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Literature Cited

- Clark, A. H. 1887. The whale-fishery. I. History and present condition of the fishery. In G. B. Goode and staff of associates, The fisheries and fishery industries of the United States, Sect. V, Vol. II, p. 3-218. Gov. Print. Off., Wash., D.C.
- Hegarty, R. B. 1959. Returns of whaling vessels sailing from American ports, 1876-1928. Old Dartmouth Hist. Soc., New Bedford, Mass., 58 p.
 Starbuck, A. 1964. History of the American
- Starbuck, A. 1964. History of the American whale fishery from its earliest inception to the year 1876. Argosy-Antiquarian Ltd., N.Y., 779 p.
- Townsend, C. H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica (N.Y.) 19, 50 p.

Minimal Historical Size of the Western Arctic Population of Bowhead Whales

L. L. EBERHARDT and J. M. BREIWICK

Introduction

The present size of the bowhead whale, *Balaena mysticetus*, population inhabiting the Bering, Chukchi, and Beaufort Seas is estimated to be at least 2,000 individuals (Braham et al., 1979). Estimates of historical levels were obtained by Breiwick et al. (In press), who used estimates of removals since 1848 and a range of values of certain parameters to reconstruct population sizes.

Two sources of concern about the trend in stock sizes since the beginning of commercial exploitation in 1848 seem worth exploration. The first concern is that the heavy exploitation may have reduced the stock to such low levels that its genetic diversity is seriously reduced. Commercial harvests effectively ended by about 1912 (Bockstoce, 1977); it is quite possible that the low point of the population occurred at about that time. If it is feasible to estimate a minimal population level, then such an estimate may permit evaluation of the issue of genetic diversity. The second concern is that the population may have continued to decrease since the cessation of commercial exploitation, due to a continuing take by Eskimos. The calculations that follow are intended to shed some light on these two sources of concern.

Materials and Methods

The basic idea is to start from the presumed low point of the population and assume a population size at that time. We then simulate the course of the growth of the population to the present, subject to available estimates of removals, and tabulate the outcomes of a number of individual simulations (500). By repeating this process with various parameter combinations, we can suggest what sets of starting population sizes and parameters will result in populations in accord with the available recent estimates. The catch history used is that reported by Marquette and Bockstoce (1980), and the loss rates are those used in Breiwick et al. (In press).

Model

The underlying model parallels that of Breiwick et al. (In press), who assumed that the current population size could be modeled as:

$$P(t+1) = [P(t) - C(t)](1 - M) + R(t)$$
(1)

where P(t+1) represents the current population size, which is equal to that of 1 year ago less the removals [C(t)], reduced by mortality [exp(-M) approximately equals 1-M], and increased by recruitment [R(t)]. Recruitment depends on population size Tyears before, reproductive rate, and survival to the present. Hence,

$$R(t) = rP(t-T).$$
(2)

Because very little is known about these parameters in bowhead whales, the only course open at present is to assume a recruitment rate and a "lag" period. The lag period (T) is inserted to reflect the fact that current births depend substantially on the size of the population some years back; i.e., reproduction is a function of the mature

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members in the population. The use of the lag term does not imply that younger animals are assumed not to be part of the population for some period of time. We thus assume two parameters (net recruitment rate [r-M] and lag time) and vary these parameters over a range of values. The net recruitment rate is taken as ranging from 0.01 to 0.05, and the lag period is taken as 0, 5, or 7 years.

Breiwick et al. (In press) assumed a logistic model for the behavior of net recruitment (varying as a function of population size). We do not include that assumption here, on the grounds that it would not be of any importance at the current low level of the population. We assume the natural mortality rate (M) to be 0.05 or 0.07. The above parameter values are essentially those used by Breiwick et al. (In press), except that they used a wider range of mortality values. Their results showed that natural mortality is the least sensitive of the parameters.

Calculations

The calculations were carried out on a CDC 6400/CYBER 173 computer¹. The model was as given in Equation (1), but stochastic elements were incorporated by approximating the expected variation in survival from year to year by a random draw from a pseudonormal (Naylor et al., 1968) population with mean zero, and binomial variance depending on current population size. That is, we calculate var (M) =M(1-M)/P(t). A similar draw was made for recruitment, for which the variance was assumed to be Poisson and equal to the current net recruitment. Each calculated population size was rounded to the nearest integer.

The year 1912 was used as the start of calculations because this appeared to be approximately the time of the minimum in the population trajectories determined by Breiwick et al. (In press). The choice of 1912 is also supported by the exploitation record, as the last substantial commercial harvest was carried out



Figure 1.—Frequency distributions of 1978 population of bowhead whales for a 1912 population of 700 and various rates of net recruitment (500 computer simulations were used for each distribution).

in 1911 (Marquette and Bockstoce, 1980).

Results

An example of the outcomes of the simulations appears in Figure 1, which shows the frequency distribution of the 1978 population for an initial population of 700 (in 1912), at various values of net recruitment (r-M). Note that the frequency distributions progressively spread wider with increasing net recruitment.

Tables 1 and 2 present the mean values of each simulation, tabulated according to the initial population size (1912), and values of (r-M), the net recruitment rate. Each of the net recruitment rate values is further subdivided by three lag periods. A comparison of individual entries in the two tables shows that the effect of postulating different overall mortality rates (M) is of minor importance. Also, lags of 5 or 7 years yield much the same results, while the absence of a lag period does result in a substantially higher simulated 1978 population. The main utility of the results is to show which 1912 population sizes would result in 1978 population sizes that are of the same order of presently available estimates, i.e., are at least 2,000 animals. Reference to Figure 1 will provide a notion of the "spread" about the mean values for various values of net recruitment (r-M).

An inspection of the tables will show that a population of 2,000 or more animals in 1978 is unlikely to have resulted if the 1912 population were less than 600 or 700 individuals, under the conditions of the simulations. Also, it seems evident that a fairly high net recruitment rate would be required to achieve current population levels on the order of 2,000 if the 1912 population were much less than 1,000 whales.

Discussion

The main conclusion supported by the simulations is that, under the present model and data, there is little reason to suppose that the 1912 population was less than 600 individuals. We expect that further refinements in the estimated catch will tend to drive the lower limit on the 1912 population upwards. The evidence does not support concern about an impact of population size on genetic diversity.

It seems to us quite unlikely that the 1912 population was greater than the present population level. If this were the case, then we would be forced to infer that even the relatively low average take by Alaskan Eskimos up to the 1970's was nonetheless sufficient to hold the population static. There is little reason to suppose that any significant man-caused environmental change had occurred that might significantly affect population growth. There is evidence, however, that mass mortality

¹Reference to trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA

Table 1.—Simulated 1978 population sizes for mortality rate (*M*) of 0.05 and various 1912 population sizes (average of 500 simulations).

Table 2.—Simulated	1978	population	sizes	for	mortality	rate	(M)	of	0.07	and
various 1912 population sizes (average of 500 simulations).										

Net re- cruitment		1912 population size							
(r-M)	Lag	600	700	800	900	1,000	2,000		
0.05	0	4,695	7,175	9,771	12,095	14,688	39,740		
	5	1,999	2,954	3,947	4,856	5,845	15,485		
	7	1,661	2,432	3,232	3,698	4,765	12,544		
0.04	0	1,373	2,699	4,021	5,326	6,656	20,055		
	5	870	1,511	2,154	2,788	3,434	9,925		
	7	787	1,327	1,871	2,407	2,952	8,433		
0.03	0	28	534	1,243	1,953	2,667	9,645		
	5	123	543	970	1,396	1,824	6,025		
	7	160	538	914	1,291	1,668	5,381		
0.02	0		_	48	331	709	4,397		
	5		13	220	484	760	3,454		
	7		37	266	510	765	3,250		
0.01	0			_	5	2	1,732		
	5	1			5	102	1,765		
	7	-	_	0	24	165	1,767		

Net re- cruitment		1912 population size							
(r-M)	Lag	600	700	800	900	1,000	2,000		
0.05	0	4,911	7,394	9,999	12,300	14,904	39,963		
	5	1,861	2,697	3,571	4,363	5,232	13,691		
	7	1.530	2,196	2,889	3,523	4,213	10,939		
0.04	0	1,519	2,842	4,163	5,463	6,796	20,208		
	5	878	1,450	2.026	2.591	3,168	8.976		
	7	787	1,264	1,743	2,215	2,696	7,533		
0.03	0	64	626	1,335	2,047	2,762	9,732		
	5	200	591	982	1,371	1,763	5,600		
	7	237	579	919	1,260	1,601	4,953		
0.02	0	_		87	392	772	4,459		
	5		63	302	549	808	3.332		
	7	1	114	346	572	809	3,117		
0.01	0		· <u> </u>		-	7	1,777		
	5			1	45	198	1,804		
	7		-	8	107	266	1,804		

due to ice entrapment has occurred in the past though the frequency and extent of this phenomenon is little known (Sleptsov, 1948, as cited by Tomilin, 1957). The Alaskan Eskimo take averaged less than 20 individuals annually prior to 1970 (Marquette and Bockstoce, 1980). This rate of take, if the 1912 population was in excess of 2,000, would indicate that this population has had a remarkably low potential for increase.

A further factor concerning the issue of continually declining levels is that the decline of commercial exploitation is frequently attributed to difficulty in finding whales. It seems improbable, given their tendency to concentrate, that a bowhead whale population numbering about 2,000 would be difficult to locate - especially by the efficient and far-ranging steam whalers operating after about 1890. However, the evidence on this point is largely anecdotal at present (Allen, 1978). Braham and Krogman² report data from Townsend (1935) that show a sharp decline in catch by 1875, with a very slight increase under steam whaling. Catch per vessel did increase appreciably from

about 1890 to 1905 (Figure 1 of Braham and Krogman, footnote 2), reflecting the increased efficiency of the steam whalers. Commercial exploitation became unprofitable by 1908 (Rice, 1974; Bockstoce, 1977; Allen, 1978) due to a drastic decline in the value of baleen.

We expect that increasing knowledge about the biology of bowhead whales will permit substantial improvements in the present model. When certain essential parameters have been estimated, it should be possible to produce a more realistic model and to improve the procedure used here. Without the lag term, our model (Equation (2)) is simply that of a difference equation for geometric growth (if catches are set to zero). Similarly, the model of Breiwick et al. (In press) reduces to the difference equation analog of the ordinary logistic growth model.

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Literature Cited

- Allen, A. J. 1978. A whaler & trader in the Arctic 1895 to 1944. My life with the bowhead. Alaska Northwest Publ. Co., Anchorage, Alaska, 213 p.
- Bockstoce, J. R. 1977. Steam whaling in the western Arctic. Old Dartmouth Hist. Soc., New Bedford, Mass., 127 p.
- New Bedford, Mass., 127 p.
 Braham, H., B. Krogman, S. Leatherwood, W. Marquette, D. Rugh, M. Tillman, J. Johnson, and G Carroll. 1979. Preliminary report of the 1978 spring bowhead whale research program results. Rep. Int. Whaling Comm. 29:291-306.
- Breiwick, J. M., E. D. Mitchell, and D. G. Chapman. In press. Estimated initial population size of the Bering Sea stock of bowhead whale, *Balaena mysticetus*: An iterative method. Fish. Bull., U.S. 78(4).
- Marquette, W. M., and J. R. Bockstoce. 1980. Historical shore-based catch of bowhead whales in the Bering, Chukchi, and Beaufort Seas. Mar. Fish. Rev. 42(9-10):5-19.
- Naylor, T. H., J. L. Balintfy, D. S. Burdick, and K. Chu. 1968. Computer simulation techniques. John Wiley & Sons, N.Y., 352 p.
- Rice, D. W. 1974. Whales and whale research in the eastern North Pacific. *In* W. E. Schevill (editor), The whale problem, a status report, p. 170-195. Harvard Univ. Press, Cambridge, Mass.
- Tomilin, A. G. 1957. Zveri SSSR i prilezhashchikh stran (Mammals of the U.S.S.R. and adjacent countries). Vol 9.
 Kitoobraznye (Cetacea). Izd. Akad. Nauk SSSR, Moskva, 756 p. [In Russ.] (Translated by Isr. Program Sci. Transl., 1967, 717 p.; avail. U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, Va., as TT 65-50086.)
 Townsend, C. H. 1935. The distribution of
- Townsend, C. H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica (N.Y.) 19, 50 p.

²Braham, H. W., and B. D. Krogman. 1977. Population biology of the bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whale in the Bering, Chukchi and Beaufort seas.

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