Center.

1. Brownell, R. L., Best, P. B. & Prescott, J. H. (1986) *Right Whales: Past and Present Status*, Reports of the International Whaling Commission (International Whaling Commission, Cambridge, U.K.), Special Issue 10.
2. Blaylock, R. A., Hain, J. W., Hansen, L. J., Palka, D. L. & Waring, G. T. (1995) *U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments*, NOAA Technical Memorandum NMFS-SEFSC-363 (National Marine Fisheries Service, Northeast Fisheries Science Center, Woods Hole, MA).
3. Waring, G. T., Palka, D. L., Mullin, K. D., Hain, J. H. W., Hansen, L. J. & Bisack, K. D. (1997) *U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments—1996*, NOAA Technical Memorandum NMFS-NE-114 (National Marine Fisheries Service, Southeast Fisheries Science Center, Miami, FL).
4. Kenney, R. D. & Kraus, S. D. (1993) *Mar. Mamm. Sci.* **9**, 445–446.
5. Knowlton, A. R., Kraus, S. D. & Kenney, R. D. (1994) *Can. J. Zool.* **72**, 1297–1305.
6. Kraus, S. D. (1997) in *Shipping/Right Whale Workshop*, eds. Knowlton, A. R., Kraus, S. D., Meck, D. F. & Mooney-Seus, M. L. (New England Aquarium Aquatic Forum Series Report 97-3, Boston). pp. 31–36.
7. Crouse, D. T., Crowder, L. B. & Caswell, H. (1987) *Ecology* **68**, 1412–1423.
8. Doak, D., Kareiva, P. & Klepetka, B. (1994) *Ecol. Appl.* **4**, 446–460.
9. Heppell, S. S., Walters, J. R. & Crowder, L. B. (1994) *J. Wildlife Management* **58**, 479–487.
10. Groom, M. J. & Pascual, M. A. (1998) in *Conservation Biology: For the Coming Decade*, eds. Fiedler, P. L. & Kareiva, P. M. (Chapman and Hall, New York), 2nd Ed., pp. 4–27.
11. Kraus, S. D., Moore, K. E., Price, C. E., Crone, M. J., Watkins, W. A., Winn, H. E. & Prescott, J. H. (1986) *Rep. Int. Whaling Commission*, Special Issue **10**, 145–151.
12. Crone, M. J. & Kraus, S. D. (1990) *Right Whales (Eubalaena glacialis) in the Western North Atlantic: A Catalog of Identified Individuals* (New England Aquarium, Boston).
13. Pollock, K. H., Nichols, J. D., Brownie, C. & Hines, J. E. (1990) *Wildlife Monogr.* **107**, 1–97.
14. Lebreton, J.-D., Burnham, K. P., Clobert, J. & Anderson, D. R. (1992) *Ecol. Monogr.* **62**, 67–118.
15. Caswell, H. (1999) *Matrix Population Models* (Sinauer, Sunderland, MA), 2nd Ed., in press.
16. Shryock, H. S. & Siegel, J. S. (1976) *The Methods and Materials of Demography* (Academic, New York).
17. Carey, J. R. (1993) *Applied Demography for Biologists* (Oxford Univ. Press, New York).
18. Cormack, R. M. (1964) *Biometrika* **51**, 429–438.
19. Jolly, G. M. (1965) *Biometrika* **52**, 225–247.
20. Seber, G. A. F. (1965) *Biometrika* **52**, 249–259.
21. Hosmer, D. W. & Lemeshow, S. (1989) *Applied Logistic Regression* (Wiley, New York).
22. Akaike, H. (1973) in *International Symposium on Information Theory*, eds. Petran, B. N. & Csaki, F. (Akademiai Kiado, Budapest, Hungary), 2nd Ed., pp. 267–281.
23. Burnham, K. P. & Anderson, D. R. (1998) *Model Selection and Inference: A Practical Information-Theoretic Approach* (Springer, New York).
24. Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C. & Pollock, K. H. (1987) *Design and Analysis Methods for Fish Survival Experiments Based on Release-Capture* (American Fisheries Society, Bethesda, MD), Monograph 5.
25. Harris, T. E. (1963) *The Theory of Branching Processes* (Springer, Berlin).
26. Brown, M. W., Kraus, S. D., Gaskin, D. E. & White, B. N. (1994) *Mar. Mamm. Sci.* **10**, 253–265.
27. Dayton, P. K. (1998) *Science* **279**, 821–822.
28. Kraus, S. D. (1990) *Mar. Mamm. Sci.* **6**, 278–291.
29. National Oceanic and Atmospheric Administration (1997) Taking of Marine Mammals Incidental to Commercial Fishing Operations; Atlantic Large Whale Take Reduction Plan Regulations, 50 CFR Part 229, 62 *Federal Register* 140, pp. 39157–39189.
30. Caswell, H. (1989) *Matrix Population Models* (Sinauer, Sunderland, MA).
31. Kenney, R. D., Winn, H. E. and Macauley, M. C. (1995) *Cont. Shelf Res.* **15**, 385–414.
32. Brault, S. and Caswell, H. (1993) *Ecology* **74**, 1444–1454.
33. Cohen, J. E. (1986) *Am. Stat.* **40**, 32–39.