Whales and Whaling in the North Pacific Ocean and Bering Sea

Oceanographic Insights and Ecosystem Impacts

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It is not clear whether or not there are enough fin whales in the North Pacific to allow the continuation of operations on such a scale. It may be wise to take measures to prevent any abrupt expansion of whaling operations. The situation should be watched closely from the viewpoint of the conservation of whale stocks.

OMURA (1955)

Hideo Omura's concern over the killing of fin whales in the early 1950s, just a few years after the resumption of whaling following World War II, foreshadowed the demise of most of the remaining great whales in the following two decades as the slaughter expanded across the North Pacific (Springer et al. 2003). His concern was warranted because of the development of an unprecedented human capability for large-scale harvests of even the fastest whales using high-speed catcher boats and mechanized factory ships designed specifically for this purpose. In 1955, the nominal harvest of fin whales was about 2,100, and it doubled over the next 10 years to a peak of some 4,000 in 1965 before declining through 1975 when the harvest was ended. Other species were similarly exploited and depleted until pelagic hunting was successively halted for humpback and blue whales in 1965, for sei whales in 1975, and for sperm and Bryde's whales in 1979. Populations of most species were severely depleted by the mid-1980s (Stewart et al. 1987; Rice and Wolman 1982). Exceptions were humpback whales in the northeastern Pacific, which had begun to recover slowly after protection was enacted in 1965 (Calambokidis et al. 2001), and bowhead whales and gray whales that had been ravaged 100 years earlier (Raferty et al. 1995; Rugh et al. 1999).

Reports of larger numbers of some species in the southeastern Bering Sea in the late 1980s in comparison with the mid- to late 1970s (Baretta and Hunt 1994) are difficult to interpret because changes in distribution rather than abundance could explain the difference in numbers between decades (Tynan 2004). Fin whales were possibly showing signs of slow recovery by the late 1990s in the northern Gulf of Alaska and Bering Sea, although sperm whales remained scarce (Moore et al. 2000; Tynan 2004).

While the rapid depletion of great whales in the North Pacific during the postwar decades was catastrophic to each species, an important ancillary issue is whether the removal of great whales had significant community-level effects (National Research Council 1996; Trites et al. 1999; Springer et al. 2003). Did the removal of megatons of upper-trophic-level consumers significantly alter food-web dynamics by (1) removing significant levels of predatory controls over prey populations, (2) removing an important prey resource for predator populations (i.e., killer whales), and (3) changing the sensitivity of the ecosystem to physical forcing because of new predator-prey functional relationships?

In order to address these questions, it is necessary to understand where and when whales were harvested in the North Pacific Ocean, and how this ultimately affected whale distribution. Whales were not uniformly distributed across this broad region, and the roles they played were concentrated in relatively small areas. Here we show where great whales formerly were found in abundance in the North Pacific, relate those distributions to oceanography, and briefly explore some examples of the magnitude of change that might have resulted from the loss of great whales in the Aleutian Islands and Bering Sea.

Data Sources and Caveats

The geographic focus of the following accounts of whales and whaling is primarily the northern and eastern North Pacific Ocean and the Bering Sea. We do not include information from the western North Pacific or its marginal seas, except for the Japanese shore-based fishery and the region including the Kurile Islands, western Aleutian Archipelago, and eastern Kamchatka Peninsula. Information on whale harvests in the 1800s and first half of the 1900s was taken from various published documents cited in appropriate locations throughout this chapter. We have plotted these data along with harvest data compiled by the International Whaling Commission (IWC) for all series where they exist. In some analyses, we have excluded information provided by the former Soviet Union (USSR), as it is known that they falsified data on the number of whales harvested, the species composition of their catches, and the locations of catches (Brownell et al. 2000a; R.L. Brownell, personal communication). The USSR data are included in the figures of harvest time series for comparative purposes, because although the USSR data were underreported and misrepresented in some cases, a better sense of the magnitude of the total harvest is achieved when these data are included than when they are excluded. Most harvest location data submitted by Japan for the pelagic harvest were reported at a resolution of 1° latitude by 2° longitude and are considered to be accurate in terms of numbers, locations, and species compositions (R.L. Brownell, personal communication).

The maps of whale distributions used in the following sections show where whales were harvested by shore-based and pelagic fisheries (excluding USSR data) since 1946. The maps thus reflect the principal summer foraging grounds of those species in the northern North Pacific, except that many of the whales taken in Japanese and Canadian coastal waters by the shore-based fisheries were actually migrating to more northerly feeding grounds (Gregr et al. 2000; Kasuya and Miyashita 1988; Nishiwaki 1966). The maps do not show the full summer range of any species, as hunting was focused on areas of greatest concentration. For example, in 1941 Japanese whalers prospected in the Chukchi Sea and killed 74 fin whales and 101 humpback whales along the Chukotka coast (Nemoto 1959), but these whales are not included in the data from which the maps were drawn. Also, because Soviet data have been excluded, harvests, and thus distributions, in the Sea of Okhotsk are poorly rendered.

Additional bias was introduced by the assignment of harvest quotas by the IWC. For example, humpback whales were apparently much more numerous in the Aleutian Islands than harvest data indicate, as the small allotment for humpbacks made it unprofitable to pursue them there (Nishiwaki 1966). The same can be said for sei whales, at least through the early 1960s; they were more abundant in the Aleutian Archipelago than it appears from harvest data.

History of Whaling in the North Pacific

Nineteenth Century

Intense commercial whaling in the northern North Pacific began in the early 1840s with the discovery of right whaling grounds in the Gulf of Alaska and off the Kamchatka Peninsula and Kurile Islands. The number of American whaling ships operating north of 50° N increased rapidly from just a few in 1840 to 108 by 1843, 292 in 1846, and 300–400 off the Kodiak Grounds between 1846 and 1851 (Scarff 1991; Gilmore 1978). In the first 10 years, between 1840 and 1850, some 11,000 right whales were taken by the fleet (Figure 19.1). Only about 3,000 were taken in the second decade from 1850 to 1860, reflecting both the depletion of the stock and the discovery of bowheads in the northern Bering Sea.

Whaling for bowheads grew equally rapidly, from one ship in the Bering Strait in 1848, to 50 in 1849, and 220 in 1852 (Bockstoce and Botkin 1983). The first few years of the fishery proved to be disastrous for bowheads, as it had for right whales, with a third of the total pelagic catch taken by 1852 and half by 1865 (Figure 19.1). The population plummeted from about 18,000 to about 3,000 by the end of the century (Woodby and Botkin 1993).

Shortly after the initial slaughter of right and bowhead whales in the northern North Pacific, gray whale calving grounds in Baja California were discovered and a commercial harvest began there (Scammon 1874). Nearly 6,600 gray whales were killed during the peak years, 1855–1870 (Figure 19.1). The population in 1846 was estimated to have been about 12,000, down from an historical high of about 24,000 because of an aboriginal take of around 600 y^{-1} just prior to the 1800s (Reilly 1981). By the 1880s the population had collapsed to about 2,000.

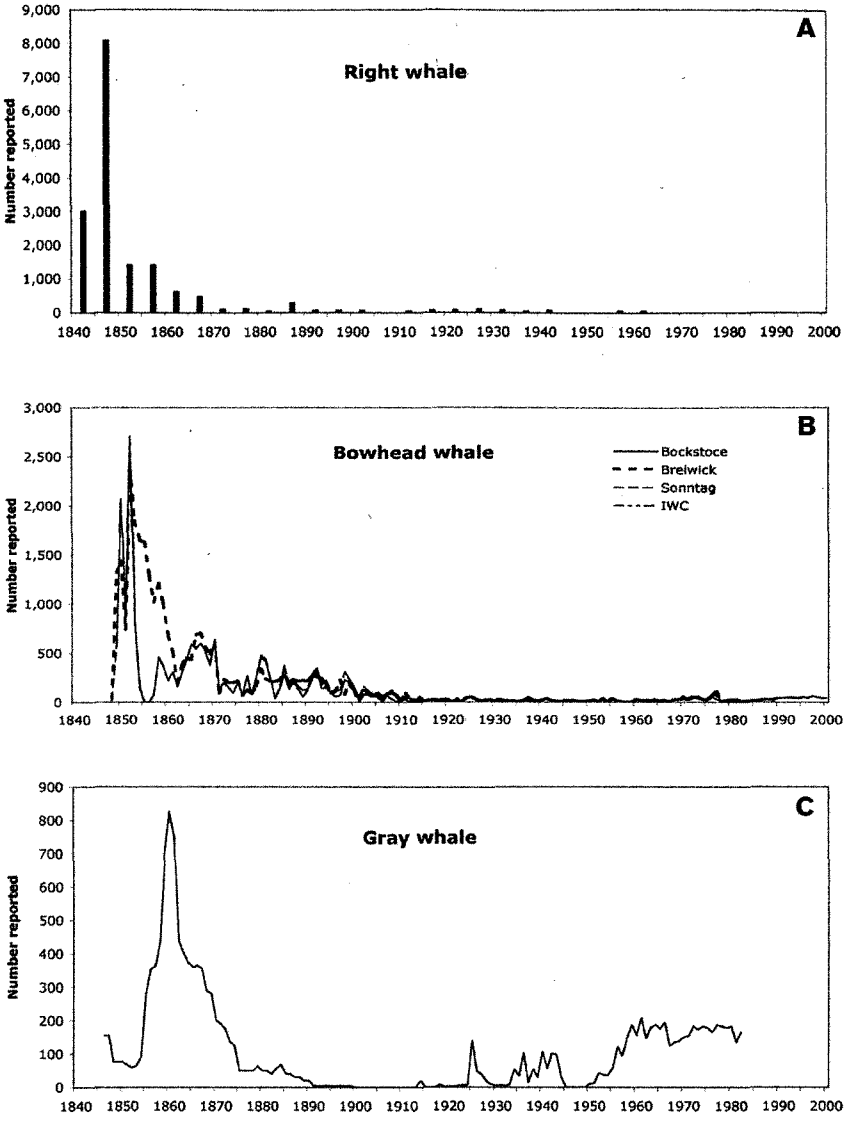

FIGURE 19.1. Annual harvests of right, bowhead, and gray whales in the North Pacific. Data from Bockstoce and Botkin (1983), Breiwick et al. (1981), Sonntag and Broadhead (1989), Best (1987), Reilly (1981), and IWC (All nations; unpublished data). Harvests of right whales compiled by 5-year intervals.

Twentieth Century Prior to World War II

Whaling in the first half of the twentieth century continued to be episodic by region and time. Modern whaling using catcher boats with mounted harpoon cannons began in Korea in 1889, in Japan in 1899, and in British Columbia and southeastern Alaska in 1905 and 1907 (Rice 1978). By the early 1900s, Japan had a flourishing coastal fishery, taking as many as 1,000 fin whales, 700 sei whales, and 250 blue whales each year. The fin whale harvest was excessive, and the population fell by an estimated 35% in just the eight years between 1910 and 1917 (Ohsumi et al. 1971). Likewise, the take of blue whales fell rapidly between 1910 and 1920 as the stock declined. The sei whale population was able to accommodate the harvest and changed little until after World War II. Right whales were afforded worldwide protection in 1935, but continued illegal hunting, particularly by the Soviet Union, after 1949 and through the early 1960s drove them nearly to extinction (Rice 1974; Wada 1979; Gambell 1976; Brownell et al. 2001).

Whalers in the eastern North Pacific in the early 1900s were hunting primarily humpback whales, which were abundant along the coast from Washington to southeastern Alaska (Figure 19.2). Catch statistics for earlier years are not available, but it has been estimated that 4,000–5,000 humpbacks were killed in Alaska and British Columbia between 1905 and 1910 (Rice 1978). Between 1920 and 1930 attention shifted south to humpbacks off Baja California and California, where during that time nearly 4,000 were killed. By 1930

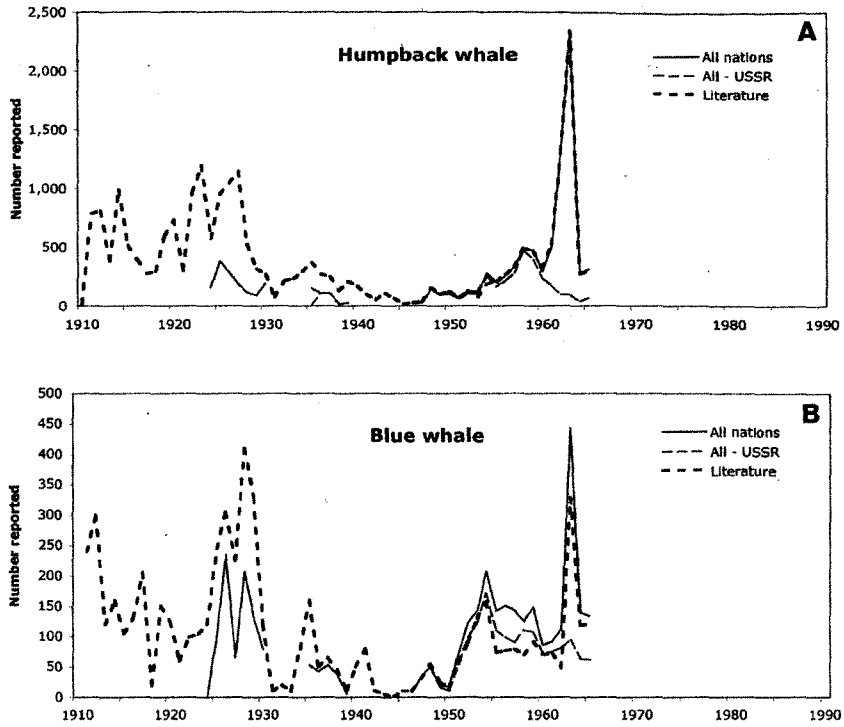

FIGURE 19.2. Annual harvests of humpback and blue whales in the North Pacific. Data from Omura (1955), Rice (1978), and IWC (All nations and All minus USSR; unpublished data).

some 18,000 humpbacks had been killed in the North Pacific, and the population had fallen from an estimated 15,000 to about 6,000 (Rice 1978).

The blue whale population in the North Pacific was historically small, and few were taken in the eastern North Pacific until the mid-1920s, when the animals congregating off Baja California in spring were targeted (Figure 19.2). The combined harvest of blue whales off Baja California and from the northern summering grounds during 1925–1930 was approximately 1,600.

POSTWAR WHALING AND THE END OF AN ERA

With the end of World War II, Japanese and Soviet pelagic whaling expanded in the North Pacific. Intensive hunting of sperm whales to the east of Kamchatka and around the Commander Islands began in 1954. Harvests increased rapidly in the years following the conversion of the Japanese fleet from solid fuel to liquid fuel in 1957. By 1963 there were three Japanese and four Russian fleets operating regularly (Rice 1978).

Humpback and blue whales were harvested heavily in Alaska in the early 1960s just prior to protection. The numbers of fin, sei, and sperm whales taken each year grew rapidly to peak levels in the middle to late 1960s (Figures 19.3 and 19.4). Bryde's whales were not hunted until the 1970s, following the depletion of larger whales in more northern waters (Figure 19.3). Pelagic fleets did not target the small minke whales; only about 12,000 were reported killed by all nations during the period 1947–1987, primarily (about 10,500) by the Japanese shore-based fishery. Other species of whales were taken incidentally between 1947 and 1987, including Baird's beaked whale (618 reported, all nations), Cuvier's beaked whale (2 reported, all nations), pilot whales (482 reported, all nations), and killer whales (319 reported, all nations).

The abrupt, intense harvest of the larger whales beginning in the early 1950s reduced to very small numbers species already depleted before the war. By 1965, when humpback and blue whales were given protection, there were approximately 1,000–1,500 of each remaining (Rice 1978, Mizroch et al. 1984). For other species with much larger initial populations—the fin, sei, and sperm whales—estimates of abundance before and after the slaughter are less reliable.

There is little doubt, however, that the overall abundance of most species declined dramatically, particularly on the northern grounds (Cook 1985; Ohsumi et al. 1971; Ohsumi 1980; Kasuya 1991). By the end of the 1950s, for example, there was a pronounced shift in size of male sperm whales taken in the Bering Sea, to smaller (younger) animals, which forewarned of the collapse of the stock (Berzin 1964). Although sperm whales were not protected until 1979, hunting of them in the Bering Sea ended in 1972 because they were so scarce (Kasuya 1991). A whale census in the northern Gulf of Alaska in summer 1980 concluded that all species of great whales were severely depleted—in an area of approximately 2.2×10^5 km^2, which formerly supported thousands

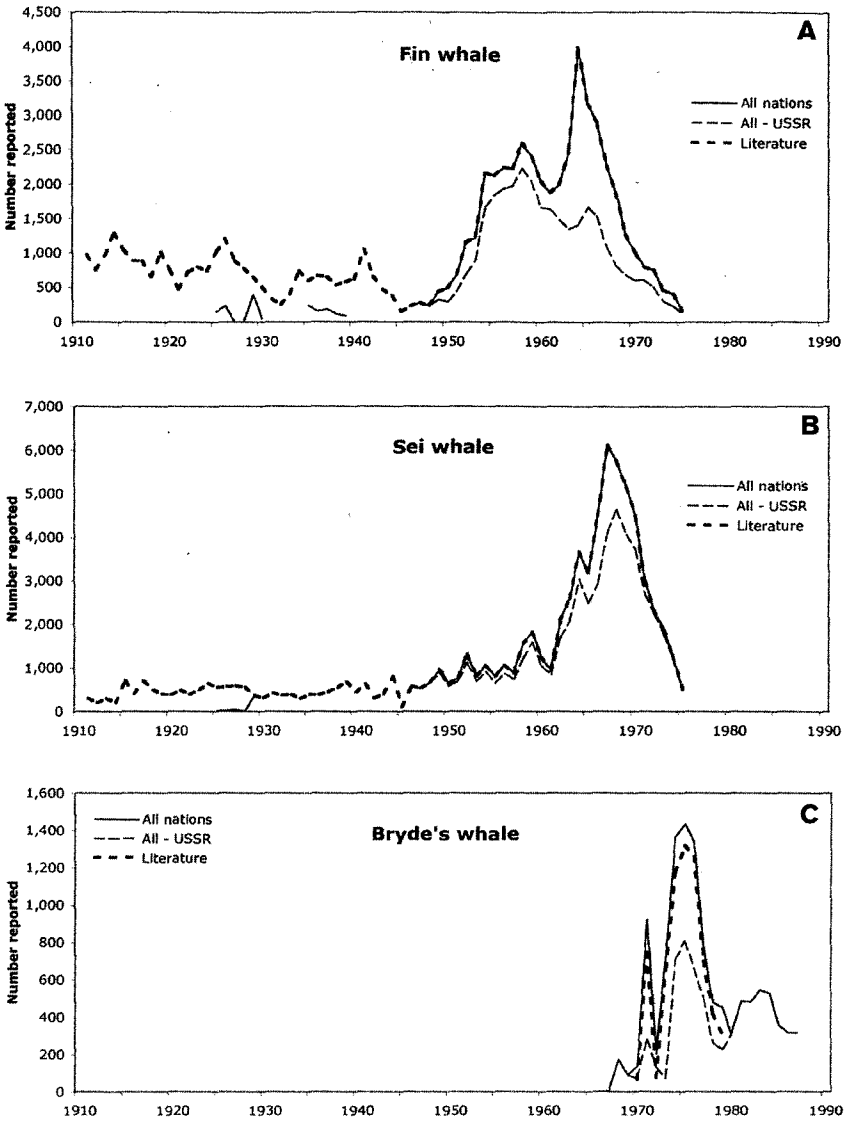

FIGURE 19.3. Annual harvests of fin, sei, and Bryde's whales in the North Pacific. Data from Omura (1955), Ohsumi et al. (1971), IWS (1930, 1937, 1948), and IWC (All nations and All minus USSR; unpublished data).

of whales, population estimates were fin, 159; humpback, 364; sperm, blue, sei, and right, few (only 36 sperm whales and none of the other species were sighted) (Rice and Wolman 1982).

Whales and Oceanography

Years ago, numerous scientists produced maps of summer distributions of whales in the North Pacific and described the patterns in relation to habitat and ocean productivity (Nasu 1966; Nemoto 1959, 1963; Nishiwaki 1966; Omura 1955; Uda 1962). We repeat that approach here, and we improve on their excellent earlier work only by broadening the horizon with locations of large numbers of whales killed in the 1960s and 1970s and with some additional insights gained from the great amount of information on oceanography obtained since those earlier studies.

Right Whales

Right whales summered in the Sea of Okhotsk south to Japan and the East China Sea, in the southeastern Bering Sea, and in the northern Gulf of Alaska south to British Columbia (Townsend 1935; Omura et al. 1969; Braham and Rice 1984; Clapham et al. 2004). In the northeastern North Pacific they were concentrated on the southeastern Bering Sea outer shelf and slope and along the shelf edge in the western Gulf of Alaska from Kodiak Island to the eastern Aleutian Islands. Today the remnant population is known to occur only in the middle shelf domain of the eastern Bering Sea, as far north

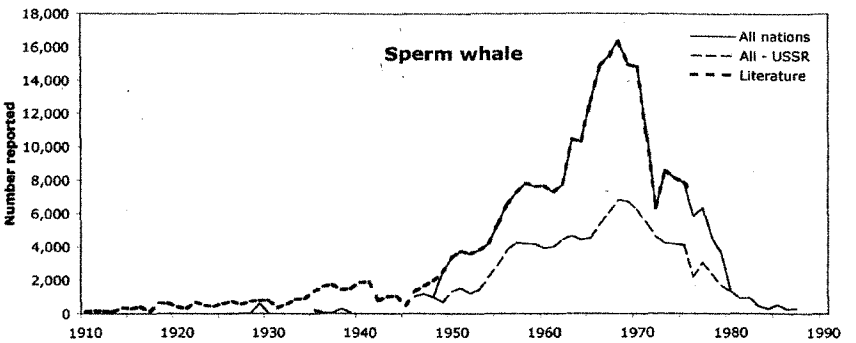

FIGURE 19.4. Annual harvests of sperm whales in the North Pacific. Data from Ohsumi (1980) and IWC (All nations and All minus USSR; unpublished data).

as St. Matthew Island (J. F. Piatt, unpublished data), where they number in the tens of individuals (Goddard and Rugh 1998; Tynan et al. 2001).

Historically, the diets of right whales consisted primarily of the copepods *Neocalanus cristatus* and *N. plumchrus*, as indicated by a small sample of whales taken during the 1950s–1970s (Nemoto and Kawamura 1977, cited in Kawamura 1980; Omura et al. 1969). These are the dominant species of copepods in the oceanic and outer shelf regions (Cooney 1981). Right whales also are known to have fed occasionally on larvae of *Euphausia pacifica*, and possibly other species of euphausiids. Recently, right whales on the middle shelf of the eastern Bering Sea are thought to be feeding on *Calanus marshallae* (Tynan et al. 2001), the large calanoid that replaced oceanic *N. cristatus* and *N. plumchrus* on the shelf (Cooney 1981). The whales may now also be feeding on euphausiids, which are abundant there (Cooney 1981; Smith and Vidal 1984).

Tynan et al. (2001) believe the present distribution of right whales on the eastern Bering Sea middle shelf is toward the periphery of their former feeding grounds, perhaps because of a change in the productivity of the different regions. They note that the abundance of *C. marshallae* in the middle shelf in the late 1990s was much higher than in the 1980s. An alternative hypothesis is that these particular animals exist where they always have, at the fringe of their range, which served as a refuge for them during the whaling days. Even in the 1980s and early 1990s right whales apparently were relatively abundant in the inner shelf domain near Bristol Bay (Vladimirov 1994). A similar situation developed with bowhead whales, where today they summer primarily only in regions where they found refuge during their era of exploitation—the ice-covered waters of the Beaufort and Chuckchi Seas, inaccessible to whaling ships.

Bowhead Whales

The historic summer range of bowheads includes the Bering, Ohkotsk, Chukchi, and Beaufort Seas (Townsend 1935; Bockstoce and Botkin 1983; Braham 1984a). In the Bering Sea, they formerly summered off Cape Navarin, south along the edge of the Kamchatka shelf in the Kamchatka Current, and north across the shallow Bering-Chukchi shelf. Today nearly all bowheads in the western Arctic still summer in the Chukchi and Beaufort seas, their refuge from whaling.

Diets of bowhead whales in the Bering Sea are not known. Contemporary diet samples have come mostly from Barrow, Alaska, in the western Beaufort Sea, and have contained approximately equal amounts of copepods and euphausiids and insignificant amounts of mysids and other invertebrates. Farther east in the Beaufort Sea at Kaktovik, Alaska, copepods contribute somewhat more, and euphausiids somewhat less, to diets (Lowry 1993, Lowry et al. 2004).

Considering the former distribution of bowheads in the northern and western Bering Sea relative to the distribution and biomass of zooplankton, it is likely that diets there consisted primarily of copepods and euphausiids as well. Bowheads lived in the Anadyr Current, the northern branch of the Bering Sea Green Belt (Springer et al. 1996), and in the headwaters of the Kamchatka Current that carries the Green Belt around the western side of the Bering Sea. Both currents originate at depth along the shelf break in the northwestern Bering Sea (Coachman et al. 1975), and the Anadyr Current transports vast amounts of nutrients and zooplankton biomass across the shallow Bering-Chukchi shelf, transforming it into one of the most highly productive marine pelagic regions in the world (Springer et al. 1989; Springer and McRoy 1993).

Gray Whales

The eastern North Pacific (ENP) stock of gray whales summers primarily in the northern Bering Sea and Chukchi Sea (Braham 1984b; Omura 1984; Rice et al. 1984). The remaining small population of western gray whales summers in the northern Sea of Okhotsk, mainly off the northwestern coast of Sakhalin Island (Rice et al. 1984; Weller et al. 1999).

ENP gray whales feed for the most part on the northern Bering-Chukchi continental shelf on benthic invertebrates, primarily ampeliscid amphipods (review by Nerini 1984;

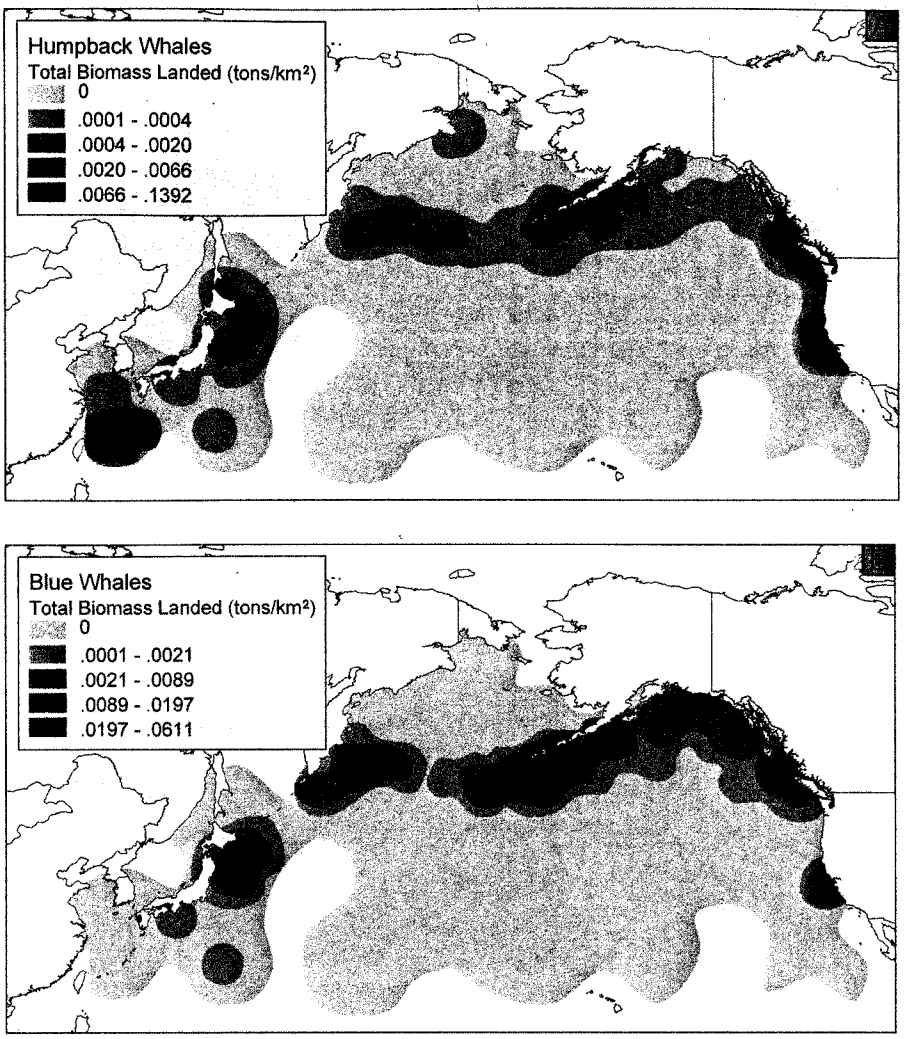

FIGURE 19.5. Summer distribution of humpback and blue whales in the North Pacific. May–September harvest locations after 1947 reported to the IWC (unpublished data) by all nations except the USSR.

Highsmith et al., Chapter 23 in this volume). Productivity of amphipods and other benthic invertebrates is extremely high in this region for the same reasons that pelagic production is high—the Anadyr Current. Nutrients supplied in the flow lead to annual primary production in the order of 500 g C m^{-2} y^{-1} (Springer and McRoy 1993), most of which falls to the sea floor and fuels the prolific benthic communities (Grebmeier et al. 1988). Although gray whales were decimated on their wintering grounds in Baja California, their loss from the Bering-Chukchi shelf undoubtedly altered benthic community structure and productivity.

Humpback Whales

Humpbacks are distributed widely in the North Pacific (Johnson and Wolman 1984). After World War II, most were killed in the eastern North Pacific (Figure 19.5). As noted previously, they were more abundant in the Aleutian Islands, as well as in the Bering Sea, than harvest records indicate. Indeed, humpbacks were, and again are, numerous in the Bering and Chukchi Seas (Moore et al. 2000; Nemoto 1959; Sleptsov 1961; Tynan 2004; Votrogov and Ivashin 1980).

Humpback whales eat a mixture of fish and euphausiids. Copepods do not appear to be important in their diet. They require dense concentrations of prey and commonly feed on schooling species of forage fishes, such as capelin, sand lance, herring, Atka mackerel, and cods, as well as on dense swarms of euphausiids (Nemoto 1959; Piatt and Methven 1992).

Because of their prey preferences, humpbacks feed closer to shore than most of the other great whales. They are presently the most abundant species of large whale in the inshore waters of the Gulf of Alaska and eastern Bering Sea.

Blue Whales

Blue whales are found around the rim of the North Pacific from Japan to California (Mizroch et al. 1984). In summer they concentrated along the edge of the continental shelf

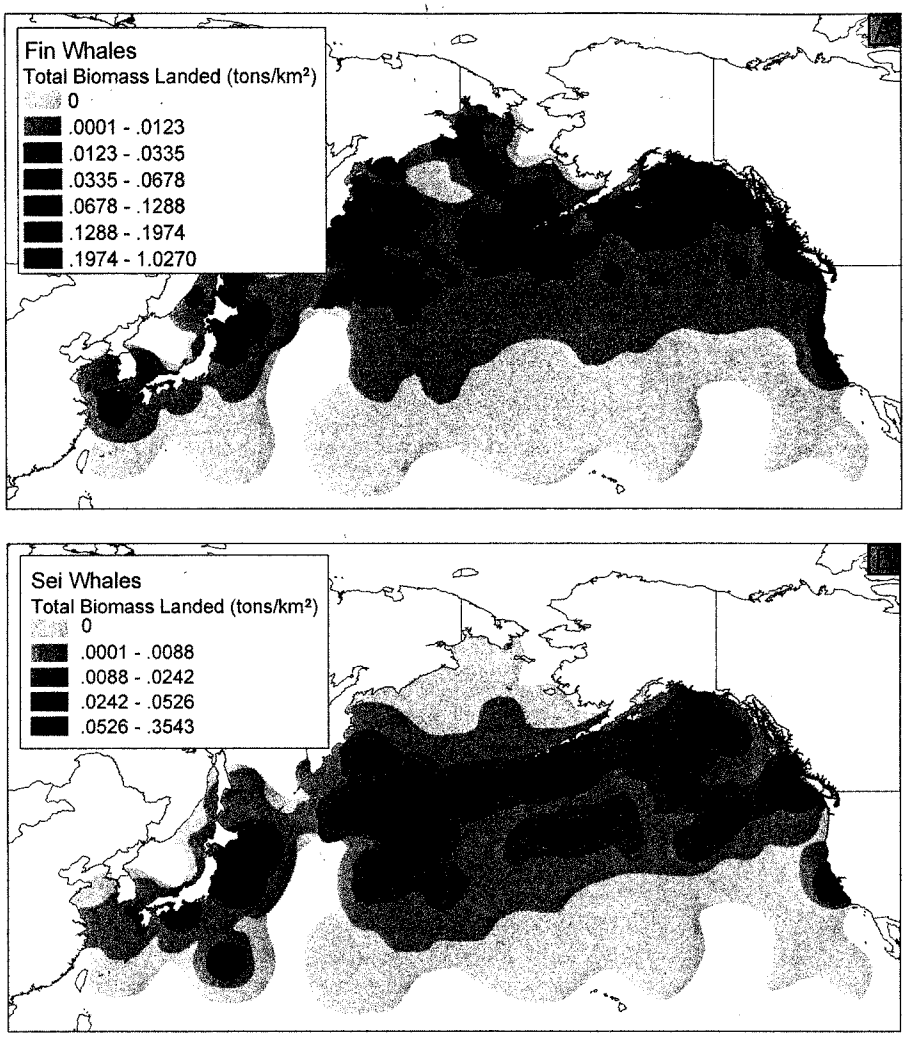

FIGURE 19.6. Summer distribution of fin, sei, and Bryde's whales in the North Pacific. May–September harvest locations after 1947 reported to the IWC (unpublished data) by all nations except the USSR.

from California to the Gulf of Alaska and along the south side of the Aleutian Archipelago (Figure 19.5). They penetrated into the Bering Sea in small numbers, and a few even ventured into the western Chukchi Sea (Sleptsov 1961), undoubtedly following the plume of the Anadyr Current northward.

Blue whales feed nearly exclusively on euphausiids in the North Pacific (Nemoto 1959; Kawamura 1980).

Fin Whales

Fin whales were very widely distributed in summer but were concentrated on their feeding grounds in a small part of the overall range (Figure 19.6). Most were found in particular locations around the rim of the North Pacific from California to Japan, including the Pacific Northwest (Washington-British Columbia), where a distinct subpopulation was exploited (Gregr et al. 2000). Also exploited in this region were whales migrating to more northern feeding grounds along the outer shelf and slope of the southeastern Bering Sea and shelf edge to the northwest, where the greatest densities of fin whales in the North Pacific occurred, and in the northwestern North Pacific south of the Aleutian Islands. Fin whales ranged into the western Chukchi Sea in substantial numbers that are not apparent in the Japanese harvest data, as noted previously. The northern distribution can be seen in the Soviet harvest data, and it has been reported by Nemoto (1959) and Sleptsov (1961).

The diet of fin whales was geographically diverse in the North Pacific (Kawamura 1980, 1982; Nemoto 1959; Nemoto and Kasuya 1965). A variety of euphausiid species provided perhaps the bulk of the diet overall. However, Nemoto (1963) saw a strong correlation between the main distribution of fin whales on their southeastern Bering Sea feeding grounds and the main concentrations of *Neocalanus cristatus*. Along the shelf edge to the northwest and in the western Bering Sea, fishes replaced zooplankton as the dominant part of the diet. Different species dominated in different areas: pollock along the shelf edge, capelin downstream off Cape Navarin and in the Gulf of Anadyr, and herring along the shelf edge southwest

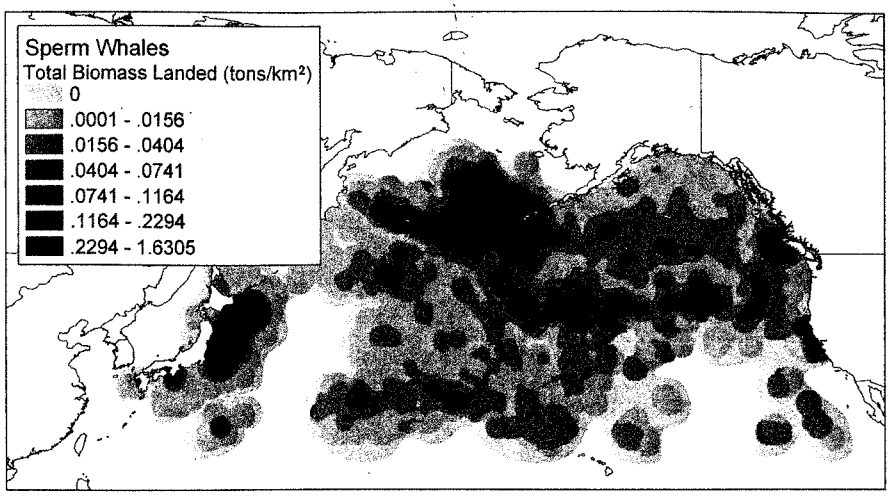

FIGURE 19.7. Summer distribution of sperm whales in the North Pacific. May–September harvest locations after 1947 reported to the IWC (unpublished data) by all nations except the USSR.

of Cape Navarin and off Cape Olyutorski. Even more so than humpbacks, fin whales require very high densities of schooling fish for successful foraging (Piatt and Methven 1992).

Diets south of the Aleutian Islands consisted primarily of euphausiids and copepods, with comparatively few fishes. *Neocalanus cristatus* was particularly important and *N. plumchrus* was common. Atka mackerel was the predominant species of fish taken in this region.

Sei Whales

Sei whales were most abundant in the western North Pacific off the coast of Japan, and south of the Aleutian Islands in the Alaska Stream (Figure 19.6). Although sei whales generally were not common north of the Aleutians, and few were taken by the fishery in the Bering Sea, they were formerly abundant on the northwestern shelf in July and August (Masaki 1976). As noted earlier, sei whales were more numerous in the Aleutian Islands than Japanese harvest records indicate because of management and economic reasons.

Sei whales are one of the smaller of the commercially exploited species and eat the smallest prey. The sei whale distribution in the northern North Pacific corresponded with the distribution of its main prey, *Neocalanus plumchrus*, although *N. cristatus* also was common prey, particularly at and beyond the shelf break in the eastern Gulf of Alaska. Euphausiids and fishes were of little importance (Kawamura 1980; Nemoto 1963; Nemoto and Kasuya 1965). The abundance of sei whales in the northwestern Bering was likely explained by the advection of the huge biomass of zooplankton, particularly *N. plumchrus*, from the basin in the flow of the Anadyr Current.

Bryde's Whales

Bryde's whales are found in tropical and warm-temperate regions of the Pacific. Their northern limit is defined generally by the 40° N parallel, although they occur somewhat north of there, particularly in the central portion of their range (Omura 1959; Ohsumi 1977; Privalikhin and Berzin 1978). They are rare in the northern part of the North Pacific but are included here because they were targeted by pelagic fleets after more valuable species were depleted on the northern grounds, and protections were enacted for most of them. Most whales taken by the fishery were in central and western temperate and subtropical regions (Figure 19.6).

Bryde's whales taken on their more southern whaling grounds fed primarily on gonostomatid fish, and secondarily on euphausiids (Kawamura 1982). Off Japan, the migration of Bryde's whales seems to be keyed to the seasonal abundance of anchovy (Nemoto 1959).

Minke Whales

Minke whales are widely distributed in the North Pacific (Brownell et al. 2000b). However, because pelagic fisheries did not target them, there are no harvest records showing whether they concentrated in particular areas. They tend to be solitary or occasionally in pairs (Buckland et al. 1992; Moore et al. 2000; Tynan 2004), indicating that they maintain a low density over broad areas. Minke whales in Japanese waters feed on euphausiids and schooling forage fishes, such as pollock, herring, sand lance, and sardines (Kasamatsu and Hata 1985).

Sperm Whales

The majority of sperm whales in the northern North Pacific were males (Figure 19.7). Most females remained in more southerly waters throughout summer, although some did migrate to the Aleutian Islands and Gulf of Alaska, particularly in El Niño years. The greatest concentration of sperm whales in summer was found in the vicinity of the Aleutian Islands, over Brower's Ridge, which extends north off the central arc, and along the edge of the continental shelf in the

Bering Sea. They were particularly dense on the north side of the Aleutians, where squid were abundant (Uda 1962). These regions are part of the highly productive Green Belt, which is so important to other cetaceans.

Sperm whales eat both squid and fish throughout their range (Whitehead, Chapter 25, this volume). In the early 1960s, squids dominated in diets of sperm whales from the Aleutians, were of similar importance as fish along the shelf edge in the Bering Sea, and were less important than fish at the shelf edge in the Gulf of Alaska (Okutani and Nemoto 1964).

Whales and Whaling in an Ecosystem Context

Great whales played roles as both consumers and prey, and the loss of both functions is thought to be consequential to ecosystem structure in the northern North Pacific (National Research Council 1996; Springer et al. 2003; Croll et al., Chapter 16 in this volume). Dead whales falling to the deep-sea floor also provide detrital oases that support complex food webs in the abyss (Smith and Baco 2003; Smith, Chapter 22 in this volume).

Estimates of their quantitative importance in the ecosystem, and the effects their loss might have had are difficult to derive. Pre-whaling and post-whaling population sizes are not well known for most species, especially for any given region, nor is it known how many whale-days each year were spent by the various species on their feeding grounds. Estimates of historic population sizes of great whales vary widely and are hotly debated (Roman and Palumbi 2003). Nonetheless, we have quantitative data on the number and lengths (and therefore biomass) of great whales harvested in well-defined areas and over relatively short periods of time after the mid-1900s, and the nutritional requirements of these large predators can be estimated reasonably well.

Whales as Consumers

Omura et al. (1969) suggested that initial depletions of bowhead and right whales in the mid-1800s could have had a beneficial effect on populations of fin and sei whales in the Bering Sea and Gulf of Alaska. Right whales likely competed for copepods with fin whales in the eastern Aleutian Islands and southeastern Bering Sea, and with fins and sei whales in the Gulf of Alaska. Bowheads would have competed for copepods and euphausiids with fins and seis in the northern Bering Sea. Rights and bowheads both would have competed for prey with several species of planktivorous forage fishes, including pollock, capelin, and herring, which in turn could have had implications for fin whales. ENP gray whales are critical to community structure and productivity on their northern feeding grounds as both consumers and habitat architects (Oliver and Slattery 1985; Highsmith et al., Chapter 23 in this volume), and their reduction and subsequent recovery must have had important effects on benthic ecology. Worm et al. (Chapter 26, this volume) hypothesize that functional dominance in the Bering Sea shifted from marine mammals to fishes with the loss of whales.

Evidence of substantial increases in prey during the modern whaling era is provided indirectly by the dramatic density-dependent responses exhibited by some whales as their populations fell. During the period of intensive whaling, from the early 1950s until 1975, the average age at sexual maturity of female fin whales declined by half, from 12 years to 6 years, and of males by nearly 65%, from 11 years to 4 years (Ohsumi 1986). Male sperm whales grew faster after modern whaling began, particularly in the 1970s when over 80% of the total post-war take occurred (Kasuya 1991). Both of these examples indicate that as whale populations fell, individuals responded to improving feeding opportunities. While part of the improvement may have resulted from diminished interference competition, much of it likely resulted from both relative and absolute increases in prey availability as total consumption declined.

A sense of the magnitude of prey released by the loss of whales, and the potential implications for them and the system, can be seen by calculating daily and seasonal consumption budgets for three important species—bowhead, fin, and sperm whales (Table 19.1).

BOWHEAD WHALES

The exact number of bowheads that formerly summered in the northwestern Bering Sea and Bering Strait region is unknown, but some 7,000–9,000 were killed there in just the first six years following their discovery in 1848 (Bockstoce and Botkin 1983; Breiwick et al. 1981; Sonntag and Broadhead 1989). The slow reproductive rate of bowheads certainly precluded substantial replacement during such a short interval, and the population likely fell by approximately the number harvested. Further evidence that supports this case is the fact that by 1856 the Bering Strait grounds were virtually deserted of whales and whalers (Bockstoce 1986).

An average bowhead is assumed here to weigh 31 t (Pfister and DeMaster, Chapter 10 in this volume), and thus would consume 0.59–0.88 t d^{-1} of zooplankton biomass consisting of a mixture primarily of large calanoid copepods and euphausiids. If 6,000 bowheads were present on any given day in summer in the region from the Gulf of Anadyr to the Bering Strait (some bowheads were southwest of Cape Navarin), they would have consumed $3.5–5.3 \times 10^3$ t d^{-1}, or, with a diet of 50% copepods and 50% euphausiids, in the order of 5–8% of the daily advective input to the Bering Strait region of *Neocalanus cristatus* and *N. plumchrus* via the Anadyr Current in early to mid-summer, and 8–13% in late summer (calculated from data in Springer et al. 1989).

Although consumption by bowheads was not a great proportion of the daily supply of zooplankton to the Bering Strait region, it may still have been an important competitor of other baleen whales, as noted previously, as well as planktivorous auklets in the region. Least and crested auklets nest on all of the islands on the northern shelf, and in aggregate, number several million individuals, making this the richest region in the world for these species (Springer et al. 1993).

TABLE 19.1

Consumption by Bowhead, Fin, and Sperm Whales in the North Pacific

	Individual Mass	*Individual Consumption (Wet Weight)*			
	t	t d^{-1}, low	t d^{-1}, high	t y^{-1}, low	t y^{-1}, high
Bowhead whales, N Bering	31	0.59	0.88	71	106
Fin whales, SE Bering	38	0.69	1.03	82	123
Sperm whales, Aleutian Is.	27	0.53	0.80	64	96

NOTE: Masses assigned to fin and sperm whales are the mean weights of animals reported in the Japanese harvest data for the Bering Sea and Aleutian archipelago. The mass of bowhead whales is taken to be 31 t from Pfister and DeMaster (this volume). Daily intake rates to meet resting, or basal, metabolic requirements were calculated from Hain et al. (1985) as consumption (g wet weight d^{-1}) = 70 × (body weight in kg)$^{0.75}$. A best estimate range of daily consumption was arrived at by applying correction factors to resting rate of 3.6 × (active metabolism = 3 × resting; assimilation efficiency = 84%) and 5.4 × (food storage requirements = 1.5 × active metabolism + assimilation efficiency). Time spent by whales on their summer feeding grounds (the effective year length) was taken to be 4 months based on information in Masaki (1976) and Ohsumi (1966), as well as the length of the principal hunting season from June to September.

Auklets specialize on *Neocalanus* and euphausiids, and their otherwise paradoxical abundance on the shallow northern shelf is made possible by the Anadyr Current conveyor belt. Despite their immense numbers, auklets are small and constitute in biomass only the equivalent of about 2–5 bowheads per million birds, depending on species, and their combined consumption of zooplankton (ca. 2.0×10^2 t d^{-1}; Piatt and Springer 2003) is more than an order of magnitude less than that of bowheads. Thus, they have an even smaller impact on the vast zooplankton stocks in the region. However, the opposite effect is plausible, that auklets benefited from the release of several thousand tonnes per day of zooplankton biomass entrained in a marine river flowing past their nesting colonies, particularly since bowheads likely targeted the same dense concentrations of zooplankton as auklets did (Hunt and Harrison 1990).

FIN WHALES

The greatest concentration of fin whales in the North Pacific in summer was over the broad slope in the eastern Aleutian Basin of the southeastern Bering Sea. At a mass of 38 t (average of fin whales harvested in the Bering Sea; IWC, unpublished data), one whale would have consumed about 0.69–1.03 t d^{-1} of zooplankton (Table 19.1). The nominal all nations harvest of fin whales from the region totaled 8,144. The instantaneous standing stock of whales is not known, so assuming two scenarios, that (1) the number of whales present in the region at any time in summer was equal to the total harvest, or (2) equal to half the total harvest, they would have consumed at least 2.8×10^3 t d^{-1} of zooplankton biomass (4,072 whales × 0.69 t d^{-1} $whale^{-1}$), and at most 8.4×10^3 t d^{-1} (8,144 whales × 1.03 t d^{-1} $whale^{-1}$).

The main distribution of fin whales in the southeastern Bering Sea corresponded with the center of the spawning distribution of the offshore segment of the pollock stock of the eastern Bering Sea, located in the Bogoslof Island area (Management area 515: Hinckley 1987; Wespestad et al. 1990; D. Arciprete in Napp et al. 2000). Diets of fin whales and pollock overlap extensively, as pollock also prey predominantly on *Neocalanus* copepods, euphausiids, and small fishes, particularly young-of-year pollock (Bailey and Dunn 1979; Dwyer et al. 1987; Livingston 1989; Takahashi and Yamaguchi 1972; Yoshida 1994). The proportion of fishes in pollock diets off the shelf is low compared to on the shelf, so assuming pollock in the Bogoslof area consume predominantly copepods and euphausiids, as do fin whales in this region, the amount of zooplankton released by the depletion of whales is equivalent to the amount consumed daily by 1.4–4.2 × 10^5 t of pollock age 1–4, or 2.8–8.4 × 10^5 t of pollock >4 years old (assuming daily consumption is 2% × body weight for 1–4 year old fish and 1% × body weight for >4 year old fish) (from Springer 1992).

Estimates of trends in biomass of pollock in the eastern Aleutian Basin have not been made. In 1989 a standing stock of about 1×10^6 t was estimated (Wespestad et al. 1990). The harvest there grew rapidly in the late 1980s, peaking at 3.8×10^5 t in 1987, but declined rapidly because of dwindling abundance. Much of the harvest in the 1980s was of fish from the unusually strong 1978 year class. The biomass of prey released by the loss of fin whales was thus of the same order as the requirement of pollock in the Bogoslof area, even at its highest.

SPERM WHALES

The center of distribution of sperm whales in the northern North Pacific was the Aleutian Arc from the Near Islands to Unimak Pass and around the eastern perimeter of the Aleutian Basin. The nominal all-nations catch from this area, including waters 100 nautical miles south of the Aleutians, was 40,850 whales, of which 29,766 were taken within

100 nautical miles on either side of the Aleutians. This is a minimum estimate, as the USSR underreported sperm whale harvests by as much as 60% (Brownell et al. 2000a).

An average male sperm whale of 27 t (mean mass of whales caught in this area; IWC, unpublished data) consumes about 0.53–0.80 t d^{-1} (Table 19.1). For the Aleutians, where sperm whales were most highly concentrated and assuming between 14,883 and 29,766 whales were present at any time in summer, they would have consumed in the order of $0.79–2.4 \times 10^4$ t d^{-1} of prey biomass. In the southeastern Bering Sea, the nominal harvest was 16,279 sperm whales, and using the same assumptions as above, the whales there would have consumed in the order of $0.43–1.3 \times 10^4$ t d^{-1}.

Squids dominated diets of sperm whales in the Aleutian Islands and Bering Sea. Squids consume a variety of prey from zooplankton to fishes to other squids depending on species and size, although larger squids of the size commonly eaten by sperm whales were likely piscivorous or teuthivorous. Although there might have been other predators available to take up the surplus biomass released by the removal of sperm whales, a more immediate result of an increase in the abundance of second- and third-order squids might have been their effect as predators on prey populations. Over the course of a 120-day season in the Aleutians absent sperm whales, $0.95–2.9 \times 10^6$ t of additional biomass would have been available as predators or prey. In the southeastern Bering Sea absent sperm whales, an additional $0.52–1.6 \times 10^6$ t would have been available to eat and be eaten and to participate in the rebalancing of food web dynamics brought on by the removal of sperm whales and fin whales.

Whales as Prey

The only significant predators of great whales, other than people, are killer whales. Notably, the commercial fishery in the North Pacific did not target killer whales, and the majority of the 391 reported to the IWC by all nations between 1949 and 1964 were taken in the northwestern Pacific off the Kamchatka Peninsula and Kurile Islands (IWC, unpublished data).

Killer whales are known to prey on all of the great whales (Jefferson et al. 1991; Reeves et al., Chapter 14 in this volume). Highly choreographed defensive formations and evasion tactics of great whales are well documented (Finley 1990; Pitman et al. 2001; Whitehead 2003) and it is argued (George et al. 1994; Corkeron and Connor 1999; but see Clapham 2001) that long seasonal migrations of some species are made primarily to avoid killer whales. Skilled, cooperative attacks on individuals and groups of great whales by pods of killer whales are obviously learned behaviors to effectively subdue large prey, and include ramming, exsanguination, and drowning (Jonsgard 1968; Jefferson et al. 1991; Pitman et al. 2001).

Sheer size does not appear to confer immunity to great whales. Nor do killer whales need to kill their prey in order to obtain benefits from an attack. In one case without confirmed mortality, a large pod of killer whales, in a highly coordinated attack, stripped long pieces of blubber from a 20-m blue whale (Tarpy 1979). In another case, killer whales bit large chunks from humpback whales without apparently killing them (Whitehead and Glass 1985).

The significance of killer whale predation to great whale abundances was probably low in general, but not necessarily always. In the eastern Canadian Arctic, bowheads are preyed upon by killer whales to the extent that their recovery from over exploitation might have been retarded (Mitchell and Reeves 1982). Finley (1990) reported that approximately 30% of bowheads in Isabella Bay, Baffin Islands, had scars from killer whales. Finley et al. suggest that although killer whales in the eastern Canadian Arctic can meet their dietary needs by feeding on other, more abundant prey, they nevertheless target bowheads when they are available. Branch and Williams (Chapter 20, this volume) have speculated that in the Southern Ocean killer whales may have reduced minke whale abundance following decimation of great whales there. Evidence that killer whales prey on great whales elsewhere also exists. Gray whales are taken across a major portion of their range—in Alaska they are killed as they migrate through the western Gulf of Alaska and southeastern Bering Sea, and while on their feeding grounds on the northern Bering-Chukchi-Beaufort shelf. In the past in southwestern Alaska, where grays are available only in spring and fall, some killer whales in summer logically could have targeted other great whales that were so highly concentrated in the Aleutian Islands and Bering Sea prior to depletion.

Other species of great whales are also attacked in Alaska. There are numerous reports, summarized by Jefferson et al. (1991), of attacks on humpback whales in southeastern Alaska; Spalding (1999) reported that some 15% of humpbacks in the Gulf of Alaska bore scars from killer whales; and a vigorous, bloody attack on humpbacks in southeast Alaska was recently observed from an Alaska ferry (G. Kruse, personal communication). George et al. (1994) examined bowhead whales taken by hunters at Barrow, Alaska, (western Beaufort Sea) for scarring by killer whales, 81 in 1976–1979 and 114 more in 1980–1992. The incidence of scarring in 1976–1979 was just 2.5%, whereas in 1980–1992 it rose to 7.9%. All whales were considered to have been "confidently examined," and it seems plausible that the difference was due to redirected killer whale predation following the demise of great whales farther south. Transient killer whales move long distances (Goley and Straley 1994) and relocation of transients from the depauperate Aleutian Islands and southern Bering Sea to areas with higher densities of marine mammals would be expected. Increases in the abundance of killer whales in the vicinity of the Pribilof Islands and in Bristol Bay in the late 1980s (Frost et al. 1992; Baretta and Hunt 1994), following the collapse of pinnipeds populations in the Aleutians, were accompanied by a resumption of the decline of fur seals following a brief interval of stability on St. Paul Island, and by numerous observations of attacks on several species of marine mammals in Bristol Bay. Residents of villages in the Bering Strait region (Russia and Alaska) are reporting unusually high numbers of killer whales in recent years

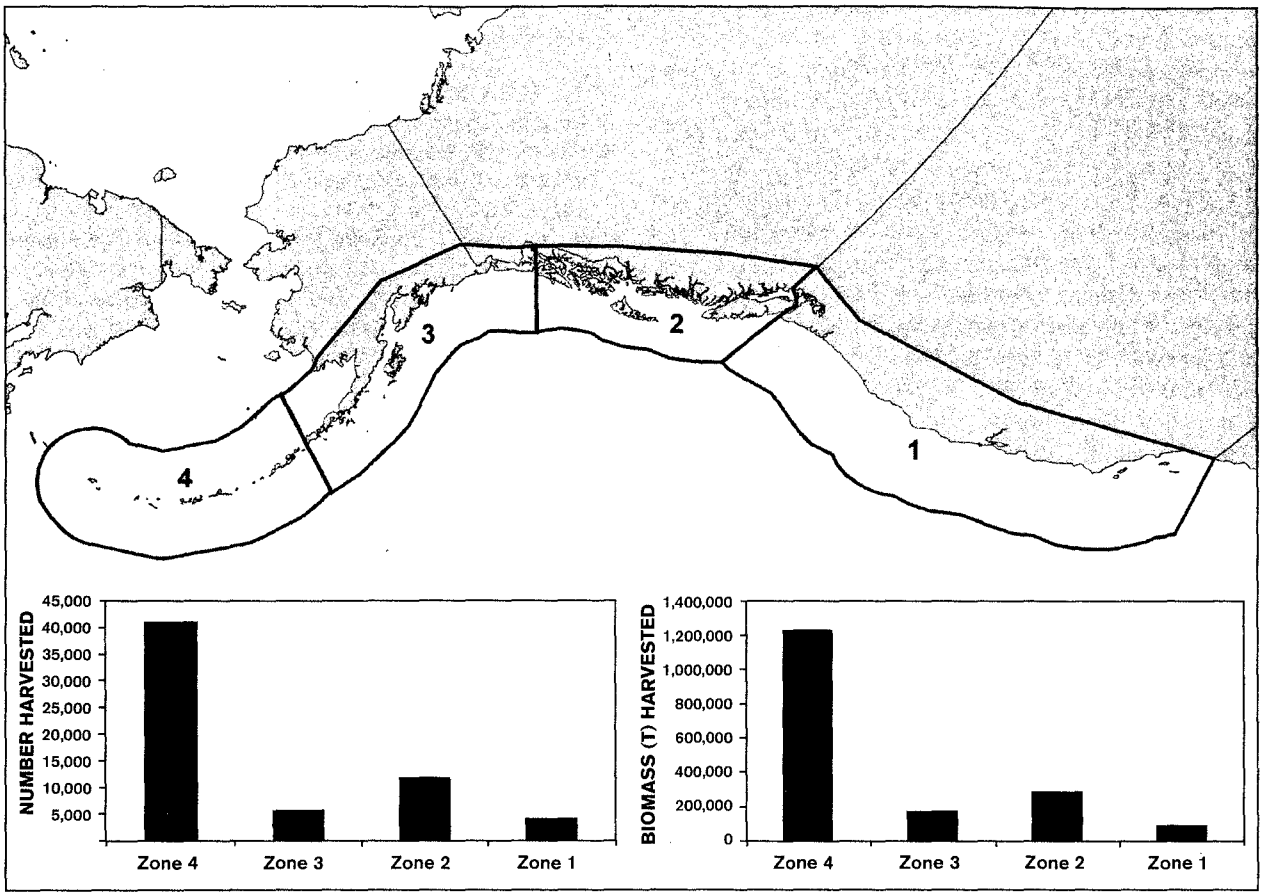

FIGURE 19.8. Numbers and biomass of whales harvested within 100 nautical miles of the coast in four regions of the North Pacific since 1947 reported to the IWC (unpublished data) by all nations except the USSR.

that are preying on bowheads, gray whales, walruses, and seals (G. Sheffield, personal communication; C. George, personal communication). Bowheads and gray whales are now the most abundant and concentrated large whales from the Aleutian Islands to Bering Strait. Minke whales also are commonly eaten by killer whales and may be particularly vulnerable because of their small size, broad distribution, and relative abundance following depletion of the larger species. There are no reliable estimates of abundance or trends in abundance of minkes, but nowadays they apparently are less numerous than many of the larger species (Moore et al. 2000; Tynan 2004), which raises the possibility that they did decline in the North Pacific, as they may have in sections of the Southern Ocean (Branch and Williams, Chapter 20, this volume).

Conclusions

Most whales were killed in the North Pacific during May–September while highly concentrated on their summer feeding grounds. These grounds are oceanographic hot spots where physical processes lead to enhanced production at numerous trophic levels (Uda 1962; Nasu 1966; Springer et al. 1996), and where prey must be concentrated for feeding to be efficient (Nemoto 1972; Piatt et al. 1989; Piatt and Methven 1992). Thus, hot spots are found along the Aleutian Arc, the slope and shelf edge of the Bering Sea and Gulf of Alaska, the northern Bering-Chukchi shelf, the mixing zone of the Kuroshio and Oyashio currents, and the Western Subarctic Gyre.

Whalers since the mid-1800s were able to quickly deplete whales in given regions of the North Pacific, generally within spans of about 10 years (Danner et al., Chapter 11, this volume). Whales served as predators and prey, and the abrupt, extreme reductions of great whales from small areas likely focused the effects of the loss of these functions on ecosystems. The great whales' chief predators, killer whales, were taken in very small numbers by the fishery and likely included all three ecotypes (resident, transient, and offshore). Unfortunately, information necessary to evaluate the extent to which killer whales were and are dependent on large whales as prey remains to be collected.

We may never be certain of the magnitude or extent of the effects of commercial whaling. Cascades of response in communities, food webs, and ecosystems likely varied depending on local and regional characteristics, including basic oceanography and production regimes, the magnitude of whale biomass removed, and the status of other species in the matrix of interactions. For example, more than three fold

more whales were killed in the modern fishery in the Aleutian Islands than in southeastern Alaska and British Columbia (Figure 19.8). By the time most whales were depleted on these grounds, the early 1970s, pinnipeds in the Pacific Northwest also were reduced to low numbers because of bounty programs and commercial hunting in the 1950s and 1960s (Bigg 1985; Olesiuk et al. 1990). But in the Aleutians, as well as the western Gulf of Alaska and Bering Sea, pinnipeds were still very abundant in the mid-1970s and did not begin to decline until about that time. Predator-prey relationships among marine mammals that existed then and that evolved in succeeding years were undoubtedly different in the two regions, and it is not surprising that conditions remain different today.

Great whale populations are recovering in the North Pacific, perhaps even the right whale stock (NMFS 2004). As population numbers grow, so too will the roles they play in the ecosystem. Whether food webs and communities return to their former condition remains to be seen, as much has changed in the intervening years. The mean climate state over the northern North Pacific has undergone three major shifts since the end of the modern whaling era (Hare and Mantua 2000; Mantua et al. 1997; Bond et al. 2003), and pinniped and sea otter populations throughout the Aleutian Islands and western Gulf of Alaska have collapsed (Estes et al. 1998; Doroff et al. 2003; Springer et al. 2003). The fundamental rules governing rates and pathways of energy exchange in the ocean are likely still the same (but see Jackson, Chapter 4 in this volume), but the constraints are certainly different now than they were in the hierarchy of the mature ecosystem 50 to150 years ago. Attention should be focused now on ways to improve our understanding of top-down oceanography (predator-prey interactions at all trophic levels, particularly high levels); how marine community structure and dynamics are influenced by those processes; and how ecosystems in their dramatically altered condition today behave in response to environmental change.

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