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Chapter 10

STOCK SIZES PRIOR TO COMMERCIAL WHALING

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The harvest of bowheads near shore and on the high seas using ships and industrial age techniques marked the beginning of the commercial exploitation of the bowhead whale, a period which opened in the early 16th century near Labrador (Barkham 1978, 1980, 1984; Chapter 13), in the early 17th century near Spitsbergen (Jenkins 1921, Chapter 13), and in the mid-19th century in the Okhotsk and Bering seas (Scammon 1874, Chapter 14). How many bowheads roamed the seas just prior to those times? The purpose of this chapter is to review the history of attempts to answer that question and to present our interpretation of the current state of knowledge, in the end providing a minimum estimate of 50,000, which is consistent with existing information.

Most authorities believe that there were several essentially independent populations of bowheads, each known as a "stock" (Tomilin 1957, Mitchell 1977, Chapter 9). The rigorous evidence of the biological independence of these populations is weak, and is based on the history of the commercial fisheries (see Chapters 9, 13, and 14). The rapid decline in bowhead numbers in one area was followed by the opening up of new areas where the whales appeared abundant and were also brought into a rapid decline, suggesting that each stock functioned more or less independently. It is also possible, but unlikely, that the whales from an exploited area sought refuge in unexploited areas, so that the "stocks" may not be distinct biological units, but simply a reflection of whaling areas exploited one at a time. Regardless of the biological reality of separate stocks, our knowledge of the catch and kill of the bowhead and its decline is segregated by divisions of geography and time. Therefore an estimate of the pre-exploitation population size must be developed as a sum of the estimates for each of the areas. The harvesting regions, or stocks, are referred to here as the Spitsbergen, the Davis Strait, the Hudson Bay, the Okhotsk Sea, and the Bering Sea stocks, and are described in Chapter 9.

Commercial bowhead harvests began in the Spitsbergen area in 1611 as a shore fishery (Reeves 1980, Chapter 13), peaking in the late 1600s as a pelagic fishery (Mitchell -1977). A productive fishery continued into the 1800s (Chapter 9, Chapter 13). The Davis Strait fishery began in the late 1600s, and was occurring at a substantial level by 1719 when reliable record keeping was begun by the Dutch (Chapter 13). Large and protracted harvests, first by Dutch and German whalers, and then by British and American vessels, continued in the Davis Strait region through the late 1800s, until it too was nearly depleted of whales by 1911 (Ross 1979, Chapter 13).

Commercial whaling in Hudson Bay began in 1860, with catches declining by the 1870s, and few whales landed after 1912 (Ross 1979, Chapter 13).

Bowhead populations in the Okhotsk, Bering, Chukchi, and Beaufort Seas were the last to be discovered by commercial whalers. In the Okhotsk, the first whaling ship took bowheads "not earlier than 1847, nor later than 1849" (Scammon 1874) with catches declining by the 1880s (Mitchell 1977). The Bering Sea stock was first exploited commercially in 1848 with catches declining through the end of the century and effectively ending by 1914 (Bockstoce and Botkin 1983, Bockstoce 1986, Chapter 14).

METHODS FOR ESTIMATING STOCK SIZES PRIOR TO COMMERCIAL EXPLOITATION

There have been several estimates of the pre-exploitation size of bowhead stocks, all of which make use of historical records, population models, or a combination of the two. Ideally, using an historical approach, one could imagine whaling records sufficiently complete so that the sightings, catch, and kill of the whalers provide a representative sample of the population from which a size at the start of the whaling period might be estimated. None of the available information is ideally complete. However, it is sufficient to have permitted prior estimates, albeit rough, for all of the exploited populations based on catch and kill records.

The pre-exploitation stock sizes might also be estimated from a population model if (1) a realistic model structure were known, (2) all population parameters could be determined with sufficient accuracy, and (3) the population size at the end of the pelagic whaling era were known accurately. With this information one could theoretically run a population model backwards (or in practice, iterate a forward solution) to determine the annual changes in abundances from the end of the whaling period to the beginning (or *vice versa).* The problem with this approach is the lack of basic information to formulate the structure of a model and to estimate the values of parameters.

As with other long-lived organisms, bowhead whales have a complex life history which can influence birth and death rates (see Chapters 7, 8, and 11). Birth and death rates might be age, sex, size, and life-stage dependent, and might be influenced by environmental factors such as ocean currents and available food supply, which themselves might vary over time, possibly in a stochastic manner. Adding to the complexity, different processes might influence birth and death rates at different time intervals, and birth rates might vary with complex behavioral characteristics of individuals. A complete population model would take all of these factors into account. An approach to a model which had the potential to consider many of these factors was suggested by Wu and Botkin (1980) for another large mammal, the African elephant. For the bowhead whale there is insufficient information from which age, sex, size, life-stage, or environmental influences on birth and death can be accurately estimated. Therefore estimates of pre-exploitation stock sizes, made with models, must be considered informal case histories with limited statistical validity. There are several model-derived estimates for the Bering Sea stock which we discuss below.

Approaches which use models to estimate pre-exploitation stock sizes of the bowhead involve a tradeoff. Either one chooses a simple, but unrealistic model formulation with parameters that can be accurately estimated, or one chooses a complex model which, although more realistic, includes parameters the values for which cannot be accurately estimated from available information and are chosen as simply plausible. One must decide which approach is appropriate to the task. For estimating the pre-exploitation stock sizes of bowheads, we favor an approach for which the assumptions are clear if unrealistic, so that estimates can be accepted or rejected on simple and objective criteria. However, we review both kinds of approaches so that readers can make their own choices.

Despite the tentative nature of the numerous estimates, they are of interest and of practical importance. In 1974 the International Whaling Commission (1976) established that the original population size of a species would be used as an index against which current population size was to be compared for the purpose of classifying each species into management categories and for setting harvest quotas (summary provided by Allen 1980).

ESTIMATES OF STOCK SIZES

The Bering Sea Stock

The historical record—The historical record of the pelagic and shore-based fishery for bowhead whales in the Bering, Chukchi, and Beaufort seas (Table 10.1) has been successively refined by several authors since an original compilation by Mitchell (1977). The principal data are from an extensive survey of journals and logbooks from an estimated 19% of the pelagic whaling cruises to the western arctic of North America from 1849 to 1914 (Bockstoce and Botkin 1983, Chapter 14). The record is augmented by tabulations of kills in the native harvests on shores of the United States, Canada, and Russia (Marquette and Bockstoce 1980, Bogoslovskaya *et al.* 1982, Braund *et al.* 1988), and with several modifications (Breiwick and Mitchell 1983, Breiwick *et al.* 1984, Sonntag and Broadhead 1989). This combined record is one of the longest time series of harvest data for any mammal.

Estimates based on extrapolations from catch records—An approach which minimized the reliance on formal models and emphasized the use of the historical record was first made by Rice (1974). He assumed that the average number of whales killed exactly equaled the net recruitment to the population, which in turn was assumed to be exactly 5 % of the total population. Records then available suggested that the kill had been 219/yr during an assumed peak harvest period from 1868 to 1884 (tabulated by Clark 1887). These assumptions led to an estimate of 219/0.05 or roughly 4,000-5,000 whales. Since these assumptions are unlikely and are not verified, and since there has been considerable improvement in our knowledge of the catch and kill, this first estimate of the Bering Sea stock has only historical interest.

Mitchell (1977) devised a simple method which has served as the basis for his attempts to estimate pre-exploitation bowhead population sizes in all stocks. As with the Leslie-DeLury method (below), this method assumes

Table 10.1. Estimated annual and cumulative total kill of bowheads from the Bering Sea stock, 1848-1987. From summary of Sonntag and Broadhead (1989); primary sources are given in endnotes.

			Cumulative total kills		
Year	Pelagic kill'	Shore-based kill'	Pelagic	Shore-based	Total
1848	18	0	18	0	18
1849	571	2	589	2	591
1850	2,067	0	2,656	2	2,658
1851	896	2	3,552	4	3,556
1852	2,682	27	6,234	31	6,265
1853	796	11	7,030	42	7,072
1854	130	36	7,160	78	7,238
1855	2	0	7,162	78	7,240
1856	0	0	7,162	78	7,240
1857	78	0	7,240	78	7,318
1858	459	2	7,699	80	7,779
1859	366	6	8,065	86	8,151
1860	221	0	8,286	86	8,372
1861	306	0	8,592	86	8,678
1862	157	0	8,749	86	8,835
1863	303	0	9,052	86	9,138
1864	434	0	9,486	86	9,572
1865	588	2	10,074	88	10,162
1866	540	14	10,614	102	10,716
1867	599	0	11,213	102	11,315
1868	516	0	11,729	102	11,831
1869	370	12	12,099	114	12,213
1870	620	17	12,719	131	12,850
1871	133	5	12,852	136	12,988
1872	194	6	13,046	142	13,188
1873	147	0	13,193	142	13,335
1874	95	0	13,288	142	13,430
1875	200	0	13,488	142	13,630
1876	76	0	13,564	142	13,706
1877	262	8	13,826	150	13,976
1878	80	0	13,906	150	14,056
1879	261	5	14,167	155	14,322
1880	460	20	14,627	175	14,802
1881	418	17	15,045	192	15,237
1882	240	2	15,285	194	15,479
1883	39	3	15,324	197	15,521
1884	133	27	15,457	224	15,681
1885	287	90	15,744	314	16,058
1886	133	35	15,877	349	16,226
1887	204	36	16,081	385	16,466
1888	133	27	16,214	412	16,626
1889	53	74	16,267	486	16,753
1890	127	9	16,394	495	16,889
1891	234	50	16,628	545	17,173
1892	317	29	16,945	574	17,519

Table 10.1. Continued.

		Shore-	Cumulative total kills		
Year	Pelagic kill'	based killb	Pelagic	Shore-based	Total
1893	141	39	17,086	613	17,699
1894	151	83	17,237	696	17,933
1895	94	23	17,331	719	18,050
1896	58	60	17,389	779	18,168
1897	73	57	17,462	836	18,298
1898	228	81	17,690	917	18,607
1899	208	26	17,898	943	18,841
1900	112	36	18,010	979	18,989
1901	29	26	18,039	1,005	19,044
1902	132	30	18,171	1,035	19,206
1903	95	21	18,266	1,056	19,322
1904	74	12	18,340	1,068	19,408
1905	93	12	18,433	1,080	19,513
1906	36	33	18,469	1,113	19,582
1907	70	26	18,539	1,139	19,678
1908	33	90	18,572	1,229	19,801
1909	10	51	18,582	1,280	19,862
1910	16	21	18,598	1,301	19,899
1911	30	18	18,628	1,319	19,947
1912	0	39	18,628	1,358	19,986
1913	0	23	18,628	1,381	20,009
1914	40	21	18,668	1,402	20,070
1915	0	23	18,668	1,425	20,093
1916	0	23	18,668	1,448	20,116
1917	0	35	18,668	1,483	20,151
1918	0	27	18,668	1,510	20,178
1919	16	17	18,684	1,527	20,211
1920	0	33	18,684	1,560	20,244
1921	0	9	18,684	1,569	20,253
1922	0	39	18,684	1,608	20,292
1923	0	12	18,684	1,620	20,304
1924	0	41	18,684	1,661	20,345
1925	0	53	18,684	1,714	20,398
1926	0	35	18,684	1,749	20,433
1927	0	14	18,684	1,763	20,447
1928	0	30	18,684	1,793	20,477
1929	0	30	18,684	1,823	20,507
1930	0	17	18,684	1,840	20,524
1931	0	32	18,684	1,872	20,556
1932	0	27	18,684	1,899	20,583
1933	0	21	18,684	1,920	20,604
1934	0	21	18,684	1,941	20,625
1935	0	15	18,684	1,956	20,640
1936	0	24	18,684	1,980	20,664
1937	0	53	18,684	2,033	20,717
1938	0	36	18,684	2,069	20,753
1939	0	18	18,684	2,087	20,771

Table 10.1. Continued.

Year	Pelagic kill'	Shore-based killb	Cumulative total kills: Pelagic	Cumulative total kills: Shore-based	Total
1940	0	20	18,684	2,107	20,791
1941	0	38	18,684	2,145	20,829
1942	0	26	18,684	2,171	20,855
1943	0	14	18,684	2,185	20,869
1944	0	8	18,684	2,193	20,877
1945	0	23	18,684	2,216	20,900
1946	0	20	18,684	2,236	20,920
1947	0	21	18,684	2,257	20,941
1948	0	8	18,684	2,265	20,949
1949	0	11	18,684	2,276	20,960
1950	0	23	18,684	2,299	20,983
1951	0	23	18,684	2,322	21,006
1952	0	11	18,684	2,333	21,017
1953	0	41	18,684	2,374	21,058
1954	0	9	18,684	2,383	2,1067
1955	0	36	18,684	2,419	21,103
1956	0	11	18,684	2,430	21,114
1957	0	5	18,684	2,435	21,119
1958	0	5	18,684	2,440	21,124
1959	0	2	18,684	2,442	21,126
1960	0	33	18,684	2,475	21,159
1961	0	17	18,684	2,492	21,176
1962	0	20	18,684	2,512	21,196
1963	0	15	18,684	2,527	21,211
1964	0	24	18,684	2,551	21,235
1965	0	14	18,684	2,565	21,249
1966	0	24	18,684	2,589	21,273
1967	0	12	18,684	2,601	21,285
1968	0	27	18,684	2,628	21,312
1969	0	32	18,684	2,660	21,344
1970	0	66	18,684	2,726	21,410
1971	0	26	18,684	2,752	21,436
1972	0	45	18,684	2,797	21,481
1973	0	57	18,684	2,854	21,538
1974	0	54	18,684	2,908	21,592
1975	0	45	18,684	2,953	21,637
1976	0	92	18,684	3,045	21,729
1977	0	111	18,684	3,156	21,840
1978	0	17	18,684	3,173	21,857
1979	0	27	18,684	3,200	21,884
1980	0	30	18,684	3,230	21,914
1981	0	26	18,684	3,256	21,940
1982	0	19	18,684	3,275	21,959
1983	0	18	18,684	3,293	21,977
1984	0	25	18,684	3,318	22,002
1985	0	17	18,684	3,335	22,019
1986	0	28	18,684	3,363	22,047

Table 10.1. Continued.

Year	Pelagic kills	Shore-based killb	Cumulative total kills Pelagic	Shore-based	Total
1987	0	29	18,684	3,392	22,076
1988	0	23'	18,684	3,415	22,099
1989	0	18	18,684	3,433	22,117
1990	0	30	18,684	3,463	22,147
1991	0	27	18,684	4,390	22,174

Pelagic kill data for 1849-1914, including both the estimated catch and the struck-and-lost data, are from Bockstoce and Botkin (1983). 1848 data are from Breiwick and Mitchell (1983), who used a catch figure of 15 and the average struck and lost rate from 1849 to 1854 from Bockstoce and Botkin (1983) to estimate a total kill of 18. Kill of 16 in 1919 is a personal communication to G. H. Jarrel from T. B. Brower, Sr., 4 January 1983, as cited in Breiwick *et al.* 1984.

[b] Shore-based kill data include landings as well as estimates of whales struck and lost from U.S., Canadian, and Soviet shores. Data are from Marquette and Bockstoce (1980) with corrections as given in Breiwick *et al.* (1984) including data from Bogoslovskaya *et al.* (1982), and additions by Braund *et al.* (1988). The record from western Canada is generally insufficient to estimate adequately the actual catch (Marquette and Bockstoce 1980, Reeves and Mitchell 1985), so that the total shore kill is likely to be underestimated. Struck-and-lost totals (subsumed in kill totals) are by method of Breiwick *et al.* (1984): prior to 1970 all whales struck were assumed killed; mortality of struck whales was computed as 50% from 1971 to 1977, and 75% from 1978 to 1987. Numbers for struck and lost whales for 1982-1987 are from International Whaling Commission reports for the appropriate years.

Shore-based landings for 1988-1991 are from records of The Alaska Eskimo Whaling Commission, P. 0. Box 570, Barrow, AK 99723.

net recruitment equals zero, so that the original population at the beginning of a decade is simply the number killed plus the number remaining. The calculations are made in three steps. The first is to sum the estimates of the number of bowheads caught during a decade of peak harvests. The peak catch is estimated as 8,852 between 1851 and 1860. This is based on an estimated 1,917 vessel-years (one vessel hunting for one season is a vessel-year, from Clark 1887, cited in Mitchell 1977), of which about 57 % were hunting bowheads, capturing an average of 8.1 bowheads per vessel-year. The second step is to correct the catch totals upwards to account for the number of whales struck but lost and assumed to have died. This was roughly estimated from logbooks and other historical records as 24% of those caught, resulting in a total kill of 11,647 during the decade. Finally, the number of whales remaining at the end of the peak decade is estimated from the number of whales harvested in the next few decades. With this method, Mitchell (1977) estimated the population size prior to commercial exploitation as 18,000. This value is roughly 1,000 greater than the midpoint of the range estimated with the simple recruitment model (below).

Estimates based on catch and effort regressions—When available, historical records of fishing effort can provide additional statistical muscle to estimate original stock abundance by means of catch-effort regressions. However, this approach has the disadvantage of stringent and ultimately unrealistic assumptions.

Estimates of pre-exploitation stock sizes of bowheads have been made using the Leslie-DeLury method, one of the more common methods used in fisheries assessments (Leslie and Davis 1939, DeLury 1947). The method is essentially a least-squares regression with kill per unit effort as the dependent variable and cumulative kill as the independent variable. This method assumes that the population is closed (without emigration, immigration, or additions due to births), and that the number of whales caught per unit of effort will decline linearly with the size of the depleted stock. These assumptions are only realistic in the case where catch and kill occur so rapidly that there is no chance for births, emigration, or immigration to influence the population dynamics. While this might be reasonable for the first 10-20 yr during which a stock is subject to the greatest depletion, it is not realistic for a stock exploited for longer periods. However, it might be reasonable if the Bering Sea population consisted of several subpopulations, each of which was depleted in a short time (one or two decades). The changing geographical distribution of the catch during the full history of the commercial fishery seems to support this possibility (see also Chapter 14). Another fundamental assumption of this method is that the entire population is available and equally likely to be caught.

Bockstoce and Botkin (1983) applied the Leslie-DeLury method and four modifications (Chapman's [1974] method, Allen's [1966] *q* method, and two versions of Allen's [1966] natural mortality and reproduction method) to their historical data. The range of estimates from all of these versions for the original Bering Sea stock of bowheads is approximately 10,900-47,000 (Table 10.2).

As Tillman *et al.* (1983) suggest, the assumption of a closed population is unlikely to hold when the entire 67-yr commercial catch history is used, especially if net recruitment (the annual difference between recruitment and mortality) were to change as the population was depleted. Using only the first 5-15 yr of pelagic catch and kill data, and mortality rates of 0.01 and 0.05, Tillman *et al.* (1983) estimated the original population to range from 6,100 to 10,500 (Table 10.2) using two of the catch-effort regression techniques (Chapman's [1974] method and Allen's [1966] method with a constant recruitment rate). These estimates seem unrealistically low because, as Tillman *et al.* (1983) note, the values are considerably lower than the cumulative catch in the first 20 yr (Table 10.1). The lowest estimate (6,100) would require a net recruitment rate of over 10% to prevent extinction (as estimated with the simple recruitment model; see below), and a rate this high is not likely for a baleen whale (a review of recruitment rates is in Breiwick *et al.* 1981).

Another approach which uses measures of effort is Allen's (1966) least-squares method, which is a hybrid between catch-effort regressions and simple population models. This technique estimates original abundance by minimizing the sums of squares between actual and expected catches, where the expected catch is the product of the available population (resulting from net recruitment from the previous year's population), the effort, and the average catch per unit of effort. This method requires an estimate of net

Table 10.2. Estimates of the Bering Sea stock size of bowheads in 1848 by various methods.

Estimate ($x 10^3$)	Method	Source
18	Sum of catches in peak decade of harvest plus residual population	Mitchell (1977)
14.2-26.4	modified logistic	Breiwick *et al.* (1981)
8.0-18.4	modified logistic	Breiwick and Mitchell (1983)
30.8-38.5	DeLury	Bockstoce and Botkin (1983)
34.7-43.6	DeLury, 3-yr averages	Bockstoce and Botkin (1983)
10.9-21.6	Chapman's modified DeLury	Bockstoce and Botkin (1983)
18.4-32.8	Chapman's "q" method	Bockstoce and Botkin (1983)
11.3-47.0	Allen's modified DeLury	Bockstoce and Botkin (1983)
23.4-24.5	Allen's modified DeLury with density-dependent recruitment	Bockstoce and Botkin (1983)
7.1-8.1	Chapman's modified DeLury	Tillman *et al.* (1983)
6.1-10.5	Allen's modified DeLury	Tillman *et al.* (1983)
10.3-21.8	Allen's least squares	Tillman *et al.* (1983)
13.6-23.0	Leslie matrix, density-dependent recruitment	Breiwick *et al.* (1984)
13.7-26.7	Leslie matrix, density-dependent recruitment	Breiwick and Braham (1990)
10.4-23.0	simple recruitment model	this study

recruitment for each year, a parameter which cannot be accurately estimated at this time. Allowing net recruitment values to range from 0 to 0.04, Tillman *et al.* (1983) estimated the original size of the Bering Sea stock as ranging from 10,284 to 21,827, using the complete record of kills and effort from 1848 to 1914 in Bockstoce and Botkin (1983). These estimates are similar to those we provide below using a simple recruitment model, suggesting that Allen's hybrid technique is not sensitive to violations of closed population assumptions (see also review by Horwood 1987).

Estimates based on population models-1. Logistic population growth models, among the oldest forms of population models, are commonly used in population estimation efforts despite their numerous limitations. Important assumptions of this model include (a) populations have a fixed, time-invariant carrying capacity (sometimes defined as an average maximum population size) set by environmental limitations; (b) populations at their lowest viable level are capable of maximal per capita net recruitment; and (c) net recruitment is a continuous, decreasing function of population size alone without regard to age structure. According to this model, an unexploited population starting at carrying capacity would have a recruitment rate equal to the mortality rate, and would have no net growth.

Breiwick *et al.* (1981) applied a modification of the logistic model (Allen 1980) to estimate the size of the Bering Sea stock in 1848. Their formulation breaks apart the intrinsic rate of increase into a constant rate of mortality and a recruitment rate which is a logistic function of a previous population size. This modification allows for changes in population size and the rate of recruitment to reflect the time it takes whales to achieve sexual maturity from birth.

Although their model is an attempt to achieve some level of realism, data are not available to provide reliable point estimates of rates of recruitment and mortality, or the lag period to account for age at sexual maturity, and these are chosen as simply plausible.

Ordinarily, this model would be used to project a future population size from a known condition, but in the case of the bowhead population, the current size is more accurately known than that in 1848, immediately prior to commercial exploitation. Therefore, Breiwick *et al.* (1981) used an iterative method to estimate the 1848 population size. They chose an initial value which, through trial and error calculations, resulted in the estimated size in 1970. Due to uncertainty in the choice of parameter values, they provide estimates of the 1848 population size ranging between 14,200 and 26,400 (Table 10.2) based on the initial catch history provided by Mitchell (1977). These estimates were superseded by the reanalysis by Breiwick and Mitchell (1983). This latter calculation used more complete kill records based primarily on the compilation by Bockstoce and Botkin (1983), but also incorporating shore-based kills tabulated by Marquette and Bockstoce (1980), with adjustments to the record for whales struck and lost in the shore fishery. The revised estimates range from approximately 8,000 to 18,400, depending on the combination of rates of recruitment and mortality, time lags, final population size, and the intensity of density dependence, all of which are unknown.

2. Age-structured, logistic-type models (Lewis 1942; Leslie 1945, 1948) were applied by Breiwick *et al.* (1984) to estimate the 1848 population size of bowheads, despite the general lack of age-specific population parameters for the species. Their estimates ranged from 13,600 to 23,000 depending on parameter values. More recent calculations using the same model with revised parameters provide estimates of 13,700-26,700 (Breiwick and Braham 1990).

Ordinarily, age-structured models require rates of fecundity and mortality for each age class. In this case, population-size estimates for bowheads were achieved by imposing several simplifying assumptions: annual fecundity is invariant across adult age classes; mortality rates are constant and take on two values, one for adults and one for immatures; and the original population was stable with a stable age distribution.

Since data are insufficient to estimate accurately the age at first breeding, or fecundity, or mortality rates of the two age classes, or the maximum age, Breiwick *et al.* (1984) provide 80 different estimates of the original population resulting from various combinations from the range of potential parameter values. Although this approach provides individually precise estimates, there is only a weak empirical basis to choose any particular parameter set among the many possibilities; a discussion of parameter choices is presented by Breiwick *et al.* (1984), Breiwick and Braham (1990), and in Chapter 11; (see also Chapters 7 and 8). Despite the lack of information on parameter values, the model is useful in testing plausible ranges for values. For example, Breiwick *et al.* (1984) show that estimates of the proportion of the population which is immature (40 % , Johnson *et al.* 1981) necessitates a late age of sexual maturity. In fact, more recent data indicate that the percentage of immature animals in the present bowhead population is over 40% and that age at sexual maturity may be within the range of 10-20 yr (Chapter 11).

To summarize, one drawback in using the age-structured model for estimating original population sizes is that even if one accepts the model structure, there is currently no clear reason to select as correct any value within the range of revised estimates, which were found to be 13,700-26,700 (Breiwick and Braham 1990). There is also little empirical support for the logistic-type model structure.

Density dependence and models of bowhead populations—Empirical evidence suggests that reproductive rates and age at sexual maturity may be density dependent for some baleen whales, including some populations of blue, fin, and sei whales *(Balaenoptera musculus, B. physalus,* and *B. borealis* respectively), and that this usually results from changing resource levels, especially food resources (Fowler *et al.* 1980; Fowler 1984, 1987). However, this evidence does not demonstrate that these mechanisms will act according to a logistic-type formulation, that is, as a continuous function of population size. Threshold responses are equally possible.

Further, while it is reasonable to assume that fecundity in a population will be inversely related to population size (Breiwick *et al.* 1984), there is no evidence for this aspect of density dependence in bowheads over the course of the fishery from 1848 to the present (Breiwick *et al.* 1981). A generalization of this sort may be useful in discussing average cases and is, of course, a simplification, but cannot be assumed to apply in a reconstruction of the specific history of the Bering Sea bowhead stock.

Effects of a variable environment, including altered food resources and increased mortality rates, may be as likely to regulate bowhead whale populations as is continuous density-dependent fecundity. For example, Mitchell and Reeves (1982) discuss a scenario, first suggested by Vibe (1967), in which ice blockages prevent migratory movements of bowheads to feeding grounds, which in turn interrupts the annual reproductive cycle.

Alternatively, reproductive rates may fall off when a population is reduced below a critical level, as suggested for bowheads by Breiwick *et al.* (1981). Declines of this nature may be due to behavioral or other limitations and are known as "Allee effects," or social dysfunctions (Allee 1931, Soule 1983).

A simple recruitment model—While it is possible to construct successful models of considerable detail with modern computer techniques *(e.g.,* Botkin *et al.* 1972), if few of the parameters can be estimated with accuracy, and if the model structure cannot be verified, then there is not an objective basis on which to accept or reject the resulting projections. Therefore, we took an approach to estimation of the bowhead stock size which uses, but does not exceed, the limits of available data. We apply a simple model without density dependence so as to infer what may have been the population size of the Bering Sea stock in 1848 (see Eberhardt 1987 for a discussion of simple population models). We assume only that the population is decreased by the annual kill, K_t, for each year, *t,* and that the difference between annual recruitment and natural mortality is a constant per capita net recruitment rate, R_{net}:

$$P_{t+}, = (1 + \qquad (P, - K,) \qquad (1)$$

Using this simple method, the goal is to attain a minimum and maximum value for the pre-exploitation population size. The estimates depend on the choice of the net recruitment rate. High values of R_{ee}, result in low estimates of original abundance, and *vice versa.* A minimum estimate for the 1848 Bering Sea stock may be obtained by assuming a maximum net recruitment rate of 0.05, which is a plausible maximum for other large baleen whales (evidence reviewed in Breiwick *et al.* 1981), although a higher rate of 0.068 has been estimated for a right whale *(Eubalaena glacialis)* population of South Africa which has been recovering from a depleted state earlier in this century (Best 1990). We restrict the time period to 1848-1914 to control the minimum possible population near the end of the fishery, and we assume that the number in 1914 may have been as low as 1,000 whales, to allow for a conservative estimate of the 1848 population.

We iterate a forward solution (per Breiwick *et al.* 1981) using the kill data in Table 10.1 (sum of pelagic and shore-based kills). Calculations begin with the 1849 population rather than the 1848 season. (The kill total of 18 in 1848 is small relative to the estimated 5% recruitment for any reasonable estimate of the initial population size, so that the population in 1849 would be larger than that in 1848.) Using this approach our minimum estimate is about 10,368 whales, which we round to 10,400. Our model projects that this population underwent a rapid decline in the first decade of commercial exploitation, followed by a less rapid decline through the end of the century (Fig. 10.1).

We cannot readily obtain an estimate of the maximum original size of the Bering Sea stock using the simple recruitment model without knowing the potential minimum net recruitment rate. Net recruitment could actually be negative due to excessive natural mortality, and the population may have been undergoing a natural decline. However, if we assume that the net recruitment rate was no lower than zero, then the original population is estimated with equation 1 as about 20,071 (for a target population of 1,000 in 1914). This estimate is simply the cumulative kill at the end of the fishery (19,071) plus the residual population, and higher initial populations are obtained for higher estimates of the residual population by addition. Whalers had difficulty in locating whales during the last years of the commercial hunt (Bockstoce 1986), so that a rough guess for the maximum residual population is 3,000. Given that this is a rough estimate, and that the estimate of the cumulative kill may be an underestimation, we round the sum of 19,071 whales killed plus 3,000 residual whales to 23,000 as an estimate of the maximum population size for the Bering Sea stock. The estimated range is therefore 10,400-23,000. The minimum estimate is relatively insensitive to the ending population. For example, if the residual population is assumed to be as low as 100 or as high as 3,000, the minimum estimate is 10,333 or 10,449 respectively (Table 10.3). Both the minimum and maximum estimates are also relatively insensitive to the year in which the smallest population occurs. A point estimate is not made because there is insufficient biological and historic information to have much confidence in the reality of a point estimate.

These projections are limited by assumptions of constant mortality and recruitment rates, which are unlikely to be true. However, they provide a range of estimates of the population size of the Bering Sea stock in 1848 with a model that does not exceed our knowledge of bowhead whale biology.

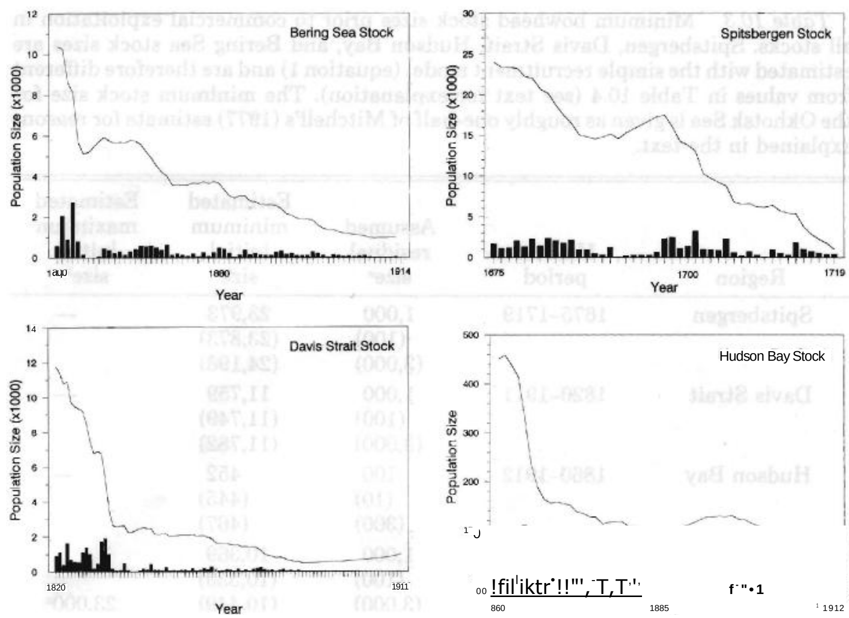

Figure 10.1. Population size projections (solid lines) for the Bering Sea, Spitsbergen, Davis Strait, and Hudson Bay stocks of bowheads estimated with the simple recruitment model (equation 1 with $R_{072} = 0.05$). These projections are iterative solutions as described in the text. The estimated number of whales killed is shown with vertical bars. The Bering Sea projection begins with a minimum population size of 10,400 in 1849 and ends with a minimum of 1,000 in 1914 when the fishery was in decline. Total annual kill of Bering Sea bowheads is the sum of pelagic and shore-based kills, corrected for whales struck and lost but assumed to have died (sources given in Table 10.1). The Spitsbergen, Davis Strait, and Hudson Bay projections begin with estimated minimum stock sizes of 24,000 in 1675, 11,800 in 1820, and 450 in 1860 respectively. Ending population sizes for all but the Bering Sea stock were chosen as 10% of the starting populations. Sources for kill data are Mitchell (1977) for the Spitsbergen stock and Ross (1979) for the Davis Strait and Hudson Bay stocks. The total annual kill for the Spitsbergen, Davis Strait, and Hudson Bay stocks are corrected for an estimated 20, 15, and 20% loss rates respectively (Mitchell 1977).

When parameter values are selected from within plausible ranges, the age-structured model provides point estimates of the 1848 population size as closer to 23,000 than to 10,400 (Breiwick and Braham 1990; Chapter 11: Table 11.11).

Other Stocks

The only objective estimates of the original abundances of bowheads in the Spitsbergen, Davis Strait, Hudson Bay, and Okhotsk Sea stocks are direct calculations from catch histories. Results from these calculations are presented in the order of historical exploitation.

North Atlantic stocks—Mitchell's (1977) three-step method (described

Table 10.3. Minimum bowhead stock sizes prior to commercial exploitation in all stocks. Spitsbergen, Davis Strait, Hudson Bay, and Bering Sea stock sizes are estimated with the simple recruitment model (equation 1) and are therefore different from values in Table 10.4 (see text for explanation). The minimum stock size for the Okhotsk Sea is given as roughly one-half of Mitchell's (1977) estimate for reasons explained in the text.

Region	Harvest period	Assumed residual size[a]	Estimated minimum initial size	Estimated maximum initial size[b]
Spitsbergen	1675-1719	1,000	23,973	
		(100)	(23,873)	
		(3,000)	(24,196)	
Davis Strait	1820-1911	1,000	11,759	
		(100)	(11,749)	
		(3,000)	(11,782)	
Hudson Bay	1860-1912	100	452	
		(10)	(445)	
		(300)	(467)	
Bering Sea	1849-1914	1,000	10,369	
		(100)	(10,333)	
		(3,000)	(10,449)	23,000[c]
Subtotal			46,553	
Okhotsk Sea			3,000	
Rounded total			50,000	

Residual stock sizes are rough estimates based on the scarcity of whales recorded for each stock following extensive commercial exploitation (Bockstoce 1986, Chapters 13 and 14), except that the Spitsbergen fishery continued with significant catches for nearly two centuries. A range of values for residual sizes are given for the first four stocks to demonstrate the great insensitivity of the minimum estimated size to the assumed residual size.

[b] Maximum sizes are not estimated for stocks other than the Bering Sea due to the greater uncertainty in the catch histories for those other stocks relative to records for the Bering Sea.

Calculated maximum for the Bering Sea is actually 22,074, and is simply the sum of the total catch plus the estimated residual size. Due to the uncertainty in estimate of the residual size, and the sensitivity of the estimated maximum to the residual size, the maximum value is rounded to the next highest 1,000 whales.

above) has been applied to estimate population sizes near the onset of commercial exploitation as 25,000 for Spitsbergen stock (Mitchell 1977, reiterated in IWC 1978); 11,000 for the Davis Strait stock (Mitchell 1977 as revised by Mitchell and Reeves 1981); and about 580 for the Hudson Bay stock (Mitchell 1977 as revised here). The calculations and resulting values are summarized in Table 10.4.

Catch statistics chosen for the estimates were generally low or conservative values, so that the resulting totals are probably minima. Using a variety of historical catch statistics, Mitchell (1977) chose 1679-1688 as a decade of peak catch for the Spitsbergen stock when at least 12,112 bow-

Table 10.4. Estimates of bowhead stock sizes prior to commercial exploitation in the Spitsbergen, Davis Strait, Hudson Bay, Bering Sea, and Okhotsk Sea regions obtained by extrapolations from catch data. Methods are explained in the notes below and an overview is provided in the text.

Region	Total peak catch•		Loss rateb	Total	Residual sized	Total'
Spitsbergen	12,112	(1679)	0.20	15,140	10,000	25,000
Davis Strait	8,510	(1825)	0.15	10,012	1,000	11,000
Hudson Bay	341 (425)f	(1860)	0.20	426 (531)f	150	575 (680)f
Bering Sea	8,852	(1851)	0.24	11,647	6,353	18,000
Okhotsk Sea	3,506	(1848)	0.24	4,613	2,000	6,500

Peak catches are for 10-year periods beginning in the year given in parentheses. Peak catches for Spitsbergen and the Okhotsk Sea are from Mitchell (1977), Davis Strait catches are from Mitchell and Reeves (1981) based on Ross (1979), and Hudson Bay catches are from Ross (1979). The Bering Sea data are Mitchell's (1977) original estimate without correction for the most recent catch compilation as given in Table 1.

b All loss rates are from Mitchell (1977). The loss rate is the number of whales struck, lost, and assumed to have died, divided by the number of all whales killed. r Total kill is catch/(1 — loss rate).

d Residual population sizes are from Mitchell (1977), except the estimate for Davis Strait, which is from Mitchell and Reeves (1981), and the estimate for the Bering Sea, which is found by subtracting the total kill from the population estimated by Mitchell (1977). The residual stock is the number remaining at the end of the peak harvest decade.

e Total is rounded from total kill + residual size. This method assumes a closed population, *i.e.,* that additions due to births and immigration are negligible during the harvest period.

f Mitchell's (1977) original values for Hudson Bay catches (based on Ross 1974) and totals are given in parentheses.

heads were taken by Dutch and German whalers. He applied a loss rate of 20 % to account for whales struck and lost and assumed to have died. This rate is based on a 15% loss rate estimated from logbooks of the Spitsbergen fishery for the years 1791-1822, but is 5% higher because he assumed the earlier fishery during the peak decade to be less efficient. Due to large sustained catches in years following 1688, Mitchell estimated the residual population size as 10,000.

Mitchell and Reeves (1981) provide a detailed review of catch statistics for the Davis Strait fishery, relying heavily on the compilation of Ross (1979). In summary, they choose 1825-1834 as the peak decade with a minimum catch of 8,510 whales, mostly by British whalers. They apply the loss rate of 15% from the 1792-1822 Spitsbergen fishery (as above), and estimate that the residual population was at least 1,000. Their resulting estimate of 11,000 whales in 1825 is surely conservative, as they note that 5,831 were taken in the preceding ten years, and that there were large catches in the previous century.

Mitchell (1977) estimated the population of bowheads in Hudson Bay as

680 based on an estimated peak catch of 425 by American and British whalers in the decade following the advent of whaling there in 1860, a loss rate of 20% as used for early Spitsbergen fishery, and an estimated residual stock of 150 in 1870. Ross (1979, Chapter 13) provides a revised estimate of 341 for the peak catch during the same decade. Use of this revised catch figure results in a pre-exploitation population size of about 575, using the same loss rate and residual size as before (Reeves and Mitchell 1990).

Mitchell's method is likely to be most accurate if a large proportion of the whales are killed in a short period of time, and only a small residual population remains to be estimated. As shown in Table 10.4, however, the residual populations are generally quite large relative to the peak catches. Despite this apparent problem, we find good agreement between the several original values extrapolated from catch data and our recalculations with the simple recruitment model (see below).

Okhotsk Sea stock—Catch data from the Okhotsk Sea are generally lacking, so that the population size prior to commercial exploitation is especially difficult to assess. Mitchell (1977) estimated the pre-exploitation population as 6,500 (Table 10.4). This estimate was derived using the same methods applied to the Bering Sea stock. These data were extracted from historical records which often included effort and catch data from the Okhotsk Sea bowhead fishery as well as the North Pacific right whale and Bering Sea bowhead fisheries, without precisely distinguishing among species and locations. For an estimated 1,882 vessel-years, of which 23 % were hunting in the Okhotsk Sea for bowheads (original vessel data in Townsend 1935), Mitchell extrapolated a catch rate of 8.1 whales per vessel-year, to estimate the catch as 3,506 whales. To this he applied a loss rate of 24%, estimated from secondary accounts of whaling records for the Bering Sea bowhead fishery, and he made a rough guess of a residual population numbering 2,000.

A pre-exploitation estimate of 6,500 in the Okhotsk Sea may be too large for several reasons. Berzin and Doroshenko (1981) note that black right whales occur in the Okhotsk Sea in areas presumed by Mitchell (1977) to be bowhead range and suggest that 6,500 is over three times the actual value (though no quantitative justification for this is given). D. Henderson (personal communication) has made an in-depth examination of logbooks from whaling vessels hunting the Okhotsk Sea in 1847 and 1848 and believes that about one-third of the whales reported killed there were actually right whales from the Sea of Japan. For these reasons, we suggest an estimate of 3,000 as a minimum population size prior to commercial exploitation as a conservative, though mostly speculative, compromise. We suggest that 3,000 may be a minimum value due to the incomplete nature of the catch records used by Mitchell (1977).

CONCLUSIONS

The most thorough analyses of bowhead populations are for the Bering Sea stock, in part because the historical information is most complete, and in part because this stock is still subjected to harvest by native subsistence hunters. Most of the methods used have overlapping ranges of estimated population sizes for this stock.

The Leslie matrix density-dependent model has received the most attention recently for projecting historical and current population trends of the Bering Sea stock (Breiwick and Braham 1990, Chapter 11). This model, which requires estimation of the greatest number of parameters, gives minimum and maximum values of about 13,700 and 26,700 (Breiwick and Braham 1990), approximately 3,000 more than minimum and maximum values given by the simple recruitment model, which requires only an estimate of net recruitment. All 1848 population sizes estimated by Breiwick and Braham (1990) in excess of 23,000 (the maximum estimate given by the simple recruitment model) require populations of between 5,800 and 8,100 in the years 1909-1914 when the commercial whaling period was ending. These may be overly generous residual population sizes in light of the apparent scarcity of bowheads on the whaling grounds at that time (Bockstoce 1986). If residual population sizes are assumed to be less than 3,000, then the Leslie matrix model projects maximum populations of less than 17,400 with the suite of parameter values used by Breiwick and Braham (1990). This comparison demonstrates the importance of the residual population size near the end of commercial whaling in estimating the maximum population size. When residual population size is the same for the two models, the simple recruitment model projections encompass the range of values projected by the age-structured model, implying that it may be unnecessary to consider explicitly the effects of age structure and density dependence if the desire is simply to estimate a range for the pre-exploitation size of stocks.

One of the modified logistic methods, and two of the DeLury methods (Chapman's and Allen's modifications), gave estimates below 10,000. These seem unreasonable because the estimates are less than the projected 11,317 bowheads killed during the first two decades of harvest (Table 10.1), and it is unlikely that net recruitment would have been sufficient to sustain such a large kill from such a small initial population.

Only the DeLury-type methods give estimates greater than 24,000 (Table 10.2, except for the Leslie matrix model as previously explained, and the modified logistic model of Breiwick *et al.* 1981, for which the estimate was decreased using a revised catch history by Breiwick and Mitchell 1983), suggesting that these high values may be the consequence of the unrealistic assumption of a closed population.

Thus, given the information available from the historical record and our limited knowledge of the natural history of the bowhead, we can reach two conclusions: (1) we can obtain similar projections of minimum and maximum stock sizes with or without assumed density dependence, time lags, and age structure, indicating that we can avoid the necessity to estimate these factors when only the minimum and maximum possible stock sizes are sought; and (2) the Bering Sea population size in 1848 was probably no less than 10,400 and no more than 23,000, as calculated from the simple recruitment model, assuming that the residual population was no greater than 3,000 near the end of commercial whaling.

The analysis of the Bering Sea stock thus suggests that we might estimate the pre-exploitation population size of all stocks using the simple recruitment model.

Reanalysis of Spitsbergen, Davis Strait, and Hudson Bay Stocks

Using the simple recruitment model (equation 1 with It_e, = 0.05) we estimate the minimum pre-exploitation stock sizes to have been about 24,000 for Spitsbergen, 11,800 for Davis Strait, and 450 for Hudson Bay (Table 10.3). These estimates are based on catches for the periods 1675-1719 for Spitsbergen (Mitchell 1977: table 2), 1820-1911 for Davis Strait (Ross 1979: table 3), and 1860-1905 for Hudson Bay (Ross 1979: table 4), with annual catches corrected upwards for loss rates of 0.20, 0.15, and 0.20 (Mitchell 1977) respectively (Fig. 10.1). These estimates are relatively sensitive to the starting year for the iterations, for the same reason as found for the analysis of the Bering Sea stock (above), and they are likewise relatively insensitive to the choice of the final year and to the population size assumed to remain following that year (examples given in Table 10.3).

The estimates for the North Atlantic regions, made with Mitchell's extrapolation method (Table 10.4), are very similar to our model-derived estimates (Table 10.3). The estimates in the two tables are not identical due to differences in methods of calculation, mainly that Mitchell's method uses catches from the peak decade during which recruitment is assumed to be negligible, whereas we used annual kill data from longer time periods and assumed an annual net recruitment rate of 0.05. Both sets of estimates are probably low due to the conservative nature of their catch histories (Mitchell 1977, Ross 1979, Chapter 13, Mitchell and Reeves 1981). Also, our estimates are minima due to the assumption of a sustained, high net recruitment rate of 0.05 for the duration of each catch period.

We have not used the simple recruitment model to estimate maximum stock sizes because the catch histories for the North Atlantic stocks are relatively incomplete and likely to underestimate the actual mortality of whales during periods of commercial harvest. The simple recruitment model was not applied to estimate the minimum or maximum population size for the Okhotsk Sea population as there is currently no adequate compilation of catch history.

Original World Population

A minimum estimate of the total bowhead abundance for all stocks prior to commercial exploitation is 50,000. This value is obtained by simple addition of estimated minimum pre-exploitation sizes for each of the stocks (Table 10.3). We emphasize that this simple sum be viewed cautiously, as it combines totals for different time periods, under the assumption that the original whale populations were stable in size over the centuries, and that the idea of whales crossing over from one stock region to another to escape hunting pressure is invalid. There is little factual basis for either assumption. We do not present a maximum value for the world population due to the mostly incomplete catch histories for all but the Bering Sea stock, as noted above.

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