The Bowhead Whale, *Balaena mysticetus*: Its Historic and Current Status

KIM E.W. SHELDEN and DAVID J. RUGH

Introduction

Bowhead whales, *Balaena mysticetus* (Fig. 1), are currently listed as endangered under the Endangered Species Act of 1973 (ESA) and depleted under the Marine Mammal Protection Act of 1972 (MMPA). The ESA, as amended in 1978, requires the status of populations listed as "endangered" or "threatened" to be reviewed every 5 years. For bowhead whales, an evaluation is to be made as to whether the status of these whales should be revised (i.e., changed to threatened) or whether specific stocks should be removed from the list of Endangered and Threatened Wildlife (50 C.F.R. § 17.11). This paper is an update of literature that has become available since the publication of Braham (1984) and a review of elements that may contribute to the evaluation of the status of stocks of bowhead whales.

Kim E.W. Shelden and David J. Rugh are with the National Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sand Point Way N.E., Bin C15700, Seattle, WA 98115-0070.

ABSTRACT—The bowhead whale, Balaena mysticetus, *is currently listed as endangered under the Endangered Species Act of 1973 and as depleted under the Marine Mammal Protection Act of 1972. Literature on the species is updated since 1984, and elements are reviewed that may contribute to the evaluation of the status of bowhead whale stocks.*

Background

Under the ESA, "endangered" status is designated to those species facing extinction "throughout all or a significant portion of [their] range. . . " (16 U.S.C. § 1532(6)). "Threatened" status is provided to ". . . any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (16 U.S.C. § 1532(20)). The definition of species within the ESA is not based on the taxonomic categories used in the field of biology. Instead the term refers to ". . . any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife that interbreeds when mature" (16 U.S.C. § 1532(16)). Subspecies and distinct population segments are not defined within the statute. In 1992, the U.S. Fish and Wildlife Service (USFWS) issued a draft policy providing a definition for "distinct population segments," reviewed by Rohlf (1994). This policy was revised and published in the Federal Register (vol. 59, p. 65885) in 1994, and the final policy was published in 1996 (Fed. Regist., vol. 61, p. 4722). Within this policy, three elements will be considered in the status designation of population segments: 1) discreteness, 2) significance, and 3) conservation status.

Historically, the distribution of these whales was almost circumpolar in the northern hemisphere (Fig. 2); however, heavy exploitation by commercial whalers seriously depleted them throughout their range. For management purposes, five stocks (geographically distinct segments of the population) are currently recognized (IWC, 1992:27). Three of these stocks are found in the North At-

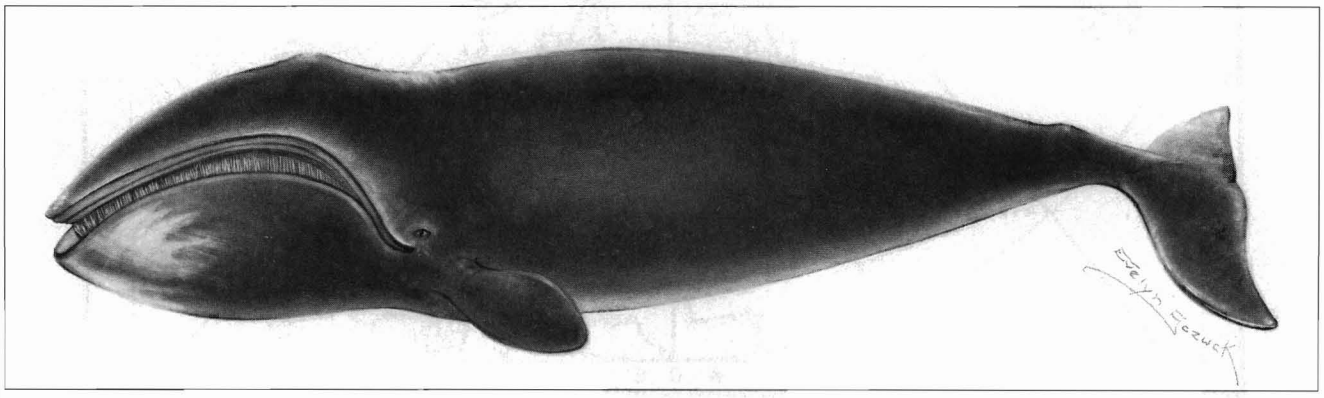


Figure 1. — The bowhead whale, *Balaena mysticetus.*

lantic and two in the North Pacific, some or all of which may be reproductively isolated.

Distribution and Abundance

Spitsbergen Stock

Commonly referred to as the Greenland whale, bowhead whales in the eastern North Atlantic have been observed in the waters north of Iceland and as far east as the Laptev Sea. Between 1940 and September 1990, 37 bowhead whale sightings have been recorded in this region, but some of these sightings were not unequivocally bowhead whales (Moore and Reeves, 1993:Table 9.2). Reviewing records from west to east, sightings were scattered along the coastline of Greenland, in the waters near Spitsbergen Island, off North Cape in northern Norway, in the waters of Zemlya Frantsa-losifa (Franz Josef Land), near Novaya Zemlya, and near Severnaya Zemlya (Fig. 3).

The majority of observations occurred between April and September. Overall, group sizes were small, ranging from 1 to 15 individuals, with the exception of two groups observed in August in Zemlya Frantsa-losifa, "sev-

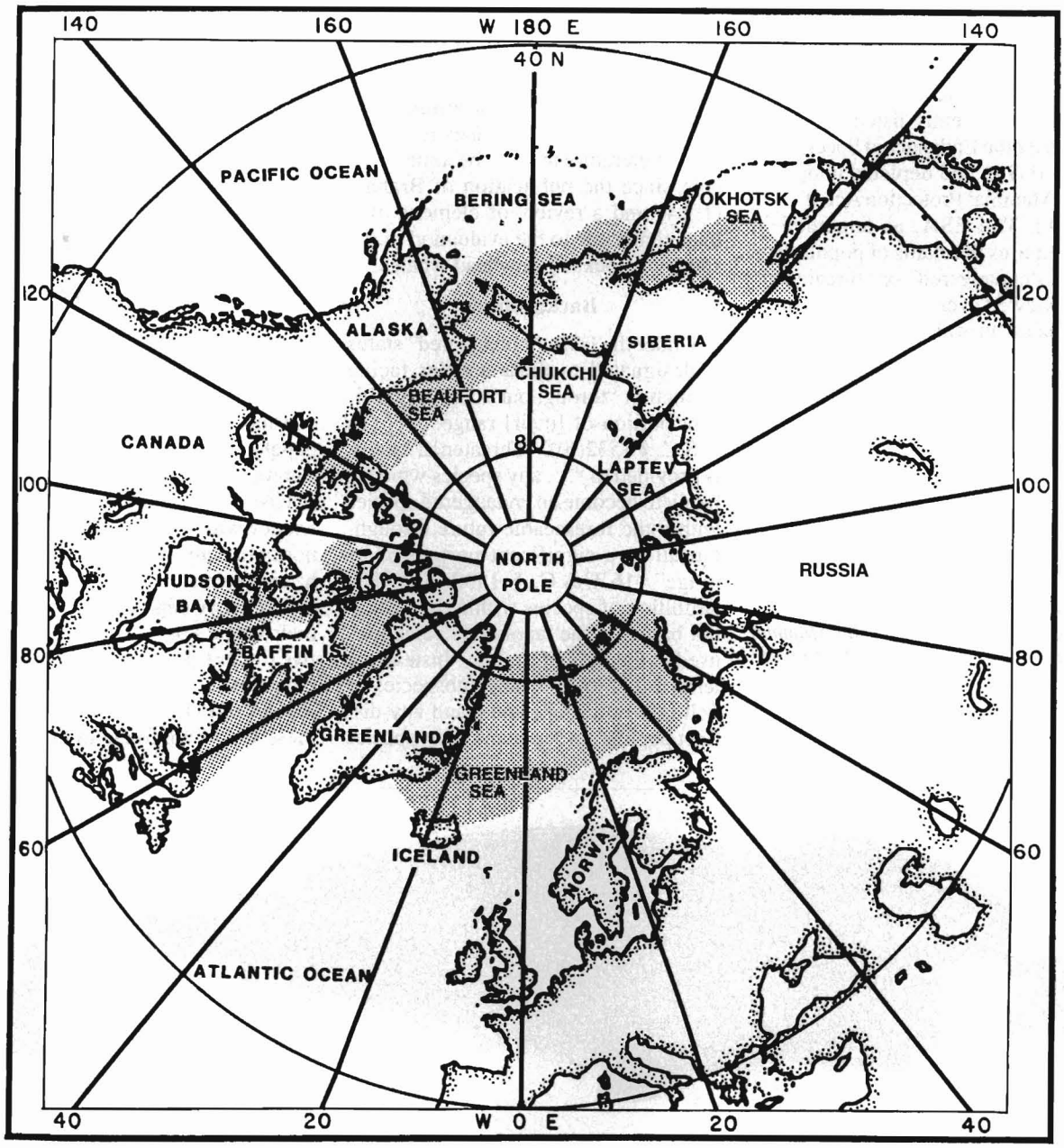


Figure 2. — Circumpolar distribution of bowhead whales (adapted from Reeves and Leatherwood, 1985).

eral tens of whales" in 1981, and "about 66 individuals" in 1983 (Belikov et al., 1989:255). In 1989, Clark et al.[1] identified at least four bowhead whales from acoustic recordings collected off Spitsbergen. Additional sightings of lone animals were reported in each year during 1990–93 in Zemlya Frantsa-losifa (de Korte and Belikov, 1994). Despite extensive research cruises conducted in the Barents Sea (McQuaid, 1986), Icelandic waters (Sigurjónsson, 1985; Sigurjónsson et al., 1988; Sigurjónsson et al.[2]), Norwegian and adjacent waters (Christensen et al.[3]), and continued Danish and Norwegian whaling activity, very few bowhead whales have been seen. It may be that some of the Spitsbergen stock overwinter within the pack ice (Moore and Reeves, 1993), in regions inaccessible to unreinforced vessels. Bowhead whales observed from aircraft were often found in polynyas or leads within solid ice (Belikov et al., 1989).

Movement patterns of bowhead whales within the eastern North Atlantic are not well known. Whalers described the migration of animals hunted between Greenland and Spitsbergen Island as following a counterclockwise circuit (Southwell, 1898, as summarized in Ross, 1993). The whales would winter in the water near Iceland and Jan Mayan, then move northeastward as the ice front retreated during March and April. From May to June, the animals summered along the ice edge between Greenland and Spitsbergen before moving south again with the advancing pack ice. Variations in the routes taken during the southbound migration have been attributed to the existence of separate

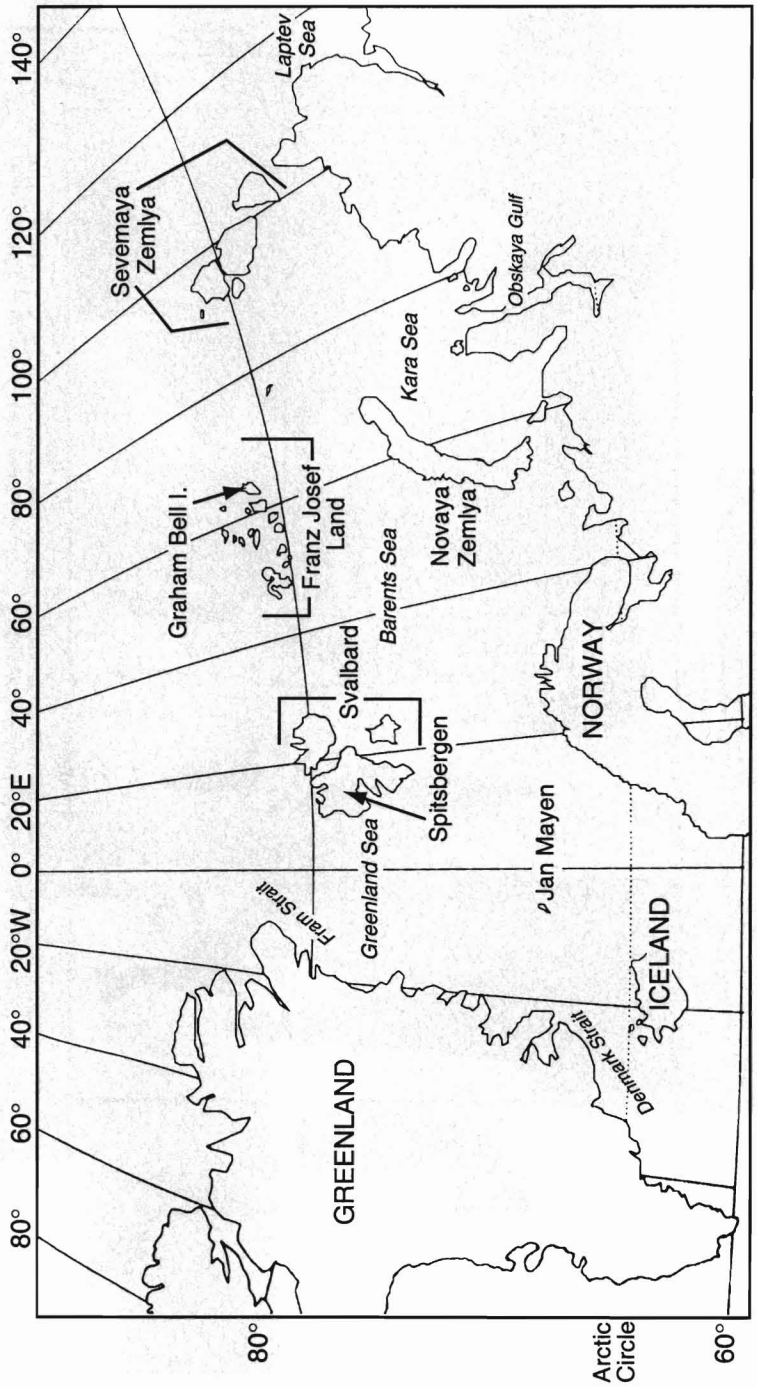


Figure 3. — Arctic seas of the northeast Atlantic with place names mentioned in the text (adapted from Moore and Reeves, 1993).

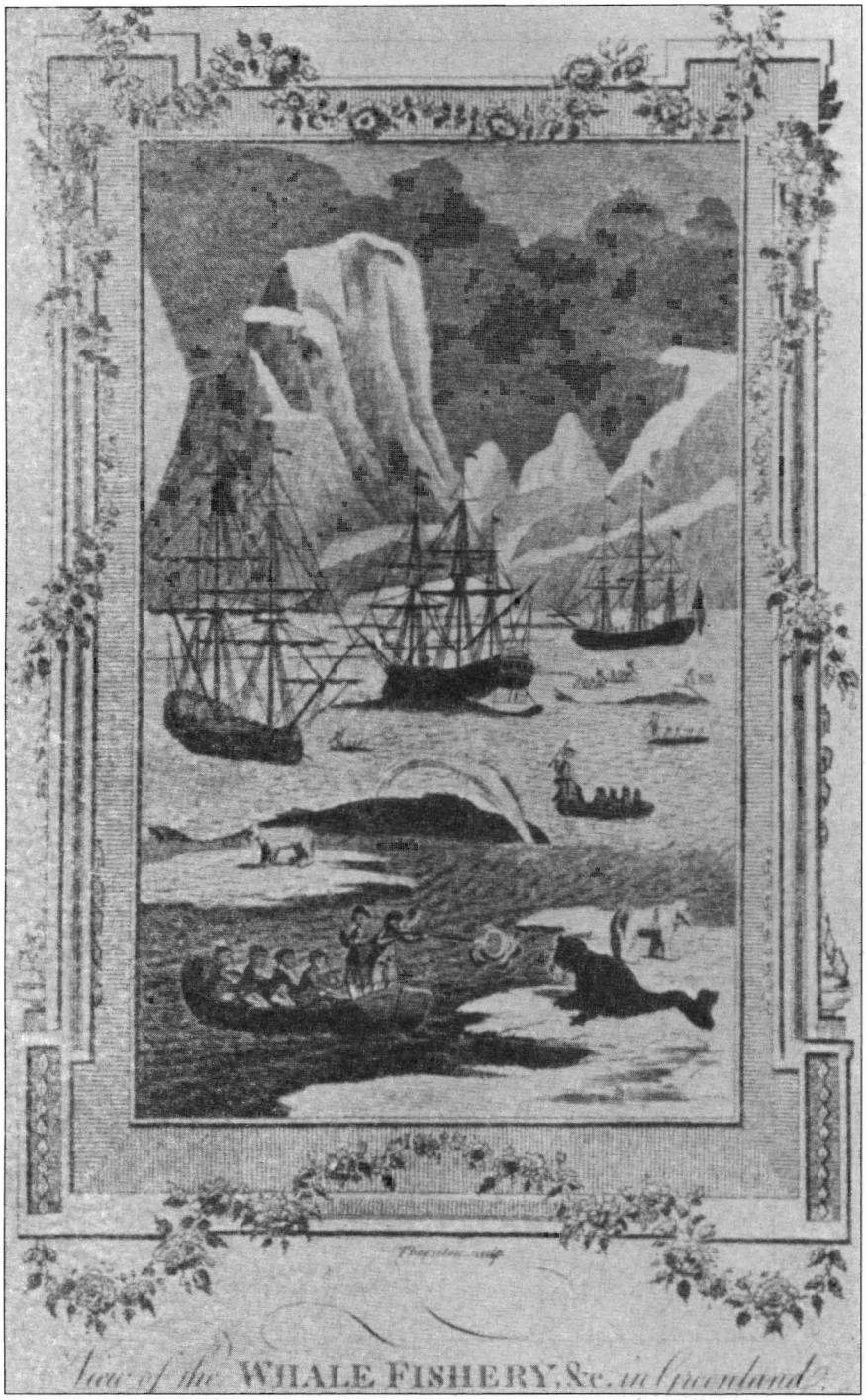
[1] Clark, C. W., L. M. Brown, K. von der Heydt, A. Baggeroer, and I. Dyer. 1991. Acoustic detections of bowhead whales from the east Greenland–Spitsbergen stock in spring 1989. Int. Whal. Comm. Unpubl. Doc. SC/43/PS19, 12 p.

[2] Sigurjónsson, J., T. Gunnlaugsson, P. Ensor, M. Newcomer, and G. Vikingsson. 1990. North Atlantic sightings survey 1989 (NASS–89): shipboard surveys in Icelandic and adjacent waters July–August 1989. Int. Whal. Comm. Unpubl. Doc. SC/42/O21, 29 p.

[3] Christensen, I., T. Haug, and N. Øien. 1990. Review of the biology, exploitation and present abundance of large baleen whales and sperm whales in Norwegian and adjacent waters. Int. Whal. Comm. Unpubl. Doc. SC/42/105, 28 p.

"tribes" (subspecies or species) of bowhead whales (Scoresby, 1820:211) or segregation of the population into age- or sex-specific groups (Southwell, 1898; de Jong, 1983).

Little is known of the migration patterns of bowhead whales found in the northern Barents Sea. Whalers described how a group of whales would arrive out of the east during heavy ice years to summer along the southern coast of Spitsbergen, then return east as the ice retreated (Zorgdrager, 1720, summarized in Eschricht and Reinhardt, 1866). These whales were said to look and behave differently from the other Spitsbergen whales. However, establishing the existence of any genetic or morphological variations between these groups would be difficult given the reduced size of the current population (Reeves, 1980).



The early whale fishery in Greenland is depicted in this 1781 engraving from Dow (1967), courtesy of and copyright by Argosy Book Store, Inc., N.Y.

There is some confusion as to whether the animals present in these waters today are representative of the historic stock. Jonsgård (1981, 1982) expressed the possibility that the Spitsbergen stock may be extinct. Past sightings may include migrants from the Davis Strait stock or the East Siberian Sea (Bering Sea stock) (Jonsgård, 1981). Whalers reported incidents in which "unsuccessfully harpooned" whales from one stock (Davis Strait or Spitsbergen) were later killed or found dead in the waters inhabited by the other stock (Eschricht and Reinhardt, 1866; Reeves et al., 1983). In times when these whales were more plentiful, such overlap in ranges may have occurred; however, it is more likely that the present population in the eastern North Atlantic is a remnant of the severely depleted Spitsbergen stock (Reeves and Leatherwood, 1985; McQuaid, 1986; Moore and Reeves, 1993).

Possibly numbering only "in the tens" now (Christensen et al.[3]), this group of animals is thought to originally have been the most populous of the bowhead whale stocks (Braham, 1984; Woodby and Botkin, 1993). The majority of islands within this region were uninhabited, and it is likely that this stock rarely experienced human predation prior to commercial whaling (Ross, 1993). From 1660 to 1912, about 90,000 bowhead whales were harvested by commercial whalers, a total that does not include mortally wounded whales that escaped, whales captured but cast adrift, or cargos of vessels that were lost or captured at sea (Ross, 1993). Woodby and Botkin (1993) reevaluated the historical harvest data and developed a minimum preexploitation estimate of about 24,000 whales (an earlier estimate

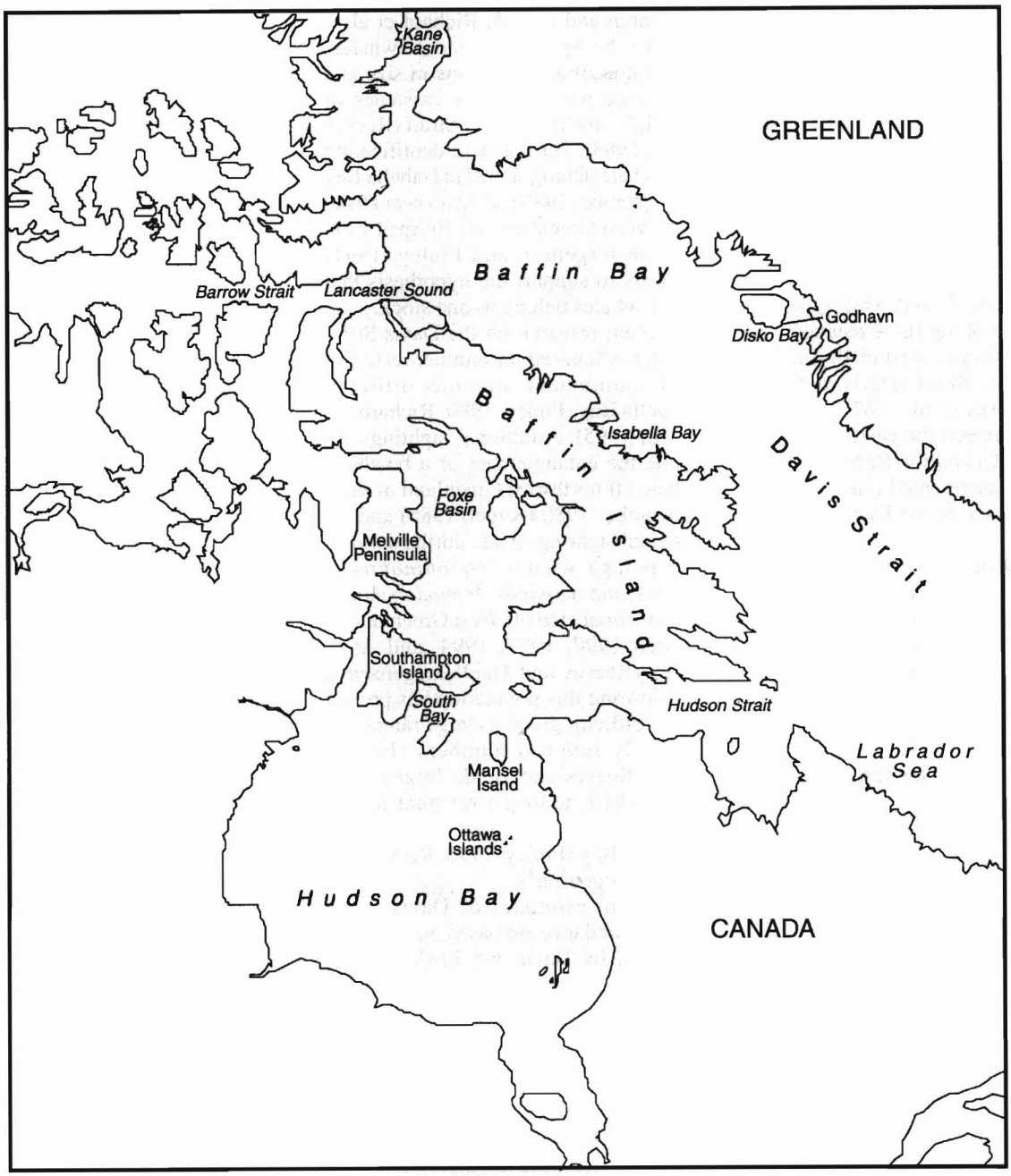


Figure 4. — Northeast Canada and Greenland with place names mentioned in the text (adapted from Moore and Reeves, 1993).

by Mitchell[4] came to 25,000). A maximum estimate was not computed because catch and voyage data (covering over 200 years of whaling) have not been fully compiled and analyzed (Ross, 1993; Woodby and Bodkin, 1993).

Davis Strait Stock

Bowhead whales in the western North Atlantic are currently segregated into two stocks, one occupying Davis Strait, Baffin Bay, and along the Canadian Arctic Archipelago (Davis Strait stock) and the other found in Hudson Strait, Hudson Bay, and Foxe Basin (Hudson Bay stock) (as defined in Moore and Reeves, 1993; Fig. 4). This distinction is uncertain given that it is not based on genetic or morphological evidence; instead the two are separated based on their summer feeding distri-

[4] Mitchell, E. D. 1977. Initial population size of bowhead whale (*Balaena mysticetus*) stocks: cumulative catch estimates. Int. Whal. Comm. Unpubl. Doc. SC/29/33, 113 p.

butions (Reeves et al., 1983; Reeves and Mitchell, 1990).

The Davis Strait stock is believed to follow a counterclockwise migration pattern similar to the Spitsbergen stock (Ross, 1993). Animals move northeast from the Labrador Sea across Davis Strait to the west coast of Greenland, following the pack ice as it recedes. Some cross Baffin Bay to Lancaster Sound, the summer feeding grounds north of Baffin Island, while others continue north along the Greenland coast to Kane Basin or west of Baffin Island into Barrow Strait (Davis and Koski, 1980; Reeves et al., 1983). Some exchange between the eastern North Atlantic stocks and the Bering Sea stock has been documented (based on whaling irons used in the Davis Strait fishery that were found in whales taken in the Chukchi Sea) (Bockstoce and Burns, 1993). Segregation by size and sex appears to occur at this time: cows with calves and subadults are found around the inlets and islands north and west of Baffin Island while other adults occupy the waters along the northeast coastline (Reeves et al., 1983; Reeves and Mitchell[5]). The summer resident population of Isabella Bay (east-central Baffin Island) has consisted predominantly of adults and large subadults (Finley, 1990; Richardson et al., 1995). Early whalers believed this segregation continued through the southbound migration (Southwell, 1898). Cows, calves, and young whales followed the east coastline of Baffin Island back to the Labrador Sea, while large adults ("old males") moved south along the western coast (Southwell, 1898, summarized in Ross, 1993). This may be true in part as calves and small juveniles (<10m in length) are rarely observed in Isabella Bay (Finley, 1990). Some whales may migrate south along the west coast of Greenland (Kapel, 1985) while others may overwinter in polynyas and flaw zones within the pack ice (Reeves et al., 1983; Turl, 1987; McLaren and Davis[6]; Richard et al.[7]). Unlike the Spitsbergen stock, whalers did not attribute variations in size and migration patterns to the existence of multiple stocks in Davis Strait (Reeves et al., 1983). The recent reidentification of a whale photographed in Isabella Bay in September 1986 and again near Disko Bay, West Greenland, on 10 April 1990 (Heide-Jørgensen and Finley, 1991) appears to support the hypothesis that these whales belong to one stock.

Recent research on the Davis Strait stock has focused on summer residents and southbound migrants utilizing Isabella Bay (Finley, 1990; Richardson et al., 1995). Additional sightings include the entanglement of a bowhead whale off northwest Greenland in early November 1980 (Kapel, 1985) and incidental sightings made during surveys for beluga whales, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, conducted off West Greenland in March 1990, 1993, 1994, and April 1991 (Reeves and Heide-Jørgensen[8]). Monitoring this population has proven to be difficult given its large range and severely reduced numbers (Finley, 1990; Reeves and Heide-Jørgensen[8]). Since 1980, no long-term studies have been made of this stock outside of Isabella Bay (Finley, 1990; Reeves and Heide-Jørgensen[8]).

Current estimates of Davis Strait stock abundance are based on sightings gathered by Davis and Koski (1980), Finley (1990), and Koski and Davis[9]. From counts obtained during the fall migration in 1978, Davis and Koski (1980) concluded that the population was "in the low hundreds at most." In 1979, an estimated 140 ± 33 bowhead whales were observed migrating through the 1978 study area, separate from another group observed summering in Isabella Bay (Koski and Davis[9]). Using the numbers gathered from aerial photo-identification surveys, Finley (1990) estimated "as many as" 107 individual bowhead whales were in the vicinity of Isabella Bay in late September 1986. To this number Finley added the Koski and Davis[9] estimate from 1979 to obtain a "conservative" estimate of 250 animals for the entire stock. Zeh et al. (1993) reanalyzed the Finley (1990) data using a mark-recapture method sampling only the best quality photo images from 1986 (77 photographs) and 1987 (21 photographs). They obtained an estimate of 214 ± 54 bowhead whales in Isabella Bay, to which they added the 1979 Koski and Davis[9] estimate, yielding a total abundance of about 350 bowhead whales in the Davis Strait stock. Because only well marked animals were used in the analysis, this estimate is considered to be "conservative" (Zeh et al., 1993). Given the low proportion of calves (2.2–3.6%) observed during these surveys, recovery from past whaling "has been, at best, exceedingly slow" (Davis and Koski, 1980), and viability of the population may be at risk (Finley, 1990). The Davis Strait stock has had no appreciable evidence of recovery since the period of commercial whaling, over 80 years ago (Reeves et al., 1983).

Almost 29,000 bowhead whales were harvested in Davis Strait between 1719 and the end of commercial whaling in 1915 (Ross, 1993) from an estimated original stock of over 11,700 (Woodby and Botkin, 1993). Between 1922 and 1975, only seven whales were taken or struck and lost by Canadian Eskimos (Mitchell and Reeves, 1982; Reeves and Heide-Jørgensen[8]), and after 1979, the Canadian government "explicitly banned the hunting of bowheads without a license" under the Federal Cetacean Protection Regulations (Reeves and Mitchell, 1990). Though bowhead whales

[5] Reeves, R. R., and E. Mitchell. 1991. Summer segregation in the Davis Strait bowhead whale stock. Int. Whal. Comm. Unpubl. Doc. SC/43/PS28, 1 p.

[6] McLaren, P. L., and R. A. Davis. 1983. Distribution of wintering marine mammals off West Greenland and in southern Baffin Bay and northern Davis Strait, March 1982. Rep. for Arctic Pilot Proj., Calgary, Alberta, by LGL Ltd., 98 p.

[7] Richard, P., J. Orr, R. Dietz, and L. Dueck. 1993. Preliminary report on an aerial survey of belugas in the North Water, 21–26 March 1993. Work. pap. pres. to Joint Commiss. Conserv. Manage. Narwhals and Belugas. Sci. Work. Group, Copenhagen, 21–23 June.

[8] Reeves, R. R., and M. P. Heide-Jørgensen. 1994. Recent observations of bowhead whales off West Greenland. Int. Whal. Comm. Unpubl. Doc. SC/46/NA11, 9 p.

[9] Koski, W. R., and R. A. Davis. 1980. Studies of the late summer distribution and fall migration of marine mammals in NW Baffin Bay and E Lancaster Sound, 1979. Rep. from LGL Ltd. to Petro-Can. Explor. Inc., 214 p. Avail. from Pallister Resour. Manage. Ltd., Suite 105, 4116–64th Ave. S.E., Calgary, Alberta, Can. T2C 3B3.

are currently designated as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Campbell, 1990), a request to harvest one whale per year by the Inuit of the eastern Northwest Territories has been made under the Nunavut Final Land Claim Agreement (Indian and Northern Affairs Canada 1993, summarized in Reeves and Heide-Jørgensen[8]). In Autumn 1994, a bowhead whale was illegally harvested from the Davis Strait stock by a Canadian native (Marine Mammal Commission[10]).

Hudson Bay Stock

As mentioned in the preceding Davis Strait Stock section, there is currently no evidence to suggest that the Hudson Bay stock is discrete from it. However, separating these two populations based on their summer distributions allows for a conservative approach to managing each one (Reeves and Mitchell, 1990). From the middle of May until September, bowhead whales of the Hudson Bay stock are commonly observed near Southampton Island in northwestern Hudson Bay and along the northern tip of the Melville Peninsula in Foxe Basin (Moore and Reeves, 1993; Fig. 4). Scattered sightings also have occurred along the western coastline of Hudson Bay and near the Ottawa Islands and Mansel Island of eastern Hudson Bay (Reeves and Mitchell, 1990). Bowhead whales observed in Hudson Strait, which connects the Bay to the Labrador Sea, are believed to be migrants leaving the Hudson Bay area in the autumn or returning in the spring (Finley et al., 1982; Reeves and Mitchell, 1990). A portion of the population overwinters in the upper Bay in leads and polynyas formed near islands (Low, 1906; Ross, 1975; Reeves and Mitchell, 1987).

Sightings usually have been of small groups of bowhead whales, rarely exceeding two individuals (Reeves et al., 1983, Reeves and Mitchell, 1990). Fifteen whales (in groups of 1, 2, 3, 4, and 5) were observed in upper Foxe Basin on 20 August 1983 (Orr et al., 1986), and in July 1981, twelve whales were seen in South Bay, Southampton Island (Reeves and Mitchell, 1990). Approximately 23 different bowheads were identified by McLaren and Davis[11] during aerial surveys conducted over Hudson Strait in winter. No single survey has adequately covered the range of this stock, and therefore it is not possible to extrapolate these counts into a population estimate. A conservative estimate by Mitchell[4] placed the current population at 100 or less. Recent observations indicate that "at least a few tens of whales" from this stock continue to occupy a large portion of their former range (Reeves and Mitchell, 1990).

Prior to commercial whaling, this population consisted of about 580 whales (Mitchell[4] as modified by Woodby and Botkin, 1993). From 1860 to 1915, 565 whales were harvested by commercial whalers (Ross, 1993). Between 1919 and 1976, 28 bowhead whales were killed or struck and lost by native hunters in western Atlantic waters (Reeves et al., 1983; Reeves and Mitchell, 1990). Of these, 23 were from the Hudson Bay stock. Since 1980, other incidents of bowheads being fired upon have been reported (as cited in Reeves and Mitchell, 1990). There has been no appreciable recovery of this stock, in part attributed to occasional hunting by natives (Reeves and Heide-Jørgensen[8]) and predation by killer whales (see section on Natural Mortality) (Reeves et al., 1983; Reeves and Mitchell, 1990).

Okhotsk Sea Stock

There has been some difficulty in assessing the historical distribution and abundance of bowhead whales in the Okhotsk Sea. Right whales, *Eubalaena glacialis*, and gray whales, *Eschrichtius robustus*, were sometimes misidentified as bowhead whales, and whaling records maintained during the short period of time this stock was hunted were incomplete (Bockstoce and Botkin, 1983). Whales in this stock were discovered by commercial whalers in 1848 (Bockstoce, 1986), but intensive hunting did not begin until 1852 when whales in the Bering Sea stock were no longer as plentiful in "traditional" whaling areas (Bockstoce and Burns, 1993). By 1860, the Okhotsk Sea stock was severely depleted, and whalers had already resumed whaling in the Bering Sea (Bockstoce, 1986). Mitchell[4] estimated the preexploitation size of the population to be 6,500 based on a total estimated catch of 3,506 whales. Ross (1993) suggested that this estimate may be too high for the reasons stated above and offered "a conservative, though mostly speculative, compromise" of 3,000 as a minimum population estimate.

Though Scammon (1874) stated that bowheads were hunted "throughout the whole extent" of the Okhotsk Sea, certain areas were occupied by concentrations of animals during the summer months (Fig. 5). In the northeastern Okhotsk Sea, whales were found in Penzhinskaya Gulf and Gizhiginskaya Gulf. The next area of concentration was to the southwest in Tauyskaya Bay. Farther south, the best whaling grounds were within the gulfs and bays south of the Shantarskiye Islands and west of Sakhalin Island; Moore and Reeves (1993) provide additional details. Almost all of the areas where summer concentrations of bowhead whales occurred in the past are still occupied today (Table 1). As recent as August 1995, during joint Russian–American surveys, a few dozen bowhead whales were observed in a feeding aggregation south of the Shantarskiye Islands (Brownell[12]). Berzin et al. (1990) estimated the population in this area to be at least 250–300 animals. An estimate of abundance of 300–400 was made for the entire Okhotsk Sea based on data collected since 1979 (Vladimirov, 1994:Table 1). However, "no quantitative data are available to confirm" these estimates

[10] Marine Mammal Commission. 1995. Annual report to Congress, 1994. Mar. Mamm. Comm., 1825 Conn. Ave. N.W., Wash., D.C. 20009, 270 p.

[11] McLaren, P. L., and R. A. Davis. 1982. Winter distribution of Arctic marine mammals in ice-covered waters of eastern North America. Rep. for Petro-Can. Explor. Inc., Calgary, Alberta, by LGL Ltd. Offshore Labrador Biol. Stud. (OLABS) program rep., 151 p. Avail. from Pallister Resour. Manage. Ltd., Suite 105, 4116–64th Ave. S.E., Calgary, Alberta, Can. T2C 3B3.

[12] Brownell, R. L. NMFS, Southwest Fisheries Science Center, La Jolla, CA, 92038. Personal commun.

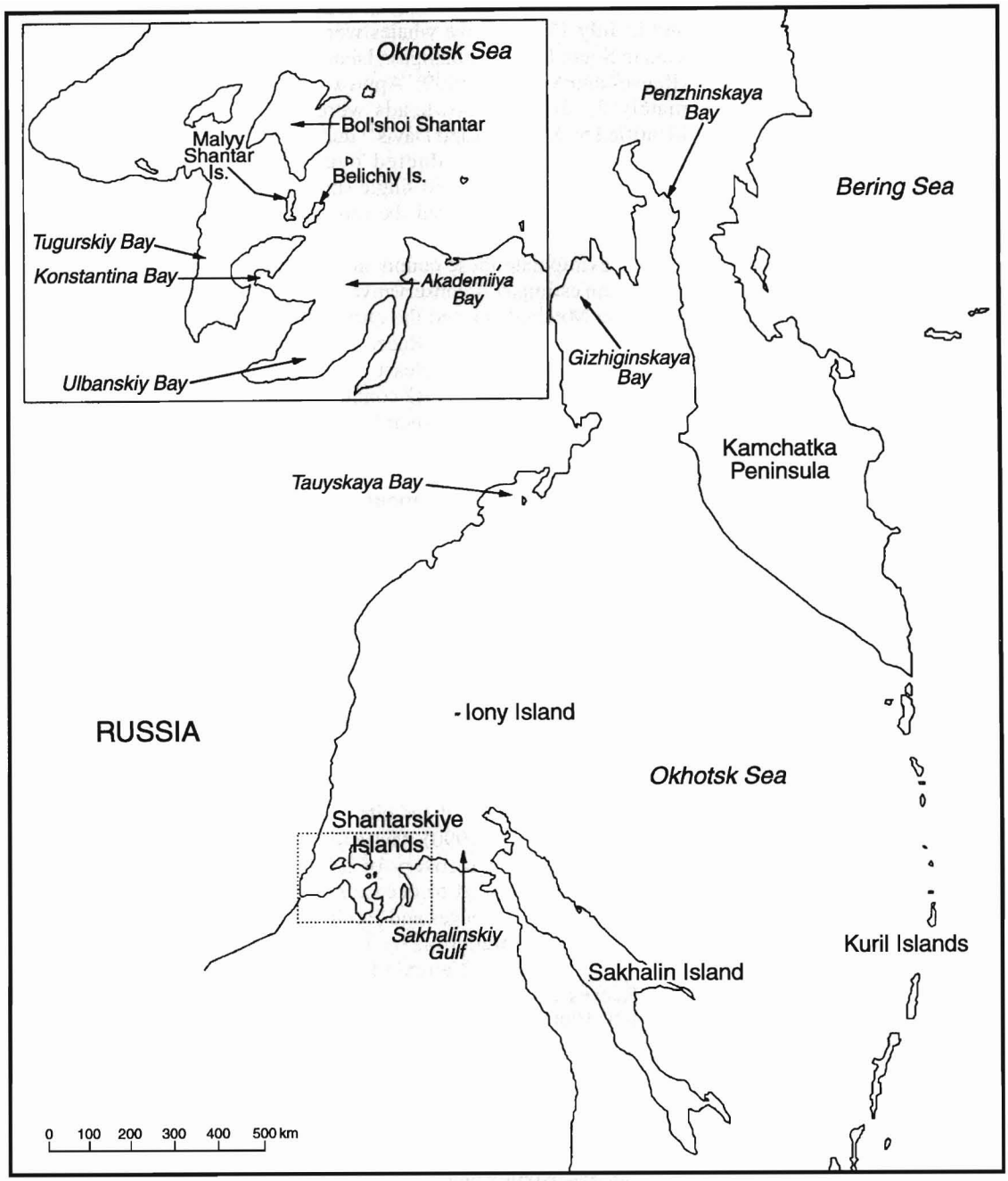


Figure 5. — Okhotsk Sea and environs with place names mentioned in the text (adapted from Moore and Reeves, 1993).

(Berzin et al.[13]). There is some speculation as to whether animals found during the summer in the northeastern Okhotsk Sea form a distinct population from those in the Shantarskiye region. The winter distribution of both of these groups is unknown.

Berzin et al. (1991) noted that by mid-November, bowhead whales were no longer found in the Shantarskiye region, despite the waters being ice-free. Fedoseev (1984) observed bowhead whales deep in the ice north of Sakhalin Island in 1969, 1981, and 1983, in addition to one sighting east of Sakhalin Island in 1981 and another a little over 200 km south of Tauyskaya Bay in 1982 (Table 2). Because whalers left the Okhotsk Sea before the onset of winter storms in early November and did not

[13] Berzin, A. A., S. A. Blokhin, H. Minakuchi, R. L. Brownell, A. M. Burdin, and V. N. Burkanov. 1995. Bowhead and gray whale populations in the Okhotsk Sea. *In* Abstracts of the North Pacific Marine Science Organization (PICES): workshop on the Okhotsk Sea and adjacent areas, Vladivostok, Russia, 19–24 June 1995, p. 44–45.

Table 1.—Recent sightings of bowhead whales in historic summer concentration areas in the Okhotsk Sea. Commas separate sightings that were made at different times (days or months) during the survey year.

General location of sightings	1982[1]	1983[1]	1984[1]	1986[2,3]	1987[2,4]	1988[2]	1989[5]	1990[5]
N.E. Okhotsk Sea								
Penzhinskaya Gulf	U[6]	U	U	U	U	2	U	U
Gizhiginskaya Gulf	U	U	U	17	U	7	19, 36	U
S.W. Okhotsk Sea								
Between Bol'shoi Shantar Island and Utichiy Island	U	U	U	18	U	U	8, 14, 21, 33	U
Tugurskiy Bay	U	3	U	U	U	U	U	1
Konstantina Bay	13	2	20	U	47	72	U	44, 7+20
Ulbanskiy Bay	15	U	11	U	40	>30	72[7], 1's	
Akademiya Bay	U	39	U	U	U	U	U	

[1] Data from Berzin et al. (text footnote 39). Surveys occurred during 1–7 September 1982, 30 August–7 September 1983, and 21–23 August, 20 October 1984.
[2] Data from Berzin et al. (1990). The 1986 sighting occurred in early June (N.E. Okhotsk Sea); the 1987 sighting was in July; the 1988 sightings occurred in late May (N.E. Okhotsk Sea), on 7 August (Konstantina Bay, including 2 calves), and on 20 October (Ulbanskiy Bay).
[3] Data from IWC (1988:113). The 1986 sighting occurred in September (S.W. Okhotsk Sea).
[4] Data from Berzin et al. (1988). The 1987 sighting occurred in October (Ulbanskiy Bay).
[5] Data from Berzin et al. (1991). The 1989 sightings occurred on 23 May (19), 24 May (36 including 2 calves), May 28 (8), the morning of 31 May (14), the afternoon of 31 May (21), 1 June (33), late August (72), and 28–30 September ("singly and far apart"). The 1990 sightings occurred on 24–25 June (1), 27 August (44 around the cape separating Konstantina and Ulbanskiy Bay), and 28 August (7 near the cape, 20 spread through Ulbanskiy and Akademiya Bay).
[6] U = unknown whether the area was surveyed or not.
[7] This sighting is incorrectly attributed to the 1989 season in Berzin et al. (1991); the sighting occurred during the 1988 season only (Brownell, text footnote 12).

Table 2.—Bowhead whales observed outside of summer concentration areas in the Okhotsk Sea (from Fedoseev, 1984).

Date	Location	Lat.	Long.	Group size
8 Apr. 1969	N. of Sakhalin Island	55°10'N	144°30E	6
11 Apr. 1981	"	55°20'N	144°15E	23
		55°15'N	144°00E	2
7 May 1981	"	56°00'N	141°20E	8+7
9 May 1981	"	54°58'N	143°15E	7
21 Dec. 1983	"	57°30'N	143°00E	2
1981[1]	E. of Sakhalin Island	Not noted in text		3
29 Dec. 1982	S. of Tauyskaya Bay	56°22'N	150°00E	4

[1] Sighting was noted on Figure 1 (Fedoseev, 1984) but not described within the text.

return until June, there are no historic records on bowhead whale distribution during this whaling hiatus, leaving the possibility that there originally was a common stock between the Okhotsk and Bering Seas (Townsend, 1935). However, other authors (Bockstoce and Botkin, 1983; Lindholm[14]) have argued that the Okhotsk Sea stock has always been a population discrete from the Bering Sea stock.

Bering Sea Stock

The Bering Sea stock, also referred to as the western Arctic stock or the Bering-Chukchi-Beaufort stock, has been studied more extensively than any of the aforementioned stocks. This stock is widely distributed in the central and western Bering Sea in winter (November to April), generally associated with the marginal ice front, and found near the polynyas of St. Matthew and St. Lawrence Islands and the Gulf of Anadyr (Bogoslovskaya et al., 1982; Brueggeman, 1982; Braham et al., 1984; Ljungblad et al.[15]; Brueggeman et al.[16]; Bessonov et al.[17]; Fig. 6). From April through June, these whales migrate north and east, following leads in the sea ice in the eastern Chukchi Sea until they pass Point Barrow where they travel east toward the southeastern Beaufort Sea (Braham et al., 1980; Braham et al., 1984; Marko and Fraker[18]). Most of the summer (June through September), bowhead whales range through the Beaufort Sea (Hazard and Cubbage, 1982; Richardson et al., 1987; McLaren and Richardson[19]; Richardson et al.[20]; Richardson et al.[21]). Spatial distribution seems to vary between years (Richardson et al., 1987; Davis et al.[22]; Thomson et al.[23]) affected in part by surface temperature or turbidity fronts and anomalies (Borstad, 1985; Thomson et al.[23]).

Very few bowhead whales are found in the Chukchi Sea in summer (Miller et al., 1986); however, there have been enough sightings to indicate that some whales do not migrate to the Beaufort Sea, at least during some years. Many small groups have been observed traveling northwest along the Chukchi Peninsula in May (Bogoslovskaya et al.,

[14] Lindholm, O. 1863. Whales and how tides and currents in the Okhotsk Sea affect them. [From an unidentified journal with news from the Far East of Russia, p. 42–43. In Russ. Transl. by L. A. Hutchinson for Univ. Calif. San Diego, La Jolla, 1965, 12 p.]

[15] Ljungblad, D. K., S. E. Moore, J. T. Clarke, and J. C. Bennett. 1986. Aerial surveys of endangered whales in the northern Bering, eastern Chukchi and Alaskan Beaufort Sea, 1985: with a seven year review, 1979–85. Rep. for U.S. Minerals Manage. Serv. by Nav. Ocean Systems Cent., NTIS No. PB87-115929, 443 p.

[16] Brueggeman, J. J., B. Webster, R. Grotefendt, and D. Chapman. 1987. Monitoring the winter presence of bowhead whales in the Navarin Basin through association with sea ice. Rep. for U.S. Minerals Manage. Serv. by Envirosphere Co., NTIS No. PB88-101258, 179 p.

[17] Bessonov, B., V. V. Mel'nikov and V. A. Bobkov. 1990. Distribution and migration of cetaceans in the Soviet Chukchi Sea. *In* Conference Proceedings, Third Information Transfer Meeting, p. 25–31. U.S. Minerals Manage. Serv., Alaska OCS Reg.

[18] Marko, J. R., and M. A. Fraker. 1981. Spring ice conditions in the Beaufort Sea in relation to bowhead whale migration. Rep. for Alaska Oil Gas Assoc., Anchorage, by LGL Ltd., 98 p.

[19] McLaren, P. L., and W. J. Richardson. 1985. Use of the eastern Alaskan Beaufort Sea by bowheads in late summer and autumn. *In* LGL and Arctic Science, Importance of the eastern Alaskan Beaufort Sea to feeding bowheads: literature review and analysis, p. 7–35. Rep. for U.S. Minerals Manage. Serv. by LGL, Inc., and Arctic Sci., Ltd., 158 p.

[20] Richardson, W. J., B. Würsig, G. W. Miller, and G. Silber. 1986. Bowhead distribution, numbers and activities. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985, p. 146–219. Rep. for U.S. Minerals Manage. Serv. by LGL Inc., OCS Study MMS 86-0026. NTIS No. PB87–124350, 315 p.

[21] Richardson, W. J., B. Würsig, and G. W. Miller. 1987. Bowhead distribution, numbers and activities. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985–86, p. 257–368. Rep. for U.S. Minerals Manage. Serv. by LGL Inc., NTIS No. PB88-150271, 547 p.

[22] Davis, R. A., W. R. Koski, and G. W. Miller. 1983. Prelimary assessment of the length-frequency distribution and gross annual recruitment rate of the western arctic bowhead whale as determined with low-level aerial photogrammetry, with comments on life history. Rep. to NMFS, Natl. Mar. Mamm. Lab., Seattle, Wash., by LGL Ltd., 91 p.

[23] Thomson, D. H., D. B. Fissel, J. R. Marko, R. A. Davis, and G. A. Borstad. 1986. Distribution of bowhead whales in relation to hydrometeorological events in the Beaufort Sea. Environ. Stud. Revolving Funds Rep. 028, 119 p. Can. Dep. Indian N. Affairs, Ottawa.

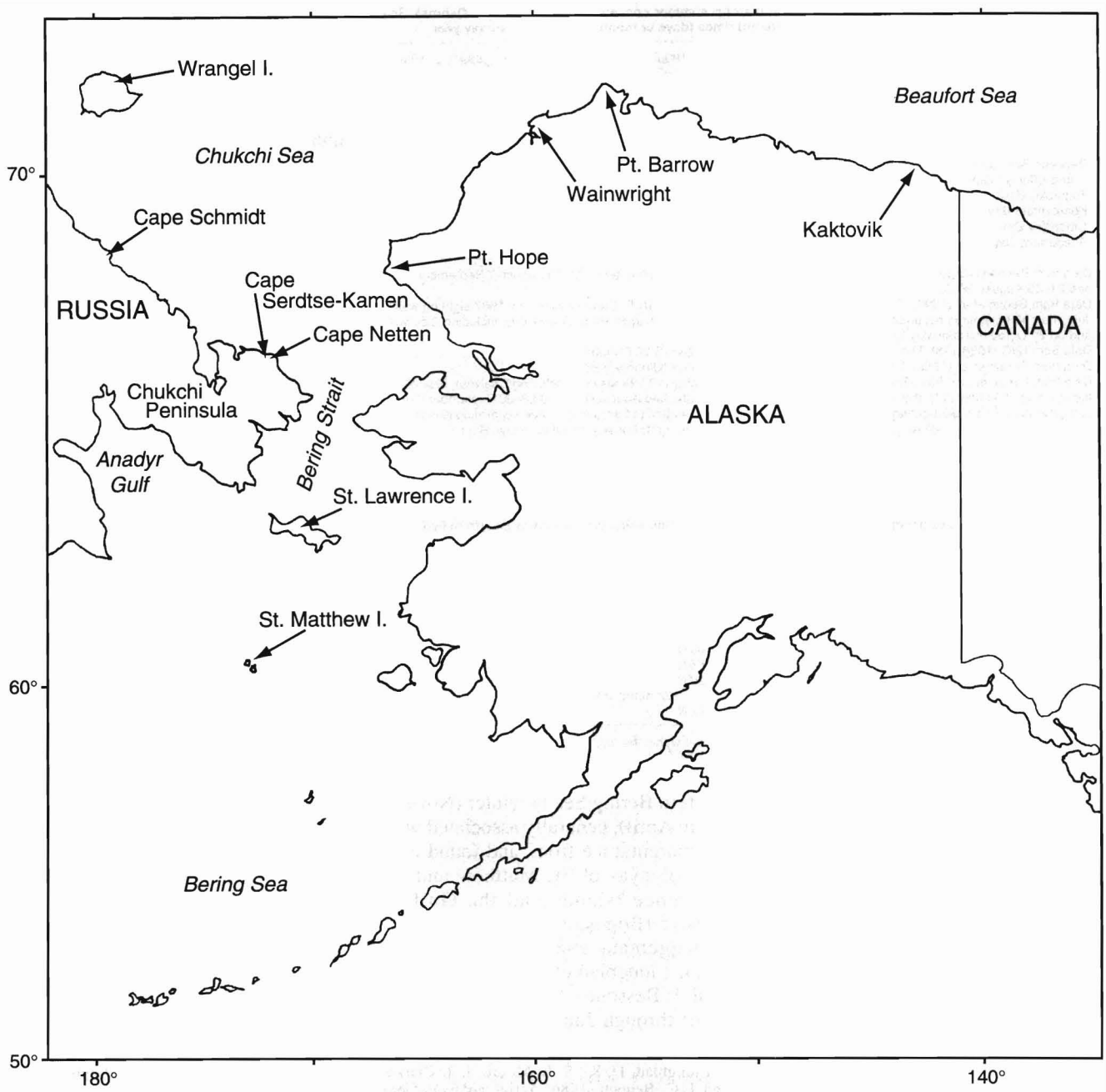
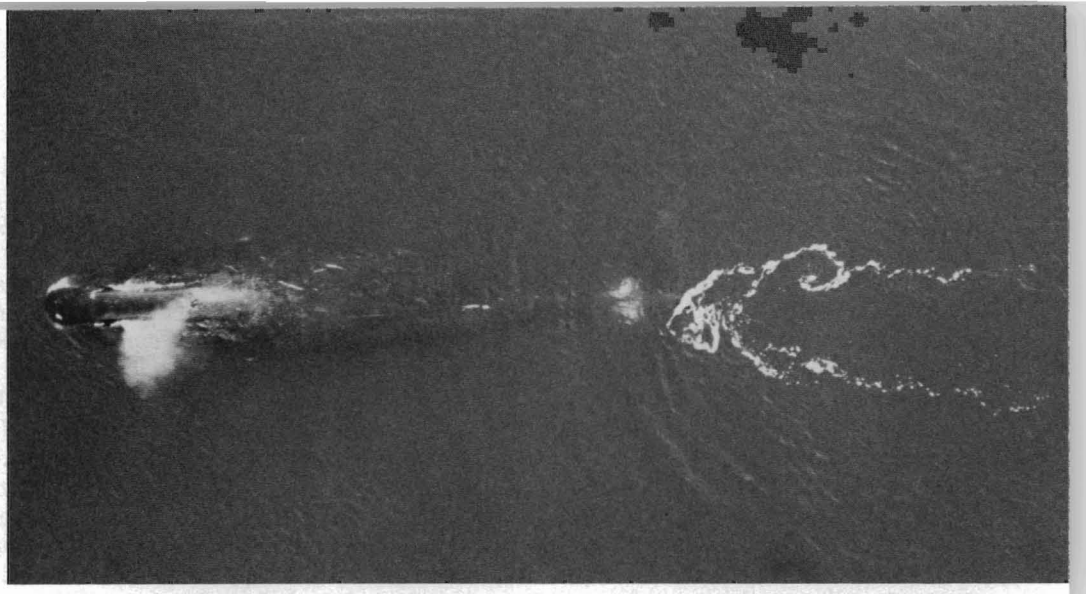


Figure 6. — Bering Sea and environs with place names mentioned in the text.

1982; Bessonov et al.[17]; Ainana et al.[24]; Zelensky et al.[25]), and about 60 whales traveled northwest past Cape Serdtse-Kamen 15–28 June 1990 (Mel'nikov and Bobkov, 1993). One group of 7 whales was observed off Cape Netten, Chukchi Peninsula, on 26 July 1991 traveling north, and a group of 7 was seen here on 27 September traveling east (Mel'nikov and Bobkov, 1994). Farther northwest, near Cape Schmidt, single animals were observed on 5 Au-

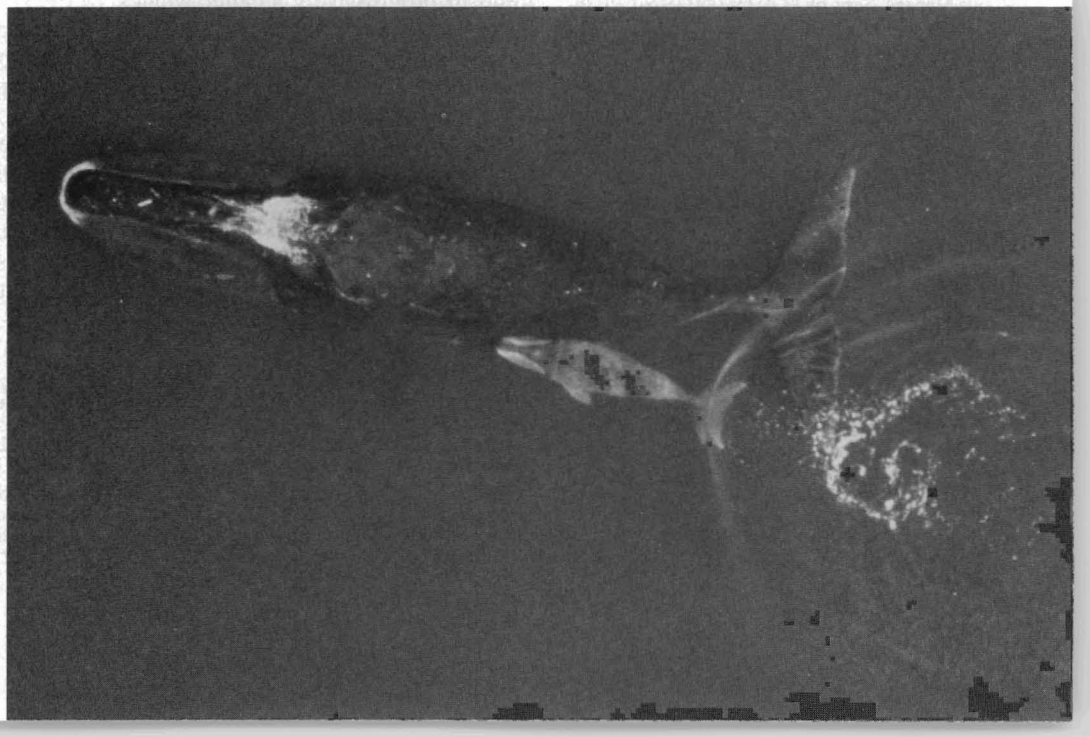
[24] Ainana, L., N. Mymrin, L. Bogoslovskaya, and I. Zagrebin. 1995. Role of the Eskimo Society of Chukotka in encouraging traditional Native use of wildlife resources by Chukotka Natives and in conducting shore based observations on the distribution of bowhead whales, *Balaena mysticetus*, in coastal waters off the south-eastern part of the Chukotka Peninsula (Russia) during 1994. Rep. to Dep. Wildl. Manage., North Slope Borough, Barrow, Alaska, by Eskimo Soc. Chukotka, Provideniya, Russia, 135 p.

[25] Zelensky, M., V. V. Mel'nikov, and V. V. Bichkov. 1995. Role of the Naukan Native Company in encouraging traditional Native use of wildlife resources by Chukotka Native people and in conducting shore based observations on the distribution of bowhead whales, *Balaena mysticetus*, in waters of the Bering Sea and Chukchi Sea adjacent to the Chukotka Peninsula (Russia) during 1994. Rep. to Dep. Wildl. Manage., North Slope Borough, Barrow, Alaska, by Eskimo Soc. Chukotka, Provideniya, Russia, 105 p.



Aerial view of a bowhead whale migrating past Point Barrow, Alaska, during the 1992 spring migration. A column of vapor, the "blow," exits the open blowholes. White on the chin and tail are characteristic of bowheads, and acquired marks along the dorsal surface allow for reidentification of this individual if photographed again. Photo by Wayne Perryman, NMFS.

A bowhead whale feeds in the Beaufort Sea (swimming to the left in this image). The high blowhole, "neck," and broad back are characteristic of this species. Photo by David Rugh, NMFS.



Aerial view of a bowhead whale adult and calf migrating past Point Barrow, Alaska, during the 1992 spring migration. The calf is in the typical swimming position beside the adult and between the pectoral flipper and fluke. Photo by Robin Westlake, NMFS.

gust and 1 September by crew members of the ice-breaker *Krasin*. Studies conducted in 1994 have shown the presence of bowhead whales throughout the summer along the southeastern portion of the Chukchi Peninsula (127 sightings in June, 59 in July, 5 in August, and 6 in September (Ainana et al.[24])) and the easternmost portion of the Peninsula (21 sightings in June and 39 in August (Zelensky et al.[25])).

During late summer (early September to mid-October), bowhead whales migrate west out of the Beaufort Sea, as evidenced during aerial surveys (Richardson [26]; Ljungblad et al.[27]), radio-tracking (Wartzok et al.[28]), and satellite- tracking (Mate and Krutzikowsky[29]). From mid-September to mid-October they are seen in the northeast Chukchi Sea, some as far north as lat. 72°N (Moore et al., 1986; Moore and Clark[30]). Whales migrate from Point Barrow into the Chukchi Sea heading toward Wrangel Island (Mate and Krutzikowsky[29]). When they reach the Siberian coast, they follow it southeast to the Bering Strait (Bogoslovskaya et al., 1982; Zelensky et al.[25]). In 1991, fall migrants, presumably returning from the Beaufort Sea, did not begin passing Cape Netten until 10 November (Mel'nikov and Bobkov, 1994). By early winter (late October and November) they arrive in the Bering Sea (Kibal'chich et al., 1986; Bessonov et al.[17]), where they remain until the following spring migration.

Segregation by size and sex class occurs in three overlapping pulses during the spring migration, the first consisting of subadults, the second of larger whales, and the third composed of even larger whales and cows with calves (Rugh, 1990; Angliss et al., 1995; Nerini et al.[31]). The reverse appears to occur along the Chukchi Peninsula; Russian natives noted the appearance of large numbers of mothers with calves in late March and early April followed by immature and adult animals (Bogoslovskaya et al., 1982). In the Beaufort Sea in summer, aggregations have usually consisted of only juveniles or of large whales that may include calves (Richardson[26], Davis et al.[32]). In 1983, Cubbage and Calambokidis (1987) found a significant inverse correlation between longitude and size class; encounter rates for larger whales increased moving west to east in the Beaufort Sea. Onshore and offshore distributions varied annually, suggesting that "sex- or age-class segregation patterns are temporally and spatially fluid and cannot be defined rigidly for any region or period" (Moore and Reeves, 1993:351). Segregation by size also occurs during the fall migration (Braham, 1995). George et al. (1995) showed a clear trend in progressively smaller whales harvested between August and November. Along the Chukchi Peninsula, the fall migration splits into two pulses (Bogoslovskaya et al., 1982; Mel'nikov and Bobkov, 1993; 1994), though segregation by size or sex class was not confirmed as the cause.

The sex ratio of whales harvested by Alaska natives from 1973 to 1992 was equal, though the proportion of adult females harvested in the spring has increased from 4.7% (1973–77) to 20.4% (1986–92) (Braham, 1995). Immature whales (<13 m) made up the largest percentage of the harvest; 80% prior to 1978 and 60% since 1978 (Braham, 1995). Records from the historical commercial catch were not as well maintained. Unlike the commercial whalers in the North Atlantic region, whalers in the North Pacific sector did not document size or sex differences between the aggregations of animals they hunted (Bockstoce and Burns, 1993).

Whales taken by commercial whalers in the Bering Sea may have been representatives of a population that did not migrate (Bockstoce and Botkin, 1983; Bockstoce, 1986; Fraker[33]). After reducing the number of bowhead whales in the Bering Sea to a point where they were uneconomical to hunt, the whalers turned their attention to the Okhotsk Sea. And when the Okhotsk Sea stock was nearly eliminated, the whalers explored the Chukchi Sea. Because they did not find whales in the western Chukchi Sea, they continued east to the Beaufort Sea where large numbers were found (Bockstoce and Burns, 1993). There has been difficulty in assessing the total number of animals killed in the Bering Sea stock. Only 19% of commercial whaling records collected from 1849 to 1914 have been extensively analyzed (Bockstoce and Botkin, 1983). Woodby and Botkin (1993) reviewed the summaries of estimated annual kills from pelagic and shore-based fisheries compiled by Marquette and Bockstoce (1980), Bogoslovskaya et al. (1982), Bockstoce and Botkin (1983), Breiwick and Mitchell (1983), Breiwick et al. (1984), Sonntag and Broadhead (1989), Mitchell[4], and Braund et al.[34]. They created a time series of harvest data showing cumulative kill records for each year

[26] Richardson, W. J. (Editor). 1987. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985–86. Rep. for U.S. Minerals Manage. Serv. by LGL Inc., NTIS No. PB88-150271, 547 p.

[27] Ljungblad, D. K., S. E. Moore, J. T. Clarke, and J. C. Bennett. 1987. Distribution, abundance, behavior and bioacoustics of endangered whales in the Alaskan Beaufort and eastern Chukchi Seas, 1979–86. Rep. for U.S. Minerals Manage. Serv. by Nav. Ocean Systems Cent., NTIS No.AD-A183934/9, 391 p.

[28] Wartzok, D., W. A. Watkins, B. Würsig, J. Guerrero, and J. Schoenherr. 1990. Movements and behaviors of bowhead whales. Rep. from Purdue Univ., Fort Wayne, for AMOCO Prod. Co., Anchorage, 197 p.

[29] Mate, B. R., and G. Krutzikowsky. 1995. Application of remote methods of large cetacean tracking: bowhead whales. Rep. for U.S. Minerals Manage. Serv. by Hatfield Mar. Sci. Cent., Oregon State Univ., Newport. OCS Study MMS 95-0053, 174 p.

[30] Moore, S. E., and J. T. Clarke. 1992. Distribution, abundance and behavior of endangered whales in the Alaskan Chukchi and western Beaufort Seas, 1991: with a review 1982–91. Rep. for U.S. Minerals Manage. Serv., Anchorage, Alaska, by SAIC, Marit. Serv. Div., 237 p.

[31] Nerini, M. K., D. Withrow, and K. Strickland. 1987. Length structure of the bowhead whale population derived from aerial photogrammetry, with notes on recruitment spring 1985 and 1986. Int. Whal. Comm. Unpubl. Doc. SC/39/PS14, 22 p.

[32] Davis, R. A., W. R. Koski, G. W. Miller, P. L. McLaren, and C. R. Evans. 1986. Reproduction in the bowhead whale, summer 1985. Int. Whal. Comm. Unpubl. Doc. SC/38/PS2, 123 p.

[33] Fraker, M. A. 1984. A brief review of recent information on the responses of bowhead whales (*Balaena mysticetus*) to offshore petroleum operations. Int. Whal. Comm. Unpubl. Doc. SC/36/PS17, 19 p.

[34] Braund, S. R., W. M. Marquette, and J. R. Bockstoce. 1988. Data on shore-based bowhead whaling at sites in Alaska. Int. Whal. Comm. Unpubl. Doc. SC/40/PS10, 9 p.

from 1848 to 1991. According to these data, 22,174 bowhead whales have been harvested from a stock that may have numbered between 10,000 and 23,000 before commercial exploitation. From 1992 to 1994, 113 bowhead whales were landed and 35 were struck but lost during native subsistence hunts in Alaska (Suydam et al., 1995).

Several different methods have been used to compute the current population size of the Bering Sea stock (reviewed by Zeh et al., 1993). In 1994, the International Whaling Commission's (IWC) Scientific Committee reviewed data collected during the 1993 visual and acoustic census (Zeh et al., 1995; Raftery and Zeh[35]) conducted near Point Barrow. They settled on a current population estimate of 7,992 bowhead whales (95% C.I.: 6,900–9,200) (IWC, 1995; Marine Mammal Commission[10]). Zeh et al.[36] continued to refine their estimate using newly available acoustic data. The 1988 Bayes empirical Bayes method yielded a population estimate of 7,500 (95% C.I.: 6,400–9,200). An alternative method, the N_4/P_4 method, which compared the estimated number of whales passing within the viewing range of census observers (N_4) and the proportion detected by the hydrophone array (P_4), resulted in an estimate of 8,000 (95% C.I.: 6,900–9,200) for the 1993 census. The Bayes empirical Bayes method "provided the best information on population size for assessment purposes" while the N_4/P_4 method provided "the best available estimate of the current size" of the Bering Sea stock (IWC, 1995; Zeh et al.[36]). An annual rate of increase of 3.1% (95% C.I.: 1.4–4.7%) was computed for the Bering Sea stock (IWC, 1995; Zeh et al.[36]).

A quota of 204 bowhead whales has been set for 1995–98 (see section on Management), based on a stated need for 51 whales per year to be divided among ten Alaskan native villages (IWC, 1995; Marine Mammal Commission[10], Zeh et al.[36]). Requests to harvest bowhead whales have also been put forth by Canadian and Russian natives. In 1991, Aklavik hunters in the western Canadian Arctic requested a permit to kill one or strike two bowhead whales from the Bering Sea stock (Freeman et al., 1992). Permission was granted by the Canadian government in August 1991, and one whale was harvested in Mackenzie Bay in the autumn of 1991 (Stoker and Krupnik, 1993; Marine Mammal Commission[10], Zeh et al.[36]). Additional licenses were granted in 1993 and 1994, though bowhead whales were not harvested in either year (Marine Mammal Commission[10], Zeh et al.[36]). Aboriginal harvests along the Chukchi Sea coasts usually yielded 8–10 bowhead whales in "good years" in the early 20th century, but by the mid-20th century, bowhead whale hunting was almost completely replaced by gray whale hunting (Krupnik, 1987). Poverty in the villages along the Chukchi Sea coast has brought about a renewed interest in hunting one or two bowhead whales a year (Bogoslovskaya et al., 1982; Bessonov et al.[17]).

Life History and Ecology

Most of what is known of the life history and ecology of bowhead whales has been derived from studies of the Bering Sea stock. The data presented in this section applies only to this stock unless otherwise stated.

Feeding

Food habits studies conducted on 35 bowhead whales (21 males and 14 females) harvested between 1975 and 1989 by Alaskan natives were reviewed by Lowry (1993). Most prey species identified from bowhead whale stomach contents were crustacean zooplankton, particularly euphausiids and copepods ranging in length from 3 to 30 mm. Epibenthic organisms, mostly mysids and gammarid amphipods, were also common in stomach contents, with only a small sampling of benthic species (Lowry, 1993). Age-related differences were difficult to establish given the limited sample size; however, slightly higher levels of epibenthic organisms were found in the stomachs of small whales (<10.5 m in length) (Lowry, 1993), and it appears that copepods become increasingly more important in the diet of larger whales (Schell et al.[37]). Crustacean zooplankton was the dominant prey in both males (89%) and females (79%) (Lowry, 1993).

As evidenced in stomach contents collected between April and June, some bowhead whales feed opportunistically during the spring migration (George and Tarpley, 1986; Carroll et al., 1987; Lowry, 1993). In most cases, half or more of the stomachs were empty (3 of 6 near St. Lawrence Island, 3 of 4 at Point Hope, 10 of 12 at Wainwright, and 23 of 36 near Point Barrow). Stomachs collected south of Point Barrow were from small whales and contained "shrimp," gammarid amphipods or very small (<3.1 mm) copepods. Stomachs collected from whales collected near Point Barrow generally contained either copepods, euphausiids, or both, though the dominant prey often varied between individuals harvested in the same year. During the fall migration, only 2 of 15 whales harvested off Kaktovik (central Beaufort Sea) and 1 of 6 taken near Barrow had empty stomachs (Lowry, 1993). Sex- and length-related differences in diet were not noted in the 11 samples collected at Kaktovik (4 females and 7 males) that underwent detailed examination. Copepods were predominant in six of the stomach samples, euphausiids in three, mysids in one, and one contained almost equal parts of all three organisms. Euphausiids were the dominant prey item found in five large whales (>14 m) harvested near Point Barrow in September.

In years when oceanographic conditions are favorable, the lead system near Point Barrow may serve as an important feeding ground in the spring

[35] Raftery, A. E., and J. E. Zeh. 1994. Bowhead whale, *Balaena mysticetus*, population size estimated from acoustic and visual census data collected near Barrow, Alaska, in 1993. Int. Whal. Comm. Unpubl. Doc. SC/46/AS13, 25 p.

[36] Zeh, J. E., A. E. Raftery, and A. A. Shaffner. 1995. Revised estimates of bowhead population size and rate of increase. Int. Whal. Comm. Unpubl. Doc. SC/47/AS10, 26 p.

[37] Schell, D. M., S. M. Saupe, and N. Haubenstock. 1987. Bowhead whale feeding: allocation of regional habitat importance based on stable isotope abundances. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales 1985–86, p. 369–415. Rep. to U.S. Minerals Manage. Serv. by LGL Ecol. Res. Assoc. Inc., NTIS No. PB88-150271.

(Carroll et al., 1987). Other important feeding grounds exist in the Beaufort Sea (Lowry and Frost, 1984; Ljungblad et al., 1986; Schell and Saupe, 1993; Würsig et al., 1985; 1989; Thomson and Richardson[38]), along the northern Chukchi Peninsula (Mel'nikov and Bobkov, 1993; 1994; Moore et al., 1995) and possibly in the Bering Sea (Schell and Saupe, 1993). Schell and Saupe (1993) and Schell et al.[37] believe that a significant amount of feeding may occur outside the eastern Beaufort Sea, particularly by older whales in the fall and early winter when they are in the Chukchi and Bering Seas. These conclusions are based on patterns of isotope variation found in the visceral fat and muscle sampled from three adults and six subadults. This variability suggests that older animals are feeding in different areas or on different prey types than younger animals. Feeding behavior has been observed during the summer in the Beaufort Sea and the fall in the Chukchi Sea but not in the winter in the Bering Sea, as summarized by Lowry (1993).

The occupation of summer concentration areas by bowhead whales in the Okhotsk Sea is believed to be influenced by distributions of prey (Berzin et al.[39]), though feeding aggregations were only reported in 1979 and 1995 (Brownell[12], Berzin et al.[39]). In the Davis Strait stock, feeding behavior was observed in bowhead whales summering in Isabella Bay, Baffin Island (Finley, 1990). Most of this activity took place in deep (>200 m), glacial troughs where large concentrations of *Calanus* copepods occurred (Finley, 1990; Nicklin, 1995; Richardson et al., 1995). Information on food habits of the Spitsbergen stock is sparce. Scoresby (1820) found Greenland whale stomachs contained predominantly small crustaceans he called "squillae and shrimps." Scoresby's drawings were examined by Ruud (1937) who determined that the "squillae" were partially digested euphausiids.

Reproduction

Although apparent sexual activity occurs among bowhead whales most months of the year, studies of bowhead fetuses indicate conception typically occurs during late winter or early spring, as summarized by Koski et al. (1993:249). Not all sexual activity leads to conception; fecundity of some bowheads is in doubt with the discovery of pseudohermaphroditism in at least two males with testicular feminization (Tarpley et al.[40]), a relatively high incidence rate as only 76 bowheads have been closely examined between 1980 and 1989 (Philo et al., 1993). Calves are usually born between April and early June during the spring migration (Koski et al., 1993) probably peaking in May (Nerini et al., 1984). Most (76%) photogrammetrically measured calves were within 1 m of their average length in late spring (4.25–5.25 m) indicating a majority are born within a restricted period (Koski et al., 1993). Pregnancy rates have been documented as 0.21 pregnancies/mature female/year (Tarpley et al.[41], which includes results from Nerini et al., 1984) or 0.20–0.35 (George et al., 1995) with a possible increase in pregnancy rates of whales harvested since 1985 (George et al., 1992). These pregnancy rates suggest that mature female bowheads have calving intervals of 3.5–7.1 years (Nerini et al., 1984) or 4 years (Tarpley et al.[41]), comparable to calving intervals of right whales (Kraus et al., 1986; Bannister, 1990; Best, 1990; Hamilton and Mayo, 1990; Payne et al., 1990). The 3–4 year calving interval in bowhead whales has been corroborated by photo-identification evidence (Miller et al., 1992; Rugh et al., 1992). The highest sighting rate of calves during the spring migration occurred in 1993. This sighting rate, when graphed with earlier shore-based census and aerial photogrammetric sightings, provides additional support for a 3–4 year variable recruitment pattern (George et al., 1995).

Gestation lasts 13–14 months (Nerini et al., 1984) or 12–16 months (Tarpley et al.[41]). Calves are 4.0–4.5 m in length when born and increase from modal lengths of 4.75–5.0 m in late May to 6.25–6.5 m in late summer, a growth rate of 1.5 cm/day (Koski et al., 1993), much less than the 2.88 cm/day calculated for southern right whales (Best and Rüther[42]). Weaning occurs 9–15 months postpartum (Nerini et al., 1984) with about 95% of the yearlings weaned by the next spring migration (Rugh et al., 1992). Yearlings are 6.6–9.4 m long in the spring according to data from harvested whales (Nerini et al., 1984) and 7.0–8.7 m in summer based on photogrammetric lengths (Koski et al., 1993). Growth rates appear to slow after weaning. Small bowheads reidentified between years had growth rates of much less than 1 m/yr (Koski et al., 1992; Davis et al.[32]). Carbon isotope analysis, using apparent oscillations in isotopic ratios in tissue samples from baleen to indicate annual cycles, also suggests bowhead whales grow slowly, taking on the order of two decades to reach sexual maturity (Schell et al., 1989; Schell and Saupe, 1993). This growth rate is much slower than that of other baleen whales (Lockyer, 1981; 1990; Payne et al., 1990). Conventional techniques to age bowhead whales have been considered unsuccessful (Nerini[43]), in part because of the poor correlation between whale size and indicated age, but some evidence, such as ivory or stone harpoon heads found in five recently

[38] Thomson, D. H., and W. J. Richardson. 1987. Integration. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales 1985–86, p. 449–479. Rep. to U.S. Minerals Manage. Serv. by LGL Ecol. Res. Assoc. Inc., NTIS No. PB88-150271.

[39] Berzin, A. A., V. L. Vladimirov, and N. V. Doroshenko. 1985. The distribution and numbers of cetacea in the Okhotsk Sea: results from aerial surveys. Int. Whal. Comm. Unpubl. Doc. SC/37/O5, 7 p.

[40] Tarpley, R. J., G. G. Stott, R. F. Sis, M. J. Shively, and G. H. Jarrell. 1985. Further observations on the morphology of the reproductive tract of the bowhead whale, *Balaena mysticetus*. *In* T. F. Albert (Editor), Third conference on the biology of the bowhead whale, *Balaena mysticetus*: extended abstracts and panel discussion, Anchorage, p. 115–119.

[41] Tarpley, R., R. Weeks, and G. Stott. 1988. Observations on reproductive morphology in the female bowhead whale (*Balaena mysticetus*). Int. Whal. Comm. Unpubl. Doc. SC/40/PS8, 50 p.

[42] Best, P. B., and H. Rüther. 1989. Aerial photogrammetry of southern right whales—a preliminary report. Int. Whal. Comm. Unpubl. Doc. SC/41/PS4, 18 p.

[43] Nerini, M. K. 1983. Age determination techniques applied to mysticete whales. M.S. thesis. Univ. Wash., 51 p.

harvested whales, suggest that bowhead whales may live >50 years (Philo et al., 1993) or >75 years (George et al., 1995).

Results from female bowhead whales examined for corpora albicantia or corpora lutea indicate sexual maturity begins when whale lengths exceed 14.2 m, and perhaps as small as 12.3 m (Nerini et al., 1984; Tarpley et al.[41]). Aerial photogrammetry indicates whales as small as 12.2 m were accompanied by calves (Davis et al.[22]). Smaller females tend to calve later in the spring migration than larger females: 1.5% (1/68) of the adults with calves photographed in the spring were <13.5 m long compared to 12% (7/59) in the summer (Koski et al., 1993). There is virtually no information on size at maturation for males, except that, in general they tend to be smaller than females (Nerini et al., 1984).

Using aerial photogrammetric techniques, Angliss et al. (1995) summarized and revised results from surveys conducted from 1985–92 (originally reported in Nerini et al.[31]; Withrow and Angliss, 1992; 1994). These show that 5.2% of the sampled population of bowhead whales in the Barrow area in the spring were calves (<6 m), 53.7% were juveniles (6–13 m), and 41.1% were adults (>13 m). These authors also showed that age segregation occurred during the spring migration: 80% of the measured animals early in the migration were juveniles, dropping to 20% by the end of the migration. Adults with calves did not appear until the last few weeks of the migration. This seasonal pattern was also evident in aerial photographic data showing increased degrees of graying on the peduncles (a sign of aging) as the migration season progressed (Rugh, 1990) and in sizes of whales harvested at Barrow (George et al., 1995). Cubbage and Calambokidis (1987) described segregation of bowheads by size in the Beaufort Sea, further confounding efforts to representatively sample the population for calving rates. On the other hand, Clarke et al. (1987) found little analytical evidence of geographic or temporal segregation of calves during the fall migration.

Population modeling by Breiwick et al. (1984) underlined the need for improved estimates of calf production and proportion of immature whales in the population. For modeling purposes, Chapman (1984) used an estimated crude birth rate of 0.072 (S.E. 0.014). Koski et al. (1993) reviewed available aerial photogrammetric data along with rates of sightings of calves from ice-based observers. These data suggested variable recruitment in bowheads with a 3–4 year cyclicity (also described in Rugh et al., 1992; Withrow and Angliss, 1992). The mean crude birth rate for all available information from 1982–89 (summarized in Koski et al., 1993:264) was 0.052. Even with this low birth rate, the Bering Sea bowhead population is increasing, suggesting a low rate of mortality (Koski et al., 1993; Whitcher et al.[44]).

Morbidity and Mortality

Although bowhead whale mortality caused by the subsistence harvest is fairly well documented (see section on Distribution and Abundance), particularly since 1977 in the Bering Sea stock, little is known about naturally occurring diseases and death in bowhead whales (e.g., Heidel and Albert, 1994). Since 1964, at least 36 cases exist in which the cause of death could not be established (Philo et al., 1993). Some of these deaths may be the result of hunter-inflicted wounds. Types of human-induced injuries include embedded shrapnel and harpoon heads from hunting attempts, rope and net entanglements from harpoon lines and crab pots, and collisions with vessels, summarized in Philo et al. (1993). Bowhead whales frequently react to being struck with a harpoon by rotating rapidly (Philo et al., 1993). This type of reaction near ropes or nets would only increase the likelihood of entanglement. Whales with ropes caught in their baleen and with scarring caused by rope entanglement have been observed during the harvest (Philo et al., 1992) and in aerial photographs of live animals (NMML, unpubl. data). Although incidental take of bowhead whales is apparently rare, there has been one reported entrapment and death of a young bowhead whale in a fishing net in Japan (Nishiwaki and Kasuya, 1970) and another in the waters of northwest Greenland in a net used to capture beluga whales (Kapel, 1985). Between 1976 and 1992, only three ship-strike injuries were documented out of a total of 236 bowhead whales examined from the Alaskan subsistence harvest (George et al., 1994). These low numbers suggest that either bowhead whales do not often encounter vessels, avoid interactions with vessels, or that interactions usually result in the death of the animal. Exposure to man-made noise and contaminants may produce short- and long-term effects (Richardson and Malme, 1993; Bratton et al., 1993) that may compromise the health and reproductive performance of some whales. The effects of repeated encounters with seismic vessels, drill rigs, hydrocarbons, and heavy metals are unknown. Anthropogenic impact is a function of the extent that industrial activities coincide with the bowhead whales' seasonal occupation of certain regions and the whales' tolerance level of the impacts (Richardson and Malme, 1993; Bratton et al., 1993).

It is not known whether bowhead whales suffer from stress-induced bacterial infections similar to those observed in captive cetaceans (Buck et al., 1987). Studies of harvested bowhead whales have provided information on bacterial, mycotic, and viral infections but not the level to which they contribute to mortality and morbidity (Philo et al., 1993). Skin lesions, found on all harvested bowhead whales, were not malignant or contagious. However, potentially pathogenic microorganisms inhabit these lesions and may contribute to epidermal necrosis and the spread of disease (Shotts et al., 1990). Exposure of these roughened areas of skin to environmental contaminants, such as petroleum products, could have significant effects (Shotts et al., 1990; Albert[45]); although, Bratton et al. (1993) con-

[44] Whitcher, B., J. E. Zeh, D. J. Rugh, W. R. Koski, and G. W. Miller. 1996. Estimation of adult bowhead whale survival rates. Int. Whal. Comm. Unpubl. Doc. SC/48/AS12, 22 p.

[45] Albert, T. F. 1981. Some thoughts regarding the possible effect of oil contamination on the bowhead whale, *Balaena mysticetus*. *In* T. F. Albert (Editor), Tissue structural studies and other investigations on the biology of endangered whales in the Beaufort Sea, p. 945–953. Rep. to Bur. Land Manage. from Dep. Vet. Sci., Univ. Md., Coll. Park, NTIS Accession No. PB86-153566.

cluded that such encounters were not likely to be hazardous.

Of 130 bowhead whales examined between 1980 and 1989, only one whale had a tumor, though this may be the result of incomplete necropsies performed on the other whales (Migaki and Albert, 1982; Philo et al., 1993). The tumor, located on the liver, was benign. According to Philo et al. (1993:295), "it is unlikely that tumors are major contributors to bowhead whale morbidity or mortality." Marine caliciviruses first discovered in California sea lions, *Zalophus californianus californianus*, are known to be widespread and transferable between terrestrial and marine hosts (Smith et al., 1986; Barlough et al., 1986; Smith et al., 1987; Smith et al.[46]). Though not isolated from bowhead whale tissues, there is evidence that these whales may be hosts for these viruses (Smith et al., 1986; Smith et al., 1987; Smith et al.[47]). Symptoms of calicivirus infection include formation of cysts, open sores, inflammation of the lungs, brain, heart, and stomach and intestine lining, and abortion (Barlough et al., 1986; Smith et al., 1986; Smith et al., 1987; Smith et al.[46]). How much these viruses contribute to natural mortality and possibly to reduced reproduction in the bowhead whale population is unknown (Philo et al., 1993).

Evidence of ice entrapment and predation by killer whales, *Orcinus orca*, has been documented in almost every bowhead whale stock. The percentage of whales entrapped in ice is considered to be small, given that this species is so strongly ice-associated (Tomilin, 1957; Mitchell and Reeves, 1982; Nerini et al., 1984; Philo et al., 1993). The ice may also provide some protection from killer whale attacks. The frequency of attacks is unknown and killer whale distribution in northern waters has not been well documented (George et al., 1994). In the Davis Strait stock, about one-third (5 of 16) of the summer residents photographed in Isabella Bay showed evidence of killer whale scarring along their flukes and sometimes their flippers (Finley, 1990). Two attacks were witnessed during Finley's study and appear to occur frequently; Inuit hunters even have a phrase for the behaviors observed during an attack, "Ardlingayuq." Of 195 whales examined during the Alaskan subsistence harvest (1976–92), 8 had been wounded by killer whales (George et al., 1994). Seven of the eight bowhead whales were greater than 13 m in length, suggesting either that scars are accumulated over time, or young animals do not survive a killer whale attack. Hunters on St. Lawrence Island reported two small (<9 m) bowhead whales found dead as a result of killer whale attacks (George et al., 1994). Overall, the frequency of attacks on bowhead whales in the Bering Sea stock appears to be low (George et al., 1994). Attacks witnessed in the Okhotsk Sea at the turn of the century are reported in Mitchell and Reeves (1982). Recent accounts include information on the distribution and abundance of killer whales in the Okhotsk Sea, but additional attacks have not been reported (Vladimirov, 1994). From the available data, it is not possible to assess the level of depredation on bowhead whales by killer whales, particularly in terms of size-class selection and encounter rates.

Management

Clearly, bowhead whale stocks are slow to recover, and some might not recover at all. The Spitsbergen stock was reduced from 24,000 to a few "tens" of whales and has not recovered in the past 80 years. The Davis Strait and Hudson Bay stocks declined from about 12,300 whales to less than 450 currently, although significant whaling has not occurred in 80 years. The Okhotsk Sea stock was originally around 3,000 whales, but after severe whaling which ended over 100 years ago, there are still only 300–400 whales. The Bering Sea may have had a stock that was eliminated, except for the component that migrated to the Beaufort Sea. This stock was reduced from at least 10,300 animals, and has been recovering slowly over the past 80 years to a current population of about 8,000. There is evidence that bowhead whales are long-lived animals. It is therefore possible that in the greatly reduced stocks, some of the animals have survived nearly since the termination of commercial whaling, but fecundity rates are so low that very few new whales are being added to the respective stocks. Calving intervals of 3–4 years and the possibility that bowheads whales do not become sexually mature until they are 20 years old may, in part, explain these slow recovery rates in stocks with only a few hundred whales.

The IWC is the primary body responsible for conservation and management of bowhead whale populations worldwide. All stocks of bowhead whales are classified as "protected" by the IWC. As mentioned in the Introduction, the United States further classified all bowhead whales as endangered under the ESA and depleted under the MMPA. Currently, the bowhead whales in the Bering-Chukchi-Beaufort Seas represent the largest surviving stock. This is the only stock, mandated by the IWC and through exemptions under the ESA and MMPA, still harvested by aboriginal hunters in Alaska. Thus far, a quota to harvest bowhead whales from the Bering Sea stock and the other stocks has not been provided to Russian or Canadian natives by the IWC (Stoker and Krupnik, 1993; IWC, 1995). As determined by the IWC's Scientific Committee, "the total of whales landed in the four years 1995–98 should not exceed 204, with a maximum number of 68 strikes in 1995, 67 in 1996, 66 in 1997, and 65 in 1998." (IWC, 1995:22). Any unused portion of the strike quota will be carried forward from that year and added to the strike quota of any subsequent years, provided that no more than 10 strikes are added to the strike quota for any one year. The average number of whales harvested per year

[46] Smith, A. W., D. E. Skilling, and K. Benirschke. 1981. Investigations of the serum antibodies and viruses of the bowhead whale, *Balaena mysticetus*. *In* T. F. Albert (Editor), Tissue structural studies and other investigations on the biology of endangered whales in the Beaufort Sea, p. 233–254. Rep. to Bur. Land Manage. from Dep. Vet. Sci., Univ. Md., College Park, NTIS No. PB86–153566.

[47] Smith, A. W. 1979. Serum antibodies and viruses. *In* J. J. Kelley and G. A. Laursen (Editors), Investigation of the occurrence and behavioral patterns of whales in the vicinity of the Beaufort Sea Lease Area, p. 445–457. Rep. to Bur. Land Manage. from Nav. Arctic Res. Lab., Barrow, Alaska, NTIS No. PB86-153582.

from 1989 to 1993, including those struck and lost, was 42 (Suydam et al., 1995).

Since 1981, the harvest has been monitored by the Alaska Eskimo Whaling Commission (AEWC) through a Cooperative Agreement with the National Oceanic and Atmospheric Administration (NOAA). This Cooperative Agreement will remain in effect until the year 2000. Also since 1981, the AEWC has channeled funds to the North Slope Borough (NSB) for censusing the bowhead whale population as it migrates past Point Barrow in the spring (Montague, 1993). The AEWC has also been responsible for allocating IWC quotas among its member communities and has worked to improve hunting methods and technology to reduce the number of whales struck but lost. Emphasis has been placed on promoting understanding of the needs of native Alaskan whalers and obtaining quotas that will meet these needs while still ensuring recovery of the bowhead whale population. Roles have included habitat management and protection in light of increased commercial activity in the Arctic (Stoker and Krupnik, 1993).

Under the 1994 reauthorization of the MMPA, the National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (USFWS) developed a method for establishing minimum allowable incidental takes of marine mammals by commercial fisheries. This potential biological removal level (PBR) is defined as "the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population" (Marine Mammal Commission[48]). Using the minimum population estimate (N_{min}) of 7,524 bowhead whales for the Bering Sea stock, one-half the maximum theoretical net productivity rate ($0.5R_{max}$) of 4%, and a recovery factor (F_r) of 0.5, resulted in a PBR of 75 animals from the current population (Small and DeMaster[49]). Because the Alaska Eskimo subsistence harvest "is managed under an international regime that differs from the MMPA amended legislation," the IWC quota supercedes any quotas set by the MMPA(Small and DeMaster[49]). Reviews of observer data and vessel logbooks indicate that no incidental takes of bowhead whales by commercial fisheries have occurred in U.S. waters (Small and DeMaster[49]). Incidental takes of bowhead whales in fisheries have rarely been reported and are thought to not be an issue of concern; in particular because the habitat selected by bowheads (ice-covered seas) limits commercial or sport fisheries activities (Small and DeMaster[49]).

Impacts from industrial development (particularly offshore oil extraction) are of concern as most habitat of the Bering stock of bowheads is within active or potential lease zones. But studies indicate that bowhead behavior is often temporarily affected when exposed to close approaches by ships, seismic vessels, and aircraft. Reactions are less obvious when the noise source is fairly constant, such as with distant seismic or drilling work, but migrating bowheads sometimes adjust their course to divert around stationary sources of man-made noise (LGL and Greeneridge[50], Hall et al.[51], Richardson et al.[52]). Although there has been concern expressed by residents of the Arctic (Ahmaogak, 1985; Ahmaogak[53]), there is insufficient evidence about cumulative and long-term effects of anthropogenic noises (Richardson and Malme, 1993). The spring season appears to be a particularly critical period in the bowheads' annual cycles as this is the time all, or most, of the population migrates, often into areas covered by dense ice, where migration routes are constrained and most likely to be blocked by noise sources (Richardson et al.[52]). Conception and parturition happen during the spring, as well as some feeding. This is also the season of the most intense harvest by subsistence hunters.

Currently, bowhead whales in the Bering Sea are classified as a "strategic stock" under the amended MMPA. Stocks are classified as strategic when one of the following three criteria are met: 1) "level of direct human-caused mortality exceeds the potential biological removal level"; 2) "based on the best available scientific information, [the stock] is declining and is likely to be listed as a threatened species under the Endangered Species Act of 1973 within the foreseeable future"; or 3) [the stock] "is listed as a threatened or endangered species under the Endangered Species Act of 1973 (16 U.S.C. 1531 et seq.), or is designated as depleted under this act" (Marine Mammal Commission[48]). The level of human-caused mortality and serious injury during the subsistence harvest of Bering Sea bowhead whales, 42 animals per year, does not exceed the PBR nor the IWC quota for 1995. The lower end of the optimum sustainable population (OSP) range was calculated to vary between 6,500 and 10,500, using an initial stock size of 12,599 (95% C.I. 10,945–17,431)(IWC, 1995) and the assumption that the maximum net productivity level (MNPL) is 60% of carrying capacity (K). Objective criteria for defining when this population should be downlisted to threatened or delisted under the ESA have not been developed to date.

[48] Marine Mammal Commission. 1995. The Marine Mammal Protection Act of 1972, as amended. Mar. Mamm. Comm., 1825 Conn. Ave. N.W., Wash. D.C. 20009, 299 p.

[49] Small, R. J., and D. P. DeMaster. 1995. Alaska marine mammal stock assessments 1995. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-57, 93 p.

[50] LGL and Greeneridge. 1987. Responses of bowhead whales to an offshore drilling operation in the Alaskan Beaufort Sea, autumn 1986. Rep. for Shell W. E. P. Inc., Anchorage, Alaska, from LGL, Ltd., King City, Ont., Can., and Greeneridge Sci. Inc., Santa Barbara, Calif, 371 p.

[51] Hall, J. D., M. L. Gallagher, K. D. Brewer, P. R. Regos, and P. E. Isert. 1994. ARCO Alaska Inc. 1993 Kuvlum exploration area site specific monitoring program: final report. Rep. for ARCO Alaska Inc., Anchorage, from Coastal Offshore Pac. Corp., Walnut Creek, Calif., 219 p.

[52] Richardson, W. J., C. R. Greene Jr., J. S. Hanna, W. R. Koski, G. W. Miller, N. J. Paternaude, and M. A. Smultea. 1995. Acoustic affects of oil production activities on bowhead and white whales visible during the spring migration near Pr. Barrow, Alaska—1991 and 1994 phases. Rep. for U.S. Minerals Manage. Serv. from LGL, Ltd., King City, Ont., Can. OCS Study MMS 95–0051, 539 p.

[53] Ahmaogak, G. 1989. Protecting the habitat of the bowhead whale. *In* L. Rey and V. Alexander (Editors), Proceedings of the sixth conference of the Comite Arctique International, New York, 13–15 May 1985, p. 593–597.

The agency plans to develop objective criteria to determine whether this stock's current classification is accurate or, if not, whether it should be listed as threatened or removed from the list of endangered and threatened wildlife. One possible approach which will be investigated is that used by IUCN-World Conservation Union. This system of classification consists of three levels (i.e., critical, endangered, and vulnerable), each level representing a different probability of extinction within a specific period of time (Mace and Lande, 1991). The IUCN criteria also take into account extent of occurrence, area of occupancy, number of locations or subpopulations, and number of mature animals. Additional objective criteria based on recently revised Recovery Plans, as appropriate, will also be considered. Because population estimates are extremely low for the Spitsbergen, Davis Strait, Hudson Bay, and Okhotsk Sea stocks, these should continue to retain endangered status.

Literature Cited

Ahmaogak, G. 1985. Comments regarding the development of a policy pertaining to research in the U.S. Arctic. Inuit Stud. 9(2):27–32

Angliss, R. P., D. J. Rugh, D. E. Withrow, and R. C. Hobbs. 1995. Evaluations of aerial photogrammetric length measurements of the Bering-Chukchi-Beaufort Seas stock of bowhead whales (*Balaena mysticetus*). Rep. Int. Whal. Comm. 45:313–324.

Bannister, J. L. 1990. Southern right whales off western Australia. Rep. Int. Whal. Comm., Spec. Iss. 12:279–288.

Barlough, J. E., E. S. Berry, D. E. Skilling, and A. W. Smith. 1986. The marine calicivirus story—part I. Compend. Continuing Educ. Practicing Vet. 8:F5-F13.

Belikov, S. E., Yu. A. Gorbunov, and V. I. Shil'nikov. 1989. Distribution of pinnipedia and cetacea in Soviet arctic seas and the Bering Sea in winter. Sov. J. Mar. Biol. 15(4):251–257.

Berzin, A. A., V. L. Vladimirov, and N. V. Doroshenko. 1988. Results of aerial surveys to study the distribution and abundance of cetaceans in the coastal waters of the Sea of Okhotsk in 1986–1987. *In* N. S. Chernysheva (Editor), Scientific research on sea mammals of the northern part of the Pacific Ocean in 1986–1987, p. 16–22. VNIRO, Moscow, U.S.S.R. [Can. Transl. Fish. Aquat. Sci. 5506, 195 p.]

_____, _____, and _____. 1990. Aerial surveys to determine the distribution and number of polar whales and beluga whales in the Sea of Okhotsk in 1985–1989. *In* A. A. Berzin (Editor), Questions relating to the rational exploitation of marine mammals in the far eastern seas, p. 22–34. TINRO, Vladivostok, U.S.S.R. Vol.112 [Environ. Can. Transl. 4083779, 109 p.]

_____, _____, and _____. 1991. Results of aerial surveys to study the distribution and abundance of whales in the Sea of Okhotsk in 1988–1990. *In* L. A. Popov (Editor), Research papers on marine mammals of the North Pacific, 1989–1990, p. 4–14. VNIRO, Moscow, U.S.S.R. [Environ. Can. Transl. 4083780, 200 p.]

Best, P. B. 1990. Natural markings and their use in determining calving intervals in right whales off South Africa. S. Afr. J. Zool. 25:114–123.

Bockstoce, J. R. 1986. Whales, ice and men: the history of whaling in the western Arctic. Univ. Wash. Press, Seattle, 400 p.

_____ and D. B. Botkin. 1983. The historical status and reduction of the western arctic bowhead whale (*Balaena mysticetus*) population by the pelagic whaling industry, 1848–1914. Rep. Int. Whal. Comm., Spec. Iss. 5:107–141.

_____ and J. J. Burns. 1993. Commercial whaling in the North Pacific sector. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 563- 577. Soc. Mar. Mamm. Spec. Publ. 2.

Bogoslovskaya, L. S., L. M. Votrogov, and I. I. Krupnik. 1982. The bowhead whale off Chukotka: migrations and aboriginal whaling. Rep. Int. Whal. Comm. 32:391–399.

Borstad, G. A. 1985. Water colour and temperature in the southern Beaufort Sea: remote sensing in support of ecological studies of the bowhead whale. Can. Tech. Rep. Fish. Aquat. Sci. 1350, 68 p.

Braham, H. W. 1984. The bowhead whale, *Balaena mysticetus*. Mar. Fish. Rev. 46(4):45–53.

_____. 1995. Sex and size composition of bowhead whales landed by Alaskan Eskimo whalers. *In* A. P. McCartney (Editor), Hunting the largest animals: native whaling in the western Arctic and subarctic, p. 281–313. Can. Circumpolar Inst. Stud. Whal. 3, Occas. Publ. 36, 345 p.

_____, M. A. Fraker, and B. D. Krogman. 1980. Spring migration of the western Arctic population of bowhead whales. Mar. Fish. Rev. 42(9–10):36–46.

_____, B. D. Krogman, and G. M. Carroll. 1984. Bowhead and white whale migration, distribution, and abundance in the Bering, Chukchi, and Beaufort Seas, 1975–78. U.S. Dep. Commer., NOAA Tech. Rep. NMFS SSRF-778, 39 p.

Bratton, G. R., C. B. Spainhour, W. Flory, M. Reed, and K. Jayko. 1993. Presence and potential effects of contaminants. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 701–744. Soc. Mar. Mamm. Spec. Publ. 2.

Breiwick, J. M., L. L. Eberhardt, and H. W. Braham. 1984. Population dynamics of western Arctic bowhead whales (*Balaena mysticetus*). Can. J. Fish. Aquat. Sci. 41:484–496.

_____ and E. D. Mitchell. 1983. Estimated initial population size of the Bering Sea stock of bowhead whales (*Balaena mysticetus*) from logbook and other catch data. Rep. Int. Whal. Comm., Spec. Iss. 5:147–151.

Brueggeman, J. J. 1982. Early spring distribution of bowhead whales in the Bering Sea. J. Wildl. Manage. 46:1036–1044.

Buck, J. D., L. L. Shepard, and S. Spotte. 1987. *Clostridium perfringens* as the cause of death of a captive Atlantic bottlenosed dolphin (*Tursiops truncatus*). J. Wildl. Dis. 23:488–491.

Campbell, R. R. 1990. Rare and endangered fishes and marine mammals of Canada: COSEWIC fish and marine mammal subcommittee status reports: VI. Can. Field-Nat. 104:1–6.

Carroll, G. M., J. C. George, L. F. Lowry, and K. O. Coyle. 1987. Bowhead whale (*Balaena mysticetus*) feeding near Point Barrow, Alaska, during the 1985 spring migration. Arctic 40:105–110.

Chapman, D. G. 1984. Estimates of net recruitment of Alaska bowhead whales and of risk associated with various levels of kill. Rep. Int. Whal. Comm. 34:469–471.

Clarke, J. T., S. E. Moore, and D. K. Ljungblad. 1987. Observations of bowhead whales (*Balaena mysticetus*) calves in the Alaskan Beaufort Sea during the autumn migration, 1982–85. Rep. Int. Whal. Comm. 37:287–293.

Cubbage, J. C., and J. Calambokidis. 1987. Size-class segregation of bowhead whales discerned through aerial stereophotogrammetry. Mar. Mamm. Sci. 3:179–185.

Davis, R., and W. Koski. 1980. Recent observations of the bowhead whale in the eastern Canadian high Arctic. Rep. Int. Whal. Comm. 30:439–444.

de Jong, C. 1983. The hunt of the Greenland whale: a short history and statistical sources. Rep. Int. Whal. Comm., Spec. Iss. 5:83–106.

de Korte, J., and S. E. Belikov. 1994. Observations of Greenland whales (*Balaena mysticetus*), Zemlya Frantsa-losifa. Polar Rec. 30(173):135–136.

Dow, G. F. 1967. Whale ships and whaling; a pictorial history of whaling during three centuries. Argosy Antiquarian Ltd., N.Y., 446 p.

Eschricht, D. F., and J. Reinhardt. 1866. On the Greenland right-whale (*Balaena mysticetus*, Linn.), with special reference to its geographic distribution and migrations in times past and present, and to its external and internal characteristics. *In* W. H. Flowers (Editor), Recent memoirs on the cetacea, p. 1–150. Ray Soc., Lond.

Fedoseev, G. A. 1984. [Encountering whales in the ice fields of the Sea of Okhotsk.] Ekologiya 3:81–83. [In Russ., partial transl. by S. Smrstik (NMML) for this review.]

Finley, K. J. 1990. Isabella Bay, Baffin Island: an important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the eastern Canadian Arctic. Arctic 43:137–152.

_____, G. W. Miller, M. Allard, R. A. Davis, and C. R. Evans. 1982. The belugas (*Delphinapterus leucas*) of northern Quebec: distribution, abundance, stock identity, catch history and management. Can. Tech. Rep. Fish. Aquat. Sci. 1123, 57 p.

Freeman, M. M. R., E. W. Wein, and D. F. Keith. 1992. Recovering rights: bowhead whales and Inuvialuit subsistence in the western Canadian Arctic. Can. Circumpolar Joint Fish. Manage. Committ., Stud. Whal. 2, 155 p.

George, J. C., L. M. Philo, R. Suydam, R. Tarpley, and T. F. Albert. 1992. Summary of the 1989 and 1990 subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos. Rep. Int. Whal. Comm. 42:479–483.

_____, _____, K. Hazard, D. Withrow, G. M. Carroll, and R. Suydam. 1994. Frequency of killer whale (*Orcinus orca*) attacks and ship collisions based on scarring on bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort seas stock. Arctic 47(3):247–255.

_____, R. S. Suydam, L. M. Philo, T. F. Albert, J. E. Zeh, and G. M. Carroll. 1995. Report of the spring 1993 census of bowhead

whales, *Balaena mysticetus*, off Point Barrow, Alaska, with observations on the 1993 subsistence hunt of bowhead whales by Alaska Eskimos. Rep. Int. Whal. Comm. 45:371–384.
_____ and R. J. Tarpley. 1986. Observations on the 1984 and 1985 subsistence harvest of bowhead whales, *Balaena mysticetus*, with a note on the fall 1983 harvest. Rep. Int. Whal. Comm. 36:339–342.
Hamilton, P. K., and C. A. Mayo. 1990. Population characteristics of right whales (*Eubalaena glacialis*) observed in Cape Cod and Massachusetts bays, 1978–1986. Rep. Int. Whal. Comm., Spec. Iss. 12:203–208.
Hazard, K. W., and J. C. Cubbage. 1982. Bowhead whale distribution in the southeastern Beaufort Sea and Amundsen Gulf, summer 1979. Arctic 35:519–523.
Heide-Jørgensen, M. P., and K. J. Finley. 1991. Photographic re-identification of a bowhead whale in Davis Strait. Arctic 44:254–256.
Heidel, J. R., and T. F. Albert. 1994. Intestinal volvulus in a bowhead whale, *Balaena mysticetus*. J. Wildl. Dis. 30:126–128.
IWC. 1988. Report of the Scientific Committee. Rep. Int. Whal. Comm. 38:32–154.
_____. 1992. Chairman's report of the forty-third annual meeting. Rep. Int. Whal. Comm. 42:11–50.
_____. 1995. Chairman's report of the forty-sixth annual meeting. Rep. Int. Whal. Comm. 45:15–52.
Jonsgård, A. 1981. Bowhead whales, *Balaena mysticetus*, observed in arctic waters of the eastern North Atlantic after the Second World War. Rep. Int. Whal. Comm. 31:511.
_____. 1982. Bowhead (*Balaena mysticetus*) surveys in Arctic northeast Atlantic waters in 1980. Rep. Int. Whal. Comm. 32:355–356.
Kapel, F. O. 1985. A note on the net-entanglement of a bowhead whale (*Balaena mysticetus*) in northwest Greenland, November 1980. Rep. Int. Whal. Comm 35:377–378.
Kibal'chich, A. A., G. A. Dzhamanov, and M. V. Ivashin. 1986. Records of bowhead and gray whales in the early winter in the Bering Sea. Rep. Int. Whal. Comm. 36:291–292.
Koski, W. R., R. A. Davis, G. W. Miller, and D. E. Withrow. 1992. Growth rates of bowhead whales as determined from low-level aerial photogrammetry. Rep. Int. Whal. Comm. 42:491–499.
_____, _____, _____, and _____. 1993. Reproduction. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 239–274. Soc. Mar. Mamm. Spec. Publ. 2.
Kraus, S. D., J. H. Prescott, A. R. Knowlton, and G. S. Stone. 1986. Migration and calving of right whales (*Eubalaena glacialis*) in the western North Atlantic. Rep. Int. Whal. Comm., Spec. Iss. 10:145–151.
Krupnik, I. I. 1987. The bowhead vs. the gray whale in Chukotkan aboriginal whaling. Arctic 40:16–32.
Ljungblad, D. K., S. E. Moore, and J. T. Clarke. 1986. Assessment of bowhead whale (*Balaena mysticetus*) feeding patterns in the Alaskan Beaufort and northeastern Chukchi Seas via aerial surveys, fall 1979–1984. Rep. Int. Whal. Comm. 36:265–272.
Lockyer, C. 1981. Growth and energy budgets of large baleen whales from the southern hemisphere. Food Agric. Organ. U. N., Fish. Ser. 5:379–484.
Lockyer, C. H. 1990. The importance of biological parameters in population assessments with special reference to fin whales from the N.E. Atlantic. *In* E. Vestergaard (Editor), North Atlantic studies: whaling communities, Vol. 2, p. 22–31. Aarhus Univ. Press, Denm., 217 p.
Low, A. P. 1906. Report on the Dominion Government Expedition to Hudson Bay and the Arctic islands on board the D.G.S. Neptune 1903–1904. Gov. Print. Bur., Ottawa, 355 p.
Lowry, L. F. 1993. Foods and feeding ecology. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 201–238. Soc. Mar. Mamm. Spec. Publ. 2.
_____ and K. J. Frost. 1984. Foods and feeding of bowhead whales in western and northern Alaska. Sci. Rep. Whales Res. Inst., Tokyo 35:1–16.
Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward re-evaluation of IUCN Threatened Species Categories. Conserv. Biol. 5:148–157.
Marquette, W. M., and J. R. Bockstoce. 1980. Historical shore-based catch of bowhead whales in the Bering, Chukchi, and Beaufort seas. Mar. Fish. Rev. 42(9–10):5–19.
McQuaid, C. D. 1986. Post–1980 sightings of bowhead whales (*Balaena mysticetus*) from the Spitsbergen stock. Mar. Mammal Sci. 2(4):316–318.
Mel'nikov, V. V., and A. V. Bobkov. 1993. Bowhead whale migration in the Chuckchee Sea. Russ. J. Mar. Biol. 19(3):180–185.
_____ and _____. 1994. On the bowhead whale migrations in the Chukchi Sea, 1991. Oceanology 33(5):643–647.
Migaki, G., and T. F. Albert. 1982. Lipoma of the liver in a bowhead whale (*Balaena mysticetus*). Vet. Pathol. 19:329–331.
Miller, G. W., R. A. Davis, W. R. Koski, M. J. Crone, D. J. Rugh, D. E. Withrow, and M. Fraker. 1992. Calving intervals of bowhead whales—an analysis. Rep. Int. Whal. Comm. 42:501–506.
Miller, R. V., D. J. Rugh, and J. H. Johnson. 1986. The distribution of bowhead whales, *Balaena mysticetus*, in the Chukchi Sea. Mar. Mammal Sci. 2:214–222.
Mitchell, E. D., and R. R. Reeves. 1982. Factors affecting abundance of bowhead whales *Balaena mysticetus* in the eastern Arctic of North America, 1915–1980. Biol. Conserv. 22:59–78.
Montague, J. J. 1993. Introduction. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 1–21. Soc. Mar. Mamm. Spec. Publ. 2.
Moore, S. E., J. T. Clarke, and D. K. Ljungblad. 1986. A comparison of gray whale (*Eschrichtius robustus*) and bowhead whale (*Balaena mysticetus*) distribution, abundance, habitat preference and behavior in the northeastern Chukchi Sea, 1982–84. Rep. Int. Whal. Comm. 36:273–279.
_____, J. C. George, K. O. Coyle, and T. J. Weingartner. 1995. Bowhead whales along the Chukotka coast in autumn. Arctic 48(2): 155–160.
_____ and R. R. Reeves. 1993. Distribution and movement. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 313–386. Soc. Mar. Mamm. Spec. Publ. 2.
Nerini, M. K., H. W. Braham, W. M. Marquette, and D. J. Rugh. 1984. Life history of the bowhead whale, *Balaena mysticetus* (Mammalia: Cetacea). J. Zool. (Lond.) 204:443–468.
Nicklin, F. 1995. Bowhead whales: leviathans of icy seas. Natl. Geogr. Mag. 188(2):114–129.
Nishiwaki, M., and T. Kasuya. 1970. A Greenland right whale caught at Osaka Bay. Sci. Rep. Whales Res. Inst., Tokyo 22:45–62.
Orr, J. R., B. Renooy, and L. Dahlke. 1986. Information from hunts and surveys of walrus (*Odobenus rosmarus*) in northern Foxe Basin, Northwest Territories, 1982–1984. Can. Manuscr. Rep. Fish. Aquat. Sci. 1899, 24 p.
Payne, R., V. Rountree, J. S. Perkins, J. G. Cooke, and K. Lankester. 1990. Population size, trends and reproductive parameters of the right whale (*Eubalaena glacialis*) off Peninsula Valdes, Argentina. Rep. Int. Whal. Comm., Spec. Iss. 12:271–278.
Philo, L. M., J. C. George, and T. F. Albert. 1992. Rope entanglement of bowhead whales (*Balaena mysticetus*). Mar. Mammal Sci. 8(3):306–311.
_____, E.B. Shotts and J. C. George. 1993. Morbidity and mortality. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 275–312. Soc. Mar. Mamm. Spec. Publ. 2.
Reeves, R. R. 1980. Spitsbergen bowhead stock: a short review. Mar. Fish. Rev. 42(9–10):65–69.
_____ and S. Leatherwood. 1985. Bowhead whale *Balaena mysticetus* Linnaeus, 1758. *In* S. H. Ridgway and R. Harrison (Editors), Handbook of marine mammals, Vol. 3, p. 305–344. The sirenians and baleen whales, Acad. Press, N.Y.
_____ and E. Mitchell. 1987. History of white whale *(Delphinapterus leucas)* exploitation in eastern Hudson Bay and James Bay. Can. Spec. Publ. Fish. Aquat. Sci. 95, 45 p.
_____ and _____. 1990. Bowhead whales in Hudson Bay, Hudson Strait, and Foxe Basin: a review. Nat. Can. 117:25–43.
_____, _____, A. Mansfield, and M. McLaughlin. 1983. Distribution and migration of the bowhead whale, *Balaena mysticetus*, in the eastern North American Arctic. Arctic 36:5–64.
Richardson, W. J., R. A. Davis, C. R. Evans, D. K. Ljungblad, and P. Norton. 1987. Summer distribution of bowhead whales, *Balaena mysticetus*, relative to oil industry activities in the Canadian Beaufort Sea, 1980–84. Arctic 40(2):93–104.
_____, K. J. Finley, G. W. Miller, R. A. Davis, and W. R. Koski. 1995. Feeding, social and migration behavior of bowhead whales, *Balaena mysticetus*, in Baffin Bay vs. the Beaufort Sea--regions with different amounts of human activity. Mar. Mammal Sci. 11(1):1–45.
_____ and C. I. Malme. 1993. Man-made noise and behavioral response. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 631–700. Soc. Mar. Mamm. Spec. Publ. 2.
Rohlf, D. J. 1994. Pacific salmon: There's something fishy going on here: A critique of the National Marine Fisheries Service's definition of species under the Endangered Species Act. Environ. Law 24(2):617–671.
Ross, W. G. 1975. Whaling and Eskimos: Hudson Bay 1860–1915. Natl. Mus. Man, Ottawa, Publ. Ethnol. 10, 164 p.
_____. 1993. Commercial whaling in the North Atlantic sector. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 511–561. Soc. Mar. Mamm. Spec. Publ. 2.
Rugh, D. 1990. Bowhead whales reidentified through aerial photography near Point Barrow, Alaska. Rep. Int. Whal. Comm., Spec. Iss. 12:289–294.
_____, G. Miller, D. Withrow, and W. Koski. 1992. Calving intervals of bowhead whales established through photographic identifications. J. Mamm. 73(3):487–490.

Ruud, J. T. 1937. Grønlandshvalen, *Balaena mysticetus* (Linné). Norsk Hvalfangst-tidende 26:254–270 [transl. by W. B. McAlister (1978), 12 p.]

Scammon, C. M. 1874. The marine mammals of the north-western coast of North America, described and illustrated, together with an account of the American whale-fishery. J. H. Carmany and Co., San Francisco, 319 p. [Repr. by Dover Publ. Inc., N.Y., 1968.]

Schell, D. M., and S. M. Saupe. 1993. Feeding and growth as indicated by stable isotopes. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 491–509. Soc. Mar. Mamm. Spec. Publ. 2.

_____, _____, and N. Haubenstock. 1989. Bowhead whale (*Balaena mysticetus*) growth and feeding as estimated by $\delta^{13}C$ techniques. Mar. Biol. 103:433–443.

Scoresby, W. 1820. An account of the Arctic regions, with a history and description of the northern whale-fishery. Archibald Constable Co., Edinb., Vol. 1, 551 p.; Vol. 2, 524 p. [Repr. by David and Charles Repr., Newton Abbot, Devon, 1969.]

Shotts, E. B., T. F. Albert, R. E. Wooley, and J. Brown. 1990. Microflora associated with the skin of the bowhead whale (*Balaena mysticetus*). J. Wildl. Dis. 26:351–359.

Sigurjónsson, J. 1985. Sightings survey in the Irminger Sea and off Iceland in 1983. Rep. Int. Whal. Comm. 35:499–503.

_____, T. Gunnlaugsson, and G. Vikingsson. 1988. Iceland, progress report on cetacean research, June 1986 to May 1987. Rep. Int. Whal. Comm. 38:190–194.

Smith, A. W., D. E. Skilling, J. E. Barlough, and E. S. Berry. 1986. Distribution in the North Pacific Ocean, Bering Sea and Arctic Ocean of animal populations known to carry pathogenic caliciviruses. Dis. Aquat. Org. 2:73–80.

_____, _____, K. Benirschke, T. F. Albert, and J. E. Barlough. 1987. Serology and virology of the bowhead whale (*Balaena mysticetus*). J. Wildl. Dis. 23:92–98.

Sonntag, R. M., and G. C. Broadhead. 1989. Documentation for revised bowhead whale catch data (1948–1987). Appendix 4 of Annex G (Report of the sub-committee on protected species and aboriginal subsistence whaling). Report of the Scientific Committee. Rep. Int. Whal. Comm. 39:114.

Southwell, T. 1898. The migration of the right whale (*Balaena mysticetus*). Part I. In the Greenland waters. Nat. Sci. 12(76):397–414.

Stoker, S. W., and I. I. Krupnik. 1993. Subsistence whaling. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 579–629. Soc. Mar. Mamm. Spec. Publ. 2.

Suydam, R. S., R. P. Angliss, J. C. George, S. R. Braund, and D. P. DeMaster. 1995. Revised data on the subsistence harvest of bowhead whales (*Balaena mysticetus*) by Alaskan Eskimos, 1973–1993. Rep. Int. Whal. Comm. 45:335–338.

Tomilin, A. G. 1957. Mammals of the U.S.S.R. and adjacent countries. Volume 9. Cetacea. Transl. by Isr. Program Sci. Transl., Jerusalem, 1967, NTIS No. TT-65-50086, 717 p.

Townsend, C. H. 1935. The distribution of certain whales as shown by logbook records of American whaleships. Zoologica 19(1):1–50.

Turl, C. W. 1987. Winter sightings of marine mammals in arctic pack ice. Arctic 40:219–220.

Vladimirov, V. L. 1994. Recent distribution and abundance levels of whales in Russian far-eastern seas. Russ. J. Mar. Biol. 20(1):1–9.

Withrow, D. and R. Angliss. 1992. Length frequency of bowhead whales from spring aerial photgrammetric surveys in 1985, 1986, 1989 and 1990. Rep. Int. Whal. Comm. 42:463–7.

_____ and _____. 1994. Length frequency of the bowhead whale population from 1991 and 1992 spring aerial photgrammetric surveys. Rep. Int. Whal. Comm. 44:343–6.

Woodby, D. A., and D. B. Botkin. 1993. Stock sizes prior to commercial whaling. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 387–407. Soc. Mar. Mamm. Spec. Publ. 2.

Würsig, B., E. M. Dorsey, M. A. Fraker, R. S. Payne, and W. J. Richardson. 1985. Behavior of bowhead whales, *Balaena mysticetus*, summering in the Beaufort Sea: a description. Fish. Bull. 83(3):357–377.

_____, _____, W. J. Richardson, and R. S. Wells. 1989. Feeding, aerial and play behaviour of the bowhead whale, *Balaena mysticetus*, summering in the Beaufort Sea. Aquat. Mamm. 15(1):27–37.

Zeh, J. E., C. W. Clark, J. C. George, D. Withrow, G. M. Carroll, and W. R. Koski. 1993. Current population size and dynamics. *In* J. J. Burns, J. J. Montague, and C. J. Cowles (Editors), The bowhead whale, p. 409–489. Soc. Mar. Mamm. Spec. Publ. 2.

_____, J. C. George, and R. Suydam. 1995. Population size and rate of increase, 1978–1993, of bowhead whales, *Balaena mysticetus*. Rep. Int. Whal. Comm. 45:339–344.

Zorgdrager, C. G. 1720. Bloeyende opkomst der aloude en hedendaagsche Groenlandsche visschery [Development of the old and contemporary Greenland fishery]. P. van Thol and R. C. Alberts, Amst., 330 p.