ESTIMATED INITIAL POPULATION SIZE OF THE BERING SEA STOCK OF BOWHEAD WHALE, *BALAENA MYSTICETUS*: AN ITERATIVE METHOD

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ABSTRACT

Initial stock sizes of bowhead whales were calculated iteratively, using an estimate of removals from the Bering Sea stock of bowheads, a range of assumed values for size of current stock, and assumed mortality and recruitment rates of $M = 0.04-0.08$ and $(r-M)_{\max} = 0.01-0.05$. Estimates of initial stock size range between 14,000 and 26,000. At a kill level of 25 per annum, time to recover to 9,000 (50% of 18,000) is a minimum of 40 years if the present stock is approximately 2,700 bowheads. A theoretical model giving the risk of extinction is also discussed.

The International Whaling Commission has recently established quotas on the aboriginal take of the bowhead whale, *Balaena mysticetus*, in the Bering, Chukchi, and Beaufort Seas. This has led to much discussion of the status of the stock both now and in relation to its original size.

Bowhead whales are distributed throughout the Arctic in several presumably discrete stock units. Tomilin (1957) recognized four circumpolar stock units and Mitchell[4] identified five. Regardless of various interpretations, the Bering-Chukchi-Beaufort Sea stock has been regarded by all authors for many years as a discrete stock (Figure 1).

This stock winters in the Bering Sea, but during the spring it moves through the Bering Strait along the northwestern and northern coasts of Alaska at least as far as the Beaufort Sea. The Beaufort and Chukchi Seas are the main feeding areas. For convenience we will refer to this stock hereafter as the Bering Sea stock. This paper concentrates solely on this stock, for which commercial exploitation began in 1848, the date to which "initial" but not "unexploited" stock refers. Eskimo utilization of bowhead whales dates back many centuries, hence the Bering Sea stock was subject to human influence prior to 1848.

After 1848 the Bering Sea stock was rapidly depleted by heavy commercial exploitation—thus following a pattern that had been established earlier with respect to the Spitzbergen, Davis Strait, and Hudson Bay stocks and which also was to occur with the putative Okhotsk Sea stock (Mitchell footnote 4). Of all these depleted stocks, that of the Bering Sea is now the most abundant, and the only one from which removals of any consequence are occurring.

There are few satisfactory estimates of current population size for other bowhead whale stocks; estimates of the population sizes of all stocks at the onset of heavy commercial exploitation are even less reliable. Accordingly, we here present one approach to verify the order of magnitude of the early Bering Sea stock. We have also used some assumed estimates of the vital parameters in a simulation study of the expected time of recovery of this stock with catches at the present level.

The basis of the method is to start with an assumed current stock size and a recruitment rate, which is a function of stock size. The same form for the recruitment function is used throughout—a linear function decreasing from its maximum value at zero stock level to the natural mortality rate, M, at the initial stock level. Given current stock size, maximum net recruitment rate, mortality rate, and lag time between birth and age at recruitment into the fishery, the program starts with an estimated initial (1848) level. The pro-

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[4] Mitchell, E. D. 1977. Initial population size of bowhead whale (*Balaena mysticetus*) stocks: cumulative catch estimates. Int. Whal. Comm. Doc. SC/29/33, 112 p. The Red House, Station Road, Histon, Cambridge CB4 4NP, Engl.

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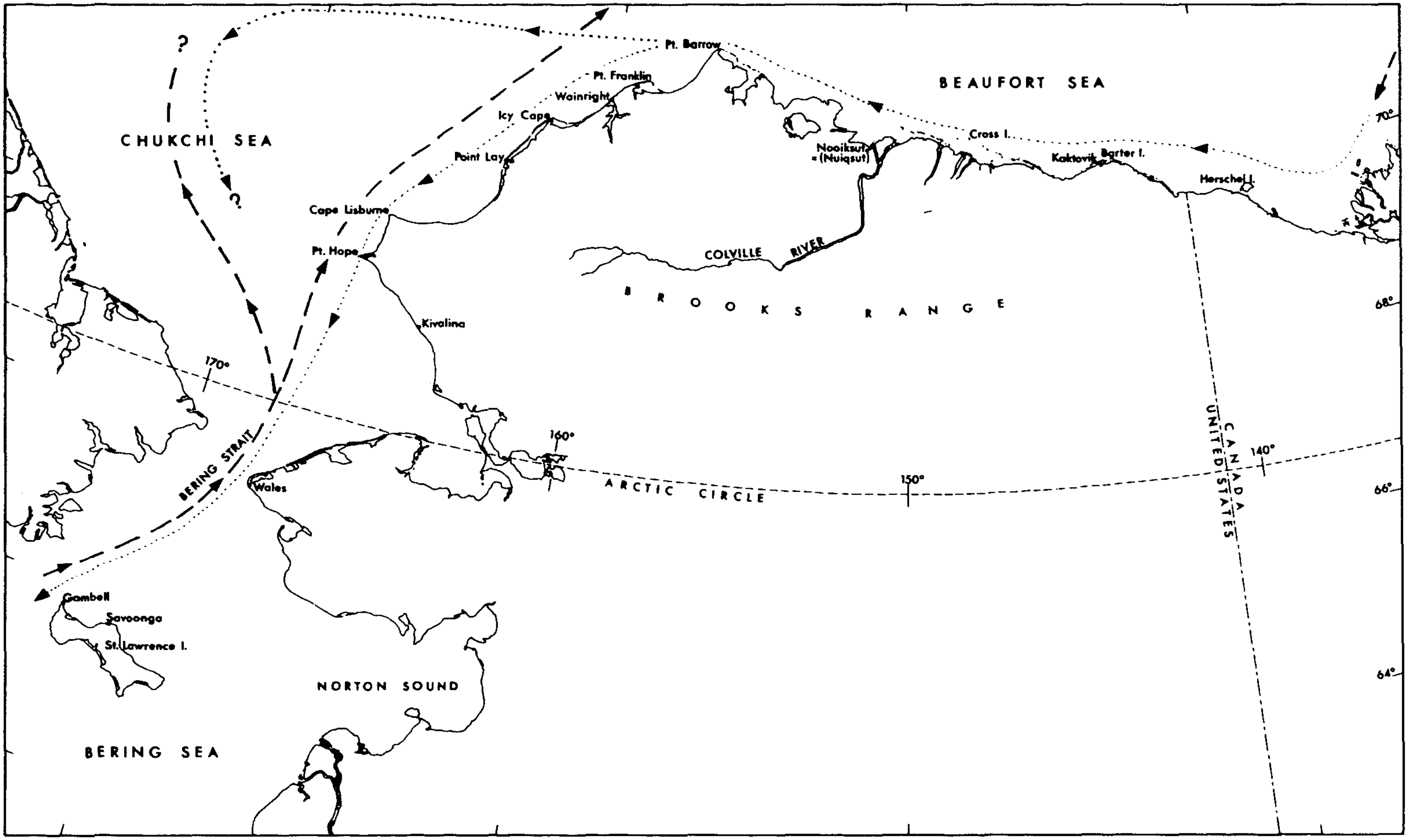

FIGURE 1.—Northern Alaska and adjacent waters, showing villages where recent whaling activities occur, and general migration trend of the bowhead whale. Dashed line, spring migration into Chukchi Sea, to summering grounds of Beaufort Sea and Amundsen Gulf; dotted line, fall migration to Chukchi Sea, and southward to Bering Sea. Bowhead migration routes based on Townsend (1935, chart D) and data of Cook (1926) as plotted in Sergeant and Hoek (1974, fig. 1).

gram then calculates forward and adjusts the initial level until it yields the correct (i.e., assumed) current stock size. Current population estimates are based on sightings and therefore are presumably for the total population.

In order to reconstruct the 1848 level, it is necessary to have a record of the catch history since that time, together with a reasonable range of estimates of the other parameters noted, i.e., mortality rate, maximum net recruitment rate, and current population size. Estimated catches and other assumed parameter values are discussed below.

METHODS

Stock Size Analysis

Estimates of Initial Stock Size

Rice (1974), using data of Clark (1887), estimated a Bering Sea stock size of 4,000-5,000 animals during a peak harvest from 1868 to 1884. Mitchell (footnote 4) concluded that the period of peak catch was earlier and, after examining methods of extrapolating catch from production statistics (oil and baleen yield) and catch per vessel, constructed a catch history (1849-1976) based on these estimates or on known catch. Mitchell summed the cumulative catch for the peak decade (1851-60), applied a loss rate of 24%, and concluded that a minimum population of 11,647 bowheads existed in 1850. He then performed the same cumulative catch summation on what he termed the "residual stock," which had survived, and exploitation of which had resulted in another peak catch period in the 1880's-1890's.

In summing the two cumulative catch estimates of population size, Mitchell corrected the latter by subtracting from it an assumed net recruitment of 5% per year over the period between the peaks. He concluded that the initial stock must have comprised approximately 18,000 bowhead whales. The calculations discussed below are a refinement of this rough procedure and show that this estimate is not unreasonable.

Catch History

We have taken the best estimate of commercial catch for each year or the known catch when available, and applied the struck but lost (and assumed moribund) rates estimated by Mitchell (footnote 4). We have added to these commercial removals the known aboriginal catch (Maher and Wilimovsky 1963; Durham 1979) with some additions (Marquette 1976, see footnotes 5 and 6; Mitchell footnote 4) and adjusted by the struck but lost (and assumed moribund) rates estimated by Mitchell (footnote 4). These are summarized in Table 1 (cf. Mitchell's table 9) for the entire period 1848-1977 (see footnotes under Mitchell's table for discussion of extrapolations and modifications to these data).

Estimates of Current Stock Size

There have been few recent surveys or counts which give quantitative estimates of total population abundance. Counts, e.g., from ice edge sightings through the season, were made by Braham and Krogman,[7] who estimated the 1976 inshore migration from 25 April to 2 June to include 796 animals. Breiwick and Chapman[8] extrapolated these data to account for animals that migrated earlier than 25 April or later than 2 June and arrived at a total population of 1,227. However, a more complete and careful census was carried out in 1978, in which whales were counted in the nearshore lead as they passed Barrow, Alaska, between 15 April and 30 May. The estimate for this component of the population was 2,264 (Braham et al. 1979). Aerial surveys were conducted in offshore leads and no whales were observed. In the model below we assumed 1978 stock levels of 900, 1,500, 2,100, and 2,700 animals.

Vital Parameters

As stated above, we assume a recruitment model with appropriate parameter values. If natural mortality is assumed to be fixed and the net recruitment rate is a linear function of stock size, the

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[5] Marquette, W. M. 1976. National Marine Fisheries Service field studies relating to the bowhead whale harvest in Alaska, 1975. Processed Rep., 31 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[6] Marquette, W. M. 1978. The 1976 catch of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos, with a review of the fishery 1973-1976, and a biological summary of the species. Processed Rep., 80 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[7] Braham, H. W., and B. D. Krogman. 1977. Population biology of the bowhead (*Balaena mysticetus*) and beluga (*Delphinapterus leucas*) whales in the Bering, Chukchi and Beaufort Seas. Processed Rep., 29 p. Natl. Mar. Mammal Lab., Natl. Mar. Fish. Serv., NOAA, 7600 Sand Point Way NE., Seattle, WA 98115.

[8] Breiwick, J. M., and D. G. Chapman. 1977. Population analysis of the Alaska bowhead whale stock. Int. Whal. Comm. Doc. SC/SPC/13, 5 p. The Red House, Station Road, Histon, Cambridge CB4 4NP, Engl.

TABLE 1.—Estimated pelagic and Eskimo kill of bowhead whales from the Bering Sea stock.

	American pelagic fishery			Eskimo fishery			
Year	Catch	Loss rate[1]	Kill subtotal	Known kill[2]	Loss rate	Kill subtotal	Kill total
1848	25	0.24	31	—	0.24	0	31
1849	1,061	0.24	1,316	—	0.24	0	1,316
1850	1,061	0.24	1,440	—	0.24	0	1,440
1851	597	0.24	740	—	0.24	0	740
1852	1,912	0.24	2,371	17	0.24	21	2,392
1853	1,482	0.24	1,838	7	0.24	9	1,847
1854	1,326	0.24	1,644	—	0.24	0	1,644
1855	1,315	0.24	1,631	—	0.24	0	1,631
1856	1,040	0.24	1,290	—	0.24	0	1,290
1857	819	0.24	1,016	—	0.24	0	1,016
1858	975	0.24	1,209	—	0.24	0	1,209
1859	811	0.24	1,006	—	0.24	0	1,006
1860	549	0.24	681	—	0.24	0	681
1861	412	0.24	511	—	0.24	0	511
1862	158	0.24	196	—	0.24	0	196
1863	307	0.24	381	—	0.24	0	381
1864	364	0.24	451	—	0.24	0	451
1865	348	0.24	432	—	0.24	0	432
1866	551	0.24	683	—	0.24	0	683
1867	569	0.24	706	—	0.24	0	706
1868	450	0.24	558	—	0.24	0	558
1869	395	0.24	490	—	0.24	0	490
1870	490	0.24	608	—	0.24	0	608
1871	75	0.24	93	—	0.24	0	93
1872	186	0.24	231	—	0.24	0	231
1873	162	0.24	201	—	0.24	0	201
1874	160	0.24	198	—	0.24	0	198
1875	173	0.24	215	—	0.24	0	215
1876	57	0.24	71	—	0.24	0	71
1877	102	0.24	126	—	0.24	0	126
1878	74	0.24	92	—	0.24	0	92
1879	130	0.24	161	5	0.24	6	167
1880	265	0.24	329	7	0.56	11	340
1881	170	0.24	211	18	0.56	28	239
1882	170	0.24	211	1	0.56	2	213
1883	170	0.24	211	2	0.56	3	214
1884	170	0.24	211	10	0.56	16	227
1885	170	0.24	211	40	0.56	62	273
1886	170	0.24	211	—	0.56	0	211
1887	170	0.24	211	11	0.56	17	228
1888	170	0.24	211	3	0.56	5	216
1889	170	0.24	211	7	0.56	11	222
1890	170	0.24	211	2	1.00	4	215
1891	184	0.24	228	19	1.00	38	266
1892	201	0.24	249	8	1.00	16	265
1893	193	0.24	239		1.00	0	239
1894	118	0.24	146	13	1.00	26	172
1895	70	0.24	87	4	1.00	8	95
1896	25	0.24	31	39	1.00	78	109
1897	173	0.24	215	5	1.00	10	225
1898	21	0.24	26	27	1.00	54	80
1899	154	0.24	191		1.00	0	191
1900	62	0.24	77	19	1.00	38	115
1901	11	0.24	14	1	0.56	2	16
1902	63	0.24	78	2	0.56	3	81
1903	58	0.24	72	8	0.56	12	84
1904	44	0.24	55	3	0.56	5	60
1905	41	0.24	51	7	0.56	11	62
1906	5	0.24	6	6	0.56	9	15
1907	58	0.24	72	9	0.56	14	86
1908	20	0.24	25	47	0.56	73	98
1909	28	0.24	35	25	0.56	39	74
1910	6	0.24	7	2	0.56	3	10
1911	72	0.24	89	4	0.56	6	95
1912	0	0.24	0	3	0.56	5	5
1913	15	0.24	19	5	0.56	8	27
1914	—	—	—	4	0.56	6	6
1915	—	—	—	3	0.56	5	5
1916	—	—	—	14	0.56	22	22
1917	—	—	—	15	0.56	23	23
1918	—	—	—	9	0.56	14	14
1919	—	—	—	4	0.56	6	6
1920	—	—	—	14	0.56	22	22
1921	—	—	—	2	0.56	3	3
1922	—	—	—	17	0.56	27	27
1923	—	—	—	3	0.56	5	5
1924	—	—	—	29	0.56	45	45
1925	—	—	—	32	0.56	50	50
1926	—	—	—	18	0.56	28	28
1927	—	—	—	7	0.56	11	11
1928	—	—	—	11	0.56	17	17
1929	—	—	—	16	0.56	25	25
1930	—	—	—	7	0.56	11	11
1931	—	—	—	18	0.56	28	28
1932	—	—	—	7	0.56	11	11
1933	—	—	—	5	0.56	8	8
1934	—	—	—	4	0.56	6	6
1935	—	—	—	6	0.56	9	9
1936	—	—	—	10	0.56	16	16
1937	—	—	—	15	0.56	23	23
1938	—	—	—	11	0.56	17	17
1939	—	—	—	8	0.56	12	12
1940	—	—	—	12	0.56	19	19
1941	—	—	—	23	0.56	36	36
1942	—	—	—	11	0.56	17	17
1943	—	—	—	7	0.56	11	11
1944	—	—	—	2	0.56	3	3
1945	—	—	—	12	0.56	19	19
1946	—	—	—	12	0.56	19	19
1947	—	—	—	11	0.56	17	17
1948	—	—	—	5	0.56	8	8
1949	—	—	—	6	0.56	9	9
1950	—	—	—	9	0.56	14	14
1951	—	—	—	14	0.56	22	22
1952	—	—	—	4	0.56	6	6
1953	—	—	—	23	0.56	36	36
1954	—	—	—	4	0.56	6	6
1955	—	—	—	23	0.56	36	36
1956	—	—	—	7	0.56	11	11
1957	—	—	—	3	0.56	5	5
1958	—	—	—	2	0.56	3	3
1959	—	—	—	1	0.56	2	2
1960	—	—	—	19	0.56	30	30
1961	—	—	—	10	0.56	16	16
1962	—	—	—	12	0.56	19	19
1963	—	—	—	10	0.56	16	16
1964	—	—	—	16	0.56	25	25
1965	—	—	—	7	0.56	11	11
1966	—	—	—	15	0.56	23	23
1967	—	—	—	4	0.56	6	6
1968	—	—	—	17	0.56	27	27
1969	—	—	—	19	0.56	30	30
1970	—	—	—	25	0.56	39	39
1971	—	—	—	24	0.48	36	36
1972	—	—	—	38	0.48	56	56
1973	—	—	—	37	0.48	55	55
1974	—	—	—	20	0.48	30	30
1975	—	—	—	15	0.48	22	22
1976	—	—	—	48	0.48	71	71
1977	—	—	—	32	—	111	[3]111
Total	21,823		27,068	1,234		2,025	29,093

[1] 100% moribund in those lost.

[2] Includes "commercial" shore-based landings in later years.

[3] 29 killed + recovered; 3 killed + lost; 79 struck + lost.

resulting recruitment in numbers generates a logistic relationship. At initial stock levels the recruitment rate is assumed to be equal to the natural mortality rate (which includes a small amount of exploitation mortality at the pre-1848 level). As the stock is reduced, recruitment rate increases proportionally, attaining its maximum level when the stock is near zero. However, it is also recognized that response in rate may occur with some lag and thus various lag periods are assumed.

In order to construct the model, various parameter estimates are needed. These are discussed below.

Net Recruitment Rate

Since information on the maximum net recruitment rate is lacking, a range of values (0.01-0.05) was used, based on analogy with other baleen whale stocks for which such data are available. For example, Allen (1972) showed calculated rates for the fin whale, *Balaenoptera physalus*, (as a proportion of exploited stock) to be mostly in the range 0.021-0.036. The Scientific Committee of the International Whaling Commission (International Whaling Commission 1978) calculated maximum gross recruitment rates for the sei whale, *B. borealis*, (as a proportion of exploited female stock) as 0.26 which implies a net recruitment rate of the exploited stock to be 0.06. If we express these rates as a proportion of the total stock, they are in the range of 0.01-0.05. (Furthermore, estimates of the 1848 stock level became unstable and did not converge if maximum net recruitment rates >0.05 were used in our iteration.)

Natural Mortality

Similarly, there is no information available on natural mortality in bowheads, and a range of values of 0.04-0.08 was used. These correspond to mortality estimates for other baleen species (Doi et al. 1967; International Whaling Commission 1971).

Lag Time

We have no data on the growth and age of this species, and there were no regulations in the fishery. Nor do we have any information on the lag that may occur between the reduction of stock density and response of the population through its presumed increase in recruitment. In a similar study carried out for porpoise stocks involved in the yellowfin tuna purse seine fishery (National Marine Fisheries Service[9]), lag periods of 1, 3, and 5 yr were used. Because the population response in larger animals might be delayed, we have arbitrarily tried four lag periods: 1, 3, 5, and 7 yr. As will be shown, this parameter has minor effect.

Model Development

The assumptions outlined above can be formulated in mathematical terms as follows. The recruitment model is

$$r_t = M + (1 - P_{t-\tau}/P_0)(r - M)_{\max}, \qquad (1)$$

where r_t = recruitment rate in season t
$P_{t-\tau}$ = population size at the beginning of season $t - \tau$ (τ = lag time assumed for population response)
P_0 = initial population size (start of 1848 season)
M = natural mortality rate
$(r - M)_{\max}$ = maximum net recruitment rate.

The extrapolation model also uses the (approximate) recursion formula (Allen 1966):

$$P_{t+1} = (P_t - C_t)e^{-M} + R_t \qquad (2)$$

where $R_t = r_t P_{t-\tau}$ is the gross recruitment between the beginning of season t and season $t + 1$, and C_t, P_t are catch in season t and population size at the beginning of season t. A further approximation made is that $e^{-M} = 1 - M$. Equation (2) provides a good approximation if the catching season is relatively short and natural mortality is low.

The iterative procedure consists of specifying a current stock level, natural mortality rate, maximum net recruitment rate, and iterating on P_0 in Equation (2). Thus

$$P_n = g(P_0, P_1, \ldots, P_{n-1}) \qquad (3)$$

where P_n is some current stock level. Due to the lag time involved in Equation (2), it is not practical to invert Equation (3) and solve for P_0 explicitly; hence the iterative solution of Equation (3) is obtained.

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[9] National Marine Fisheries Service. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. Adm. Rep. LJ-76-29, 54 p. Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, P.O. Box 271, La Jolla, CA 92038.

Risk Analysis

For any population there is a positive probability of its extinction, though for most populations this is negligibly small. However, the probability will increase as the population size is reduced, e.g., by direct or indirect action of man. Such direct action may be a harvest which is uncontrolled or one which is controlled by fixed rules that do not consider stochastic fluctuations in the environment.

Random fluctuations in the environment or population which cause increased mortality or reduced births can lead to extinction, particularly if the population is at a very low level. Moreover, the longer the population is maintained there, the greater the probability of extinction. Such risks of extinction have for a long time been the subject of study in population theory, but most such models are rather simple and include only statistical variation within the population but not externally imposed stresses. We now develop a model that expresses probabilities of extinction as a function of average population growth and variability of environmental stresses. In this model we assume that there is an average increment for each year but, superimposed on this, a variability of the environment which may result in the actual change being positive or negative. We define a stochastic process which is the sum of annual increments which are normally distributed with mean μ and variance σ^2, and with successive increments independent. It is known from the theory of stochastic processes (c.f., Cox and Miller 1965:58) that the probability of the process being absorbed by barriers at levels "a" above the initial value or "b" below the initial value are equal to

$$\frac{1 - \exp(2\,\mu\, b/\sigma^2)}{\exp(-2\,\mu\, a/\sigma^2) - \exp(2\mu b/\sigma^2)}$$

and

$$\frac{\exp(-2\,\mu\,/\sigma^2) - 1}{\exp(-2\,\mu\, a/\sigma^2) - \exp(2\,\mu\, b/\sigma^2)}\ ,$$

respectively. If b is set equal to the initial value, the second of these represents the probability of extinction. It is difficult to specify appropriate values for σ. For example, $\sigma = 100$ implies that with 95% probability the actual increase might vary from 200 above to 200 below the mean. Such variations are not unreasonable in the Arctic environment. We do not know if they are this large or not but catastrophic mortality due to ice conditions has been recorded (Sleptsov 1948, as cited by Tomilin 1957, in text but no citation given). We have assumed that stresses are independent events from year to year. To apply this we consider the female population which, in a total of 2,000, will number about 1,000. Extinction clearly occurs if this component falls to zero. We arbitrarily have assumed that if the female population reaches 2,000, the population is safe from extinction. If a larger "safe" upper limit is chosen, then the probabilities of extinction will be greater. It should be noted that the level of 2,000 females (or any other upper limit) is not an absorbing barrier in the sense that zero, the lower limit, is. However, to simplify the model, we have chosen a range within which it is reasonable to assume average growth is approximately constant—over a wider range the growth parameter must change. Because we have assumed constant μ (average increment), the probabilities of a population becoming extinct with 1,000 females are easily computed from the given formula for various levels of average annual increase and various levels of environmental stress as expressed by standard deviation.

RESULTS

Risk Analysis

The effect of the level of exploitation on the risk of extinction is shown in Table 2. A catch of 10 whales shifts the average increase downward by that amount; i.e., one moves one column to the left in the table. A continuing kill of 30 whales shifts the probabilities three columns to the left. Thus, if present net recruitment were 50 whales and the environmental perturbation were represented by $\sigma = 141.4$, the probability of extinction according to this model would be increased from 0.01 to 0.12 with a continuing 30 whale kill.

Initial Stock Size

It can be seen that the initial stock estimates are little affected by the estimates or assumptions of

TABLE 2.—Probabilities of extinction for stochastic process with normally distributed independent additive increments.

	Average annual increase, μ					
Stress variability σ	10	20	30	40	50	60
0.7	0.02	—	—	—	—	—
100	.12	0.02	0.002	—	—	—
141.4	.27	.12	.05	0.02	0.01	0.002
173.2	.34	.21	.12	.06	.03	.02

the current (1978) stock level given the same values of the other parameters $(r - M)_{\max}$, M, and τ (Figure 2, Table 3). Table 4 shows the initial stock size estimates from Table 3 (1978 stock level of 2,700) reexpressed as deviations from row and column medians. The magnitude and direction of changes in the estimates as a function of the different parameter combinations indicate that in-

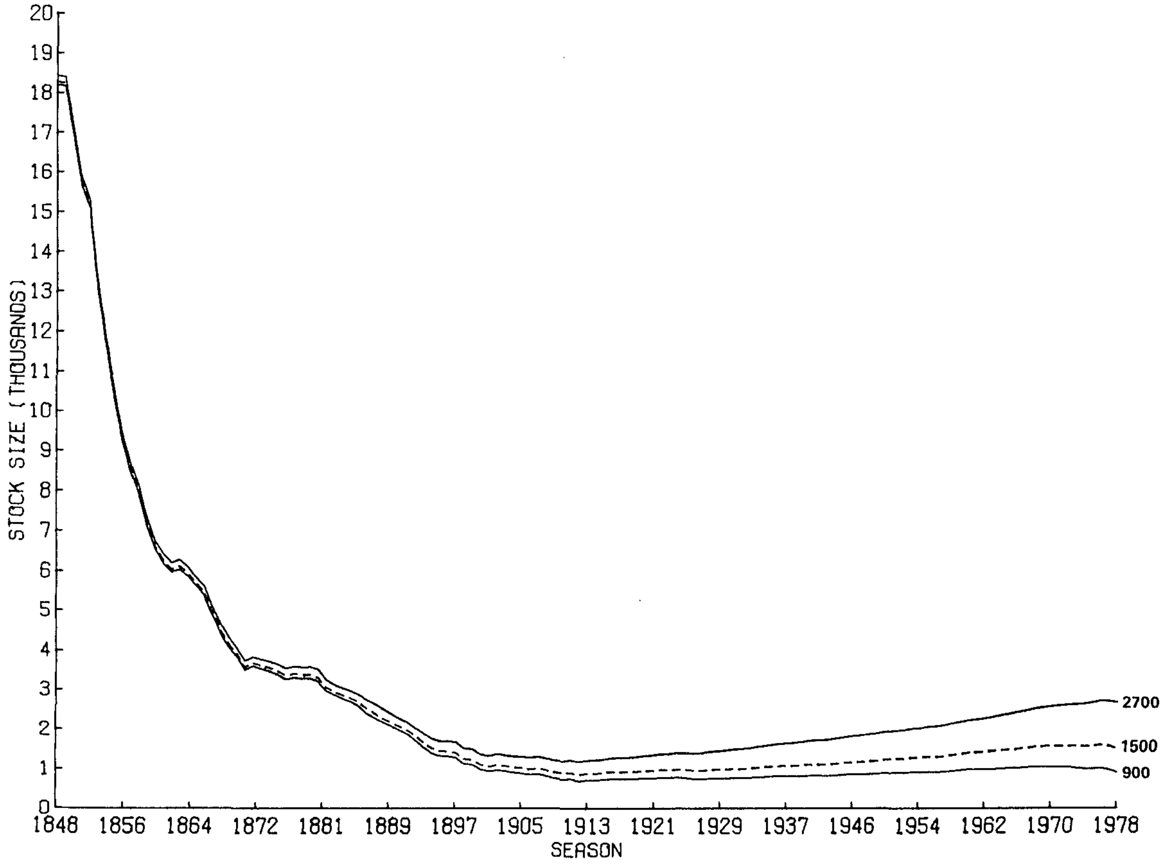

FIGURE 2.—Population back projections (where $M = 0.06$, Lag = 5 yr, $(r - M)_{\max} = 0.03$) which would theoretically result in current stock sizes of 900, 1,500, and 2,700 bowhead whales according to the model (see text).

TABLE 3.—Results of iterative solution of Equation (3). Initial stock size estimates (in thousands) for various values of vital parameters (M, lag time, and maximum net recruitment rate) and 1978 stock level.

		1978 stock level of 900			1978 stock level of 1,500			1978 stock level of 2,100			1978 stock level of 2,700		
		$(r - M)_{\max}$			$(r - M)_{\max}$			$(r - M)_{\max}$			$(r - M)_{\max}$		
M	Lag time (yr)	0.01	0.03	0.05	0.01	0.03	0.05	0.01	0.03	0.05	0.01	0.03	0.05
0.04	1	25.67	21.95	19.64	25.91	21.98	19.64	26.15	22.02	19.65	26.40	22.05	19.65
.06		25.15	21.90	19.23	25.38	21.90	19.23	25.63	21.56	19.24	25.88	21.60	19.24
.08		24.62	21.41	18.82	24.86	21.44	18.82	25.10	21.10	18.83	25.35	21.14	18.83
.04	3	24.01	20.72	18.68	24.27	20.76	18.69	24.54	20.81	18.69	24.81	20.86	18.70
.06		22.77	19.69	17.78	23.04	19.74	17.79	23.31	19.80	17.80	23.60	19.85	17.81
.08		21.61	18.73	16.93	21.89	18.78	16.94	22.17	18.64	16.96	22.47	18.90	16.97
.04	5	22.56	19.63	17.83	22.84	19.69	17.84	23.13	19.76	17.86	23.43	19.82	17.87
.06		20.82	18.19	16.56	21.12	18.26	16.58	21.43	18.33	16.59	21.74	18.41	16.61
.08		19.29	16.90	15.42	19.60	16.98	15.44	19.92	17.11	15.57	20.25	17.16	15.49
.04	7	21.29	18.67	17.07	21.59	18.75	17.09	21.90	18.83	17.11	22.22	18.91	17.14
.06		19.21	16.92	15.52	19.53	17.02	15.55	19.86	17.11	15.57	20.20	17.21	15.61
.08		17.44	15.43	14.18	17.78	15.54	14.22	18.13	15.65	14.25	18.49	15.77	14.29

TABLE 4.—Reexpressed stock sizes of Table 3 (1978 stock level of 2,700).

		Row values minus medians				Column values minus medians		
		$(r - M)_{\max}$				$(r - M)_{\max}$		
M	Lag time (yr)	0.01	0.03	0.05	Median	0.01	0.03	0.05
0.04	1	4.35	0.00	−2.40	22.05	0.52	0.45	0.41
.06		4.28	.00	−2.36	21.60	.00	.00	.00
.08		4.21	.00	−2.31	21.14	− .53	− .46	−0.41
					Median	25.88	21.60	19.24
.04	3	3.95	.00	−2.16	20.86	1.21	1.01	0.89
.06		3.75	.00	−2.04	19.85	.00	.00	.00
.08		3.57	.00	−1.93	18.90	−1.13	− .95	− .84
					Median	23.60	19.85	17.81
.04	5	3.61	.00	−1.95	19.82	1.69	1.41	1.26
.06		3.33	.00	−1.80	18.41	.00	.00	.00
.08		3.09	.00	−1.67	17.16	−1.49	−1.25	−1.12
					Median	21.74	18.41	16.61
.04	7	3.31	.00	−1.77	18.91	2.02	1.70	1.53
.06		2.99	.00	−1.60	17.21	.00	.00	.00
.08		2.72	.00	−1.48	15.77	−1.71	−1.44	−1.32
					Median	20.20	17.21	15.61

creasing values of M, lag time, and maximum net recruitment tend to decrease the estimate of initial stock size.

Vital Parameters

The natural mortality rate has somewhat less of an effect on initial stock estimates than does the maximum net recruitment rate. This can be seen from Table 4 where initial stock estimates have been reexpressed as deviations from row and column medians. As noted above, net recruitment rates >0.05 often did not result in convergence of the iterative procedure. In general, convergence occurred only if fractions of animals were allowed in Equation (2). If only integer numbers were used, it was virtually impossible to arrive at a prescribed stock level in 1978 from a given stock level. This is because the time series consists of over 100 yr, and rounding-off errors become critical if the convergence criterion is too stringent. We assumed convergence if the difference between two successive initial stock estimates was <0.1.

Maximum net recruitment rate and lag time are the most sensitive of the parameters we use in the model and natural mortality rate the least. We have used all combinations of the range of values of the parameters, although we recognize that certain combinations are likely to be unreasonable (for instance, a lag time of 1 yr with a maximum net recruitment rate of 0.01 is unlikely and therefore the initial stock size is unreasonable for these parameter values).

Bockstoce[10] examined a sample of maritime newspapers and logbooks of whaling voyages and estimated that 22,111 bowheads were killed by pelagic whalers in the "commercial" fishery between 1848 and 1915. Mitchell (footnote 4) estimated 27,714 whales killed in both the "commercial" and the "aboriginal" fisheries during this period. Initial stock size estimates using the data in Bockstoce (footnote 10) for 1848-1915 and our Table 1 for 1916-77 are about 15% lower than the results given in Table 3.

Recovery Times

Using the basic model of Equation (2) and assuming that the maximum net recruitment rate applies in the current season (assuming a population of 1,500 and 2,700 animals), the time required to recover to one-half of an initial stock level of 18,000 was calculated for various parameter values. These are presented in Table 5 as a ratio of time to recover to 9,000 with a constant kill (5, 10, 15, 20, 25, and 30 animals) compared with the time to recover without a kill.

If the current stock level were 1,500 animals and the maximum net recruitment rate was 0.05, M = 0.04, time lag 3 yr, the stock would take 58 yr to recover to a level of 9,000 with no kill vs. 75 yr with a kill of 30/year. These numbers are increased to 94 and 153 yr, when the maximum net recruitment rate is only 0.03 (other parameters unchanged).

DISCUSSION

We believe our model is useful but not fully adequate. We have reservations about the data used, limitations of the model, and aspects of the fishery that we did not have time or data to adequately address.

Limitations of the Data

The commercial catch data are based mainly on extrapolations of a consistent number of whales caught per ship. The statistics for the number of vessels operating in the bowhead fishery component of the North Pacific Ocean are also subject to

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[10] Bockstoce, J. 1978. A preliminary estimate of the reduction of the western Arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry: 1848-1915. Report submitted to U.S. Marine Mammal Commission, Washington, D.C. Available U.S. Dep. Commer., Natl. Tech. Inf. Serv., Springfield, VA 22161, as PB-286-797.

TABLE 5.—Estimated recovery times for Bering Sea bowhead whale stock. Recovery time is that calculated with the parameters indicated, assuming zero kill. The relative increases in recovery time that occur with various levels of constant kill are tabulated in the last six columns.

Assumed current stock level	Lag time used in model	$(r - M)_{max}$	M	Recovery time (yr) to 9,000	Annual kill 5	10	15	20	25	30
1,500	3	0.01	0.04	273	1.22	1.63	(1)	—	—	—
			.08	302	1.21	1.58	—	—	—	—
		.03	.04	94	1.06	1.14	1.22	1.33	1.46	1.63
			.08	104	1.06	1.13	1.20	1.30	1.41	1.57
		.05	.04	58	1.05	1.09	1.12	1.17	1.22	1.29
			.08	64	1.03	1.06	1.11	1.16	1.20	1.27
	7	.01	.04	315	1.22	1.63	—	—	—	—
			.08	381	1.21	1.58	—	—	—	—
		.03	.04	110	1.06	1.14	1.22	1.33	1.45	1.63
			.08	131	1.06	1.13	1.21	1.31	1.43	1.59
		.05	.04	69	1.03	1.07	1.12	1.16	1.22	1.28
			.08	81	1.04	1.07	1.12	1.16	1.21	1.27
2,700	3	.01	.04	197	1.16	1.39	1.75	2.45	—	—
			.08	218	1.15	1.36	1.69	2.28	—	—
		.03	.04	68	1.04	1.09	1.15	1.22	1.29	1.38
			.08	74	1.05	1.09	1.16	1.22	1.28	1.36
		.05	.04	42	1.02	1.05	1.07	1.12	1.14	1.19
			.08	46	1.02	1.04	1.09	1.11	1.13	1.17
	7	.01	.04	226	1.16	1.39	1.74	2.45	—	—
			.08	274	1.15	1.36	1.69	2.28	—	—
		.03	.04	78	1.05	1.10	1.15	1.22	1.29	1.38
			.08	93	1.04	1.10	1.15	1.22	1.29	1.37
		.05	.04	48	1.04	1.06	1.08	1.13	1.17	1.21
			.08	57	1.04	1.05	1.09	1.12	1.16	1.19

[1] Stock goes to zero.

much interpretation (Mitchell footnote 4), but at least the extrapolations will approximate true trends.

The aboriginal catch data for some years may represent only the minimum landed catch. The pre-1960 aboriginal catch fluctuates from 0 to 47 (1908) per annum, where presently known. From 1978 back to 1854 there are many years for which no data were recorded or obtainable. Also, for many years for which data are available, the numbers given may not represent the true total landed catch. In our analysis, these unrecorded kills have implications only for the data from 1908 or 1912, near the end of the commercial pelagic fishery when the aboriginal catch begin to represent the majority of the total catch. However, during the much earlier period of high commercial catches, the aboriginal catch composed a small percentage of the total (5% or less of the pelagic catch at its highest). Thus any analysis of recovery patterns dependent upon the post-1900 data is entirely dependent upon the completeness of the aboriginal catch. Since few contemporary written records have been kept and continued library research yields new figures for given years, the aboriginal catch must be regarded as minimum and provisional.

Limitations of the Model

All models with published results previously used on whale populations have been applied to odontocetes, balaenopterids, or eschrichtiids, but not to balaenids. Because we are dealing with a separate zoological family (much older than the balaenopterids and apparently different in many behavioral features), caution should be used when applying balaenopterid vital parameter values, by analogy, to the balaenid model. No other reasonable estimates are available, however.

Although the model (Equation 2) used to estimate initial abundance is relatively simple, it does account for fishing and natural mortality and recruitment as a function of the time-lagged population size. It is quite possible, though, given the 130 yr we are considering, that the natural mortality rate has changed. Such a change, if it has occurred, probably would have had a relatively small effect on the initial stock estimates. We have also not considered the effect of a differential sex ratio in the large pelagic catches, which could have resulted in the 1912 population consisting of (in the worst possible cases) mostly males, mostly old females of low fertility, or young animals of either sex.

Although Figure 2 shows a minimum population size occurring around 1912, we have not calculated the minimum size the population might have declined to, for the following reasons: assumptions that the population was much smaller then (and has appreciably recovered) cannot be proven, and represent only one alternative explanation of the history of the fishery and of the population since the early 1900's. For example, we do not know how the 1912 population was structured. If, as seems likely with high prices for baleen, selection mainly for large animals with long baleen occurred near the end of the fishery, then the remnant population might have comprised a large proportion of young animals. The 1977 population might represent a considerable proportion of this 1912 population, now old, and we would know little about net recruitment or failure thereof.

The most difficult parameter to estimate in any whale population is the recruitment rate. In the absence of better knowledge, we have used a simple linear model and specified a range of maximum net recruitment rates. Given that the recruitment rate function varies between some maximum value at stock level near zero and M at P_0, the shape of the curve has less effect than the value of $(r - M)_{\max}$. During the early history of the fishery, catches exceeded recruitment, and during the last half-century the stock was at a relatively low level. Thus, the recruitment rate was close to its maximum and varied little. A further study could consider the effect of a dome-shaped recruitment curve.

Given our results, it appears likely that stock size between 1910 and 1978 was probably <10% of the initial stock level. According to most classical models used with baleen whale populations, the net recruitment should have been near its maximum for about the last 60 yr. Because the population does not appear to have grown substantially since then, either the recruitment rate has been low or the kills have been higher than currently estimated. It is also possible that the catches during the last half-century represent survivors of the then young animals.

Aspects of the Fishery

We may have to consider very low net recruitment rates because the changing nature of the fishery suggests that, as the worst case, the whalers efficiently decimated a structured population successively over its geographic range. The argument is as follows: females with calves migrate farther north (later, in the migration stream) and also inhabit ice fields. They might not have been as available to the early fishery, 1850-ca. 1870's, which used sailing vessels at the ice edge and which was mainly a midsummer to late season fishery. The greatest removals were during this time and for a short period. Subsequently, with the development of steam whaling, overwintering of the fleet became possible, and heavy fishing occurred in the ice fields at all times. The fishing season was effectively increased in length between the 1880's and 1910's. (Even if the population were not so structured by sex or age, the present spring and summer distribution is confined to a much smaller area compared with the data of Townsend (1935).)

Due to the unique geography, stratification, and timing of this fishery, the possibility exists that once the stock is fished to some low level, recruitment failure could occur and that net recruitment since about 1900 could indeed be as low as 0.01, the minimum figure used in our calculations.

Any subsequent analysis of annual catch and effort data (e.g., including number of vessels, etc.) should consider changing technology. The fishery changed radically from one of a sailing vessel-ice edge-early season fishery to a steam vessel-ice pack-nearly year round fishery. The best measure of change in effort between sailing and steam vessels to catch the same number of whales might be the monthly duration of the respective voyages.

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