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Declining carrying capacity in the Bering Sea: Isotopic evidence from whale baleen

Abstract—The Bering Sea is a rich marine ecosystem with 1995 U.S. landings of finfish and shellfish in excess of 2×10^6 tons. Recently, major declines of marine mammal and bird populations have occurred, with the question arising as to whether the causes were top down, i.e., from fishing pressure, or bottom-up, i.e., driven by climate-change effects. We assessed the latter scenario by using the inverse relationship between phytoplankton cell-growth rates and carbon isotope fractionation to compare seasonal rates of primary productivity. The isotope ratios in the long baleen plates from bowhead whales (*Balaena mysticetus*) laid down while the whales fed in the Bering and Chukchi seas were used as a proxy for the average annual isotope ratios in their zooplankton prey and, by extension, phytoplankton. Plates from 37 whales produced a continuous isotopic record from 1947–1997 and indicate that seasonal productivity was higher in 1947–1976, peaking in 1966. Since that time, average $\delta^{13}\text{C}$ values have declined by over 2.7‰ until 1997, inferring a drop in seasonal carbon fixation of ~30–40%. Alternatively, lowered isotope ratios could arise if phytoplankton stocks significantly increased over time while cell-growth rates declined. However, long-term literature estimates for phytoplankton in the Western and Eastern Pacific Ocean and Eastern Bering Sea show either no trend or a decrease over time. Archaeological samples of baleen from ca. 100 and 2,200 yr. B.P. showed average $\delta^{13}\text{C}$ values higher than any in the last five decades, implying still higher productivity in the past. The lowered carrying capacity is a likely contributor to the decline of top consumers in the region.

During the past two decades, population declines of harbor seals (*Phoca vitulina*), fur seals (*Callorhinus ursinus*), and Steller sea lions (*Eumetopias jubatus*) have occurred in the Bering Sea and Western Gulf of Alaska along with decreases in some sea bird stocks (Pitcher 1990; Alaska Sea Grant 1993; Merrick et al. 1997). In spite of apparent strong correlations between the rapid rise of fisheries in the region with intense pressure on herring and gadid stocks (especially pollock), no definitive links or cause and effect relationships have been established (Lowry et al. 1989; Loughlin 1998). Concurrently, a major shift has occurred in the physical environment of the region with pronounced effects on the biota. Years prior to 1976 were typified by more extensive ice cover in the winter and colder average temperatures, whereas subsequent years were warmer and marked by shifts in the species compositions of benthic fishes and invertebrates (Niebauer 1988; Ebbesmeyer et al. 1991; Anderson et al. 1997). Recent syntheses of historical nutrient and weather data indicate that mixed layer depths and nitrate supply to the euphotic zone in the North Pacific Ocean have decreased (Freeland et al. 1997). Models such as the one proposed by Polovina et al. (1995) have been proposed to incorporate the

meteorological causes of the climatic shift and project the biological responses, but no robust tests of these models have been undertaken.

There are no easy means of measuring the carrying capacity of marine ecosystems. Improved assessments of relative chlorophyll concentrations by remote sensing have been used for seasonal and longer term estimates, and the routine techniques of ^{14}C uptake or other means of estimating primary productivity provide short-term measurements. From these measurements approximations of annual primary production can be derived, but the best results are still highly extrapolated numbers. Recently, however, the relationships between carbon isotope ratios ($\delta^{13}\text{C}$) in phytoplankton and the growth characteristics in phytoplankton have been better defined in the laboratory (Laws et al. 1995; Popp et al. 1998) and in the marine environment (Bidigare et al. 1997). A roughly linear relationship exists between algal $\delta^{13}\text{C}$ and algal cell-growth rates in vitro and in various ocean locations. This correlation encouraged a retrospective analysis in the Bering Sea where a long-term proxy record was available in whale baleen.

Bowhead whales (*Balaena mysticetus*) provide a nearly ideal source of long-term isotope ratio records from the western arctic and subarctic marine environments. The western arctic population overwinters in the northern Bering Sea and then moves northward in the spring, entering the Beaufort Sea for the summer months (Schell and Saupe 1993). In early fall, the return migration is westward along the coast of the Beaufort Sea and into the Chukchi Sea. Northward flow through the Bering Strait of a “displaced pelagic ecosystem” (Springer et al. 1989) transports large amounts of zooplankton prey (primarily euphausiids and large calanoid copepods) upon which the whales feed heavily. As the ice cover increases, the whales continue southward through the Bering Strait to overwinter in the Bering Sea. The whales feed most heavily in the fall and early winter months on zooplankton stocks composed of the integrated primary productivity from the previous summer season. Each adult whale consumes on the order of 100 metric tons of zooplankton prey (Thomson 1987), which in turn represents a much larger (~10 times) biomass of phytoplankton. The isotope ratios of the assimilated food are incorporated in the keratin being deposited in the growing baleen plate.

The availability of a large number of baleen plates derived from Alaskan Inupiat whaling over the past 35 yr offered a means of obtaining a continuous record of relative changes in carbon isotope ratios in Bering/Chukchi sea zooplankton from the late 1940s to present. A large plate may contain isotope ratio cycles derived from feeding along the migra-

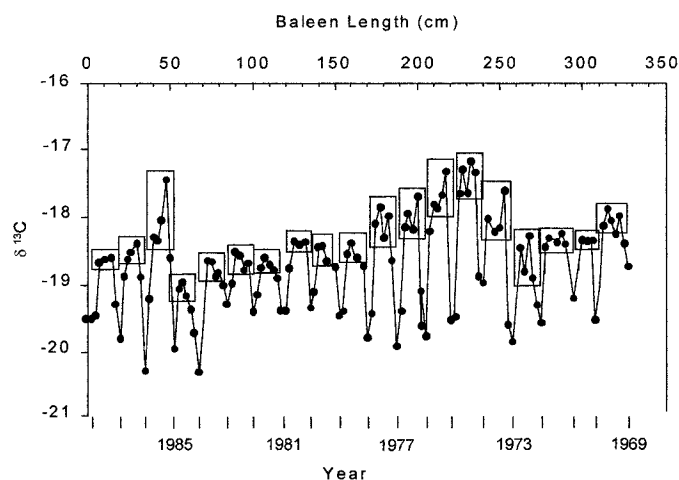


Fig. 1 Carbon isotope ratios along a baleen plate from *B. mysticetus* 88B10, killed at Barrow, Alaska in fall 1988. Each oscillation is an annual cycle and boxes enclose $\delta^{13}\text{C}$ values from feeding in the Bering and Chukchi seas.

tory route that span >20 yr (Schell et al. 1989). Baleen plates grow at rates of 16 to 25 cm yr^{-1} in subadult and adult whales with the faster rates occurring in younger whales. Thus whales taken in the 1960s showed isotope records extending back to the 1950s and 1940s, and more recent takes allowed continuing the record to near present.

Sampling—Baleen plates from bowhead whales ($n = 31$) were obtained from the Alaskan native subsistence hunts during the period 1986–1998. The North Slope Borough Department of Wildlife Management provided one of the longest baleen plates from the baleen rack of adult and large subadult whales taken in the subsistence hunt at Barrow, Alaska. Plates collected in the 1960s and early 1970s ($n = 6$) were sampled at the Los Angeles County Museum. The latter plates enabled extending the record back to 1947.

Isotope ratio analysis—Baleen plates were scrubbed with steel wool and sampled at 2- or 2.5-cm intervals along the length using an engraving tool. Powdered baleen samples were analyzed either via manual isolation of carbon dioxide and nitrogen from the sealed tube combustion of samples followed by discreet analysis or by using a Europa 20/20 continuous flow mass spectrometry system. Data are reported in standard del notation referenced against PDB (carbon) or air (nitrogen). Replication for the entire sampling process and mass spectrometry was about 0.2‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$.

An example of the isotope ratio trace from a bowhead whale killed in fall 1988 at Point Barrow is shown in Fig. 1. The portions of the plate with enriched $\delta^{13}\text{C}$ values were grown while the whale was feeding in the Bering and Chukchi seas and are identified by the boxes. By overlapping the records from whales killed in different years, a continuous record was constructed. The initial purpose of the isotopic analysis was for age determination of individual animals, and the sampling frequency was not directed toward maximizing analysis of specific sections of the plates. Typically each trace provided 3–5 Bering/Chukchi $\delta^{13}\text{C}$ values yr^{-1}

Table 1. Average $\delta^{13}\text{C}$ values and standard deviations for baleen grown while feeding in the Bering and Chukchi Seas by year. Each baleen plate spans several years and was sampled at 3–5 points for each year. Standard deviations are for all points in a given year.

Year	$\delta^{13}\text{C}$ (‰)	Standard deviation	Number of whales
1947	-18.07		1
1948	-17.61		1
1949	-17.34		1
1950	-17.61		1
1951	-17.68	0.02	2
1952	-17.70	0.34	2
1953	-17.92	0.45	2
1954	-17.27	0.17	3
1955	-17.68	0.51	4
1956	-17.63	0.42	4
1957	-17.92	0.73	4
1958	-17.63	0.83	4
1959	-17.66	0.52	4
1960	-17.68	0.65	4
1961	-17.65	0.68	4
1962	-17.70	0.43	4
1963	-17.52	0.31	4
1964	-17.46	0.43	4
1965	-17.19	0.31	3
1966	-16.54	1.04	2
1967	-16.85	0.18	4
1968	-16.69	0.38	5
1969	-17.05	0.56	5
1970	-17.66	0.39	8
1971	-17.77	0.80	10
1972	-17.99	0.40	12
1973	-17.71	0.60	13
1974	-17.50	0.43	14
1975	-17.16	0.24	14
1976	-17.18	0.43	14
1977	-17.57	0.32	14
1978	-17.46	0.54	14
1979	-17.72	0.51	14
1980	-17.84	0.44	14
1981	-17.91	0.48	14
1982	-18.23	0.43	14
1983	-18.23	0.42	14
1984	-18.39	0.41	14
1985	-18.79	0.37	14
1986	-17.78	0.29	15
1987	-18.47	0.29	13
1988	-18.27	0.27	9
1989	-18.55	0.36	4
1990	-18.02	0.31	6
1991	-17.94	0.34	4
1992	-18.03	0.26	4
1993	-18.08	0.22	4
1994	-19.07	0.56	4
1995	-18.79	0.54	13
1996	-19.11	0.49	9
1997	-19.27	0.22	3

depending upon baleen growth rate and sampling frequency for the individual whale. For years prior to 1966, data were averaged from 2–4 whales yr^{-1} with only one animal extending back prior to 1950. Table 1 lists the number of

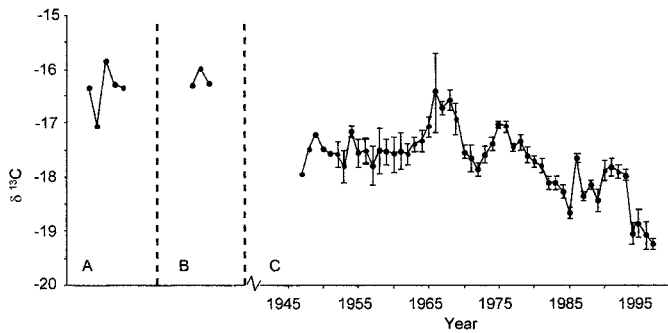


Fig. 2 Average annual Bering/Chukchi carbon isotope ratios in baleen from (A) partial baleen plate from Penuk Island, (2200 yr B.P.); (B) partial plate from St. Lawrence Island (ca. 1870 A.D.) and (C) from 37 whales taken over the past four decades (from Table 1).

whales sampled for each year, average $\delta^{13}\text{C}$ values, and standard deviations. The plotted data are shown in Fig. 2.

An older comparison was obtained from two pieces of baleen recovered from archaeological sites in the Bering Sea. One strip of 120 cm, part of a sled runner, was recovered from a Yupik house site on St. Lawrence Island, abandoned in 1871 (Geist and Rainey 1936). Another coiled piece of baleen, 75 cm in length, came from a house site on Penuk Island in association with artifacts radiocarbon dated at 2,200 yr B.P. (Rainey 1941). Both pieces of baleen were well preserved and showed minimal signs of decomposition. These baleen samples yielded isotope ratio records of 6 and 3 yr, respectively, with average $\delta^{13}\text{C}$ values of -16.45 and -15.69 ‰ (Fig. 2).

Considering the extensive regions in the Bering and Chukchi seas in which the bowhead whales can feed, the consistency in isotope ratios between whales for a given year is remarkable. The premise that the isotopic record is environmental in origin and not due to physiological responses in the whale is supported by the close agreement in isotope ratios between multiple whales, adult and subadult, for a given year. The zooplankton prey of the Beaufort Sea north of Canada where the whales spend the summer have much lower $\delta^{13}\text{C}$ values (Saupe et al. 1989; Schell et al. 1998) and constitute the remainder of the record. Adult whales derive only a minor fraction of their food from the Eastern Beaufort Sea based upon muscle tissue isotope ratios (Schell and Saupe 1993), and there is little correlation between the isotope records for that region between whales. Thus the isotopic data from several whales represent the secondary production derived from a wide area and a large fraction of the Bering/Chukchi Sea euphotic zone. Keratin $\delta^{13}\text{C}$ in baleen is typically ~ 1.1 ‰ higher than whale muscle tissue and 1.5 ‰ higher than the diet (Schell et al. 1989).

The decrease in $\delta^{13}\text{C}$ of approximately 2.7 ‰ in the average $\delta^{13}\text{C}$ that occurred between 1966 and 1997 can be compared with the data of Laws et al. (1995) and Bidigare et al. (1997) to estimate the magnitude of average phytoplankton growth rate changes that have occurred over the 31 yr since 1966. The major assumptions are that phytoplankton species compositions have remained similar over the years and that the $\delta^{13}\text{C}$ and seasonal concentrations of dissolved free CO_2 in the euphotic zone have remained relatively con-

stant. If these assumptions are correct, the data imply that the ecosystem has undergone a decrease of between 30–40% in average seasonal primary productivity. The limited additional data from the archaeological samples implies that productivity may have been higher in the past than at any time in recent decades. The annual $\delta^{13}\text{C}$ values from 7 of the 8 yr represented exceed the maximum values in the 50-yr continuous record except for 1966, which was nearly as high.

The causes for the decline in carbon isotope ratios could arise from several sources singly or in combination. Nutrient concentrations on the shelf are dependent upon winter re-supply to surface waters via deep mixing followed by on-shelf advection in summer months (Overland et al. 1996). Net flow northward is determined by wind-forcing and sea surface differentials between the Bering Sea and the Arctic Ocean. Maximum primary productivity is believed to occur near the shelf break as this nutrient-rich water is mixed with water containing trace elements derived from Alaskan rivers and stabilized by stratification (Springer et al. 1996). Over the past 40 yr, however, the estimated transport through the Bering Strait has decreased from 0.85 to $0.6 \times 10^6 \text{ m}^3 \text{ sec}^{-1}$ (Roach et al. 1995; T. Weingartner pers. comm.). If the net on-shelf advection is directly linked to flow through the Bering Strait, this decline may account for much of the decrease in productivity.

The $\delta^{15}\text{N}$ data are incomplete for the last decade, but for 1966–1986 they do not show the large interannual variations apparent in the $\delta^{13}\text{C}$ record. A slight declining trend in $\delta^{15}\text{N}$ of the baleen is evident of approximately 0.7 ‰, which indicates that no major shift in trophic status in the whales occurred over the two decades represented. A more extensive synthesis of the data will be undertaken when analyses are complete.

The alternative hypothesis of a top-down change driven by fishing pressure would posit a large increase in small fishes arising from removal of the large predatory adults (primarily gadids) from the system. The small fishes would then crop zooplankton to the point that phytoplankton stocks significantly increase. A larger standing stock of phytoplankton with a constant nutrient supply would yield slower growth rates in individual cells but similar net primary productivity overall. Comparing estimates of zooplankton and phytoplankton (chlorophyll) standing stocks over the same period tested this hypothesis. Sugimoto and Tadokoro (1997) present the only long-term estimates of these variables from the central and western subarctic Pacific Ocean and Eastern Bering Sea. They estimated chlorophyll concentrations based on Secchi disk depths and zooplankton stocks from net tow volumes and related these observed changes to other physical and biological conditions. In contrast to the above hypothesis, the Pacific regions show a decline in chlorophyll between 1965 to 1994 and no significant trend in the Eastern Bering Sea over the same interval. Zooplankton data are less comprehensive but show a general decline in standing stocks in the Eastern Bering Sea over the same period, similar to the trend in baleen $\delta^{13}\text{C}$, implying decreased secondary productivity as well (Sugimoto and Tadokoro 1997).

Other potential causes of the decrease in average $\delta^{13}\text{C}$ values include a progressive shift in bowhead feeding habitat to regions of lower average $\delta^{13}\text{C}$ values in prey or a large decrease in phytoplankton cell sizes. Neither of these latter

scenarios is plausible. Large blooms of coccolithophores on the Southeastern Bering shelf have been apparent in the past 3 yr, but the decrease in isotope ratios began over 30 yr ago. Bowhead whales do not frequent the Eastern Bering Sea and tend to overwinter in the central and western regions within the edge of the winter sea ice (Braham 1984).

The large food requirements of whales and close agreement between the isotope ratios of different individual whales in context with estimates of phytoplankton standing stocks argue that the isotope ratios accurately record the variability in seasonal primary production. The marked declines in the numbers of top consumers in the Bering Sea imply that the magnitude of seasonal primary production and its coupling to consumers have significantly decreased.

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