The many threads of evidence, inquiry, and hypothesis . . . pattern themselves into a tapestry of history—the history of the landscape of Beringia, at one time dominated by sea, at another by a great plain; once covered with forest, then with treeless tundra; once populated by mammoth, horse, and bison, hunted by Paleolithic man; now the home of sea, walrus, and polar bear, sought by the world’s most skillful sea-mammal hunters.

David M. Hopkins (1967)

1. A SHORT HISTORY OF DRAMATIC CHANGE

This chapter addresses the natural histories of Bering Sea pinnipeds (seals, fur seals, sea lions, and walruses), and their responses to human impact and rapid climate change. Aleut, Yukon, Hupa, and Chukchi peoples have exploited pinnipeds for millennia, and continue to do so, but in the modern era, climate change has become the dominant issue that affects living sea natural resources and indigenous people.

The value and extent of the Bering Sea became known to the Western world only in the mid-18th century. Peter the Great of Russia, appointed Captain Commander Vitus Bering in 1725 to explore unknown eastern shores beyond Russia and to claim resources and lands. On his second expeditions Bering reached Alaska, accompanied by German physician-theologian Georg Wilhelm Steller. Steller documented many discoveries and several species that bore his name: Steller sea cow, Steller’s jay, Steller sea lion, and others. Bering’s ship was wrecked on the Commander Islands, where he died in 1741. The news of rich resources spread rapidly among fur traders, and by 1743 the hunt was on, principally for sea otters (Enhydra lutris) and northern fur seals (Callorhinus ursinus). On Bering Island, Steller described the huge Steller sea cow (Hydrodamalis gigas; Fig. 1.3), which hunting crews wastefully exploited for food, leading to its extinction by 1768. A century later in 1867, the United States purchased Alaska from Russia—labeled “Seward’s folly,” as the region was thought to hold little value—presenting an opportunity to expand U.S. territory. New England whalers, who had been active in the Bering and Chukchi Seas since the 1840s, rapidly increased their exploitation. And by the 1880s, bowhead whales (Balaena mysticetus) were so reduced that whalers turned to Pacific walruses (Odobenus rosmarus divergens), depleting them to less than a quarter of their estimated former population (Fay, 1982). Due to loss of these resources, indigenous peoples starved, exacerbated by alcoholism and diseases introduced by the whalers. By 1900, few whaling ships ventured to the Arctic for resources. By the end of the 19th century, the northern fur seal was critically depleted, and the sea otter was presumed extinct. The wasteful slaughter of
these valued species led to the international 1911 Treaty for the Preservation and Protection of Fur Seals and Sea Otter (Fur Seal Treaty, Ch. 3), initiating a remarkable recovery for both species.

Presently, climate change has introduced a high degree of uncertainty into Bering Sea conservation and management. The changing climate is affecting both marine ecosystems and indigenous peoples, and is occurring more rapidly in the Arctic than for any other large region on Earth (Fig. 7.1). Climate change raises questions about sea-ice diminution, northward expansion of fisheries, intensified efforts to exploit oil and gas, legislative conflicts, the sustainability of healthy pinniped populations, and the ecological consequences of their changing status. From a socio-political point of view, conservation in the Bering Sea is undertaken against a backdrop of two contrasting, unequally positioned, cultural systems of non-common antecedence: one founded on historical beliefs and subsistence needs, the other on industry, profits, and national-to-global economies. Fishing in the southern Bering Sea is presently the dominant commercial enterprise. By the 1980s, Alaska’s seafood industry produced 40% of the world’s salmon supply, and walleye pollock (Theragra chalcogramma) has now become the world’s largest single-species fishery. Northward expansion of commercial fishing could carry substantial ecological concerns.

Among these, pinnipeds are potential indicators of environmental change for reasons of their diversity of habitat choice, their widespread distributions, and their collectively very high consumption rates that demand continuing high ocean production.

The Bering Sea is separated from the North Pacific by the Aleutian Islands, covering 2.3 million km², and extending approximately 1500 km from the Aleutians to the 85 km-wide Bering Strait (Fig. 7.2). This sea is almost equally divided into two distinct ecological regimes: a southern deep-ocean basin heavily utilized by commercial fisheries, and a northern, relatively shallow shelf portion characterized by winter-spring sea ice, and not yet heavily fished. The southern basin is up to 3600 m deep and almost totally ice-free year-round. A steep continental margin, incised by seven of the largest submarine canyons in the world, is transitional between the shallow, gently sloping shelf and the deep basin. Volcanic intrusions—Pribilof Nunivak, St. Matthew, St. Lawrence, and the Diomede islands—are important breeding habitats for some of the largest populations of seabirds on Earth. Landward margins include mountainous shores, terrestrial lowlands, extensive wetlands, barrier islands, lagoons, and river deltas. Seasonal river flows influence the timing of river-ice entry and sediment delivery into the sea, as well as migration and spawning of the largest native salmon populations remaining today.

Physical factors heavily influence Bering Sea ecology. Ocean currents bring warm North Pacific waters into and through the Bering Sea (Fig. 7.3a) and directly influence oceanic productivity (Fig. 7.3b). The Bering Sea’s climate is made complex by regional to global weather phenomena that determine species distributions. Atmospheric winds are seasonally dominated by the semi-permanent Aleutian Low (Fig. 7.4), which strongly influences storm tracks coming from the North Pacific. Usually, winter storms move eastward along the Aleutian Islands chain and into the Gulf of Alaska, with a

**Fig. 7.1** Climate warming has been considerably greater in the Arctic than for any other large region on Earth. The bar on the right indicates increases in degrees Celsius from 2002–8. Image provided by the NOAA/ESRL Physical Sciences Division, Boulder Colorado: at www.esrl.noaa.gov/psd/
**Fig. 7.2** Bering Sea geography and place names. The entire Sea is under U.S. and Russian jurisdiction, with the exception of the international "donut hole" outside U.S. and Russian EEZs. The dashed line indicates the separation of these two nations' jurisdictions at the International Date Line. Shades of blue indicate ecologically distinct domains where physical, chemical, and biotic factors influence reproduction, growth, and survival of marine organisms: light blue = Alaska coastal domain; medium blue = mid-shelf and Anadyr domains; darker blue = outer shelf domain; deep blue = Bering deep domain, surrounded by blue-gray shelf slope domain. From Loughlin and Ohtani (1999).

**Fig. 7.3** (a) Bering Sea currents. Weak currents in the central and western Bering Sea increase the residence time of warm North Pacific waters, with significant effects on sea-ice melt. (b) Generalized pattern of primary production in the Bering Sea. The "green belt" is the region of high productivity at the shelf edge, with northwest and southwest branches. The northward extension reflects high productivity that is augmented by inputs from large rivers. From Springer et al. (1996). Reproduced with permission from John Wiley & Sons.
frequency of about four to five per month, producing cold outbreaks that are often followed by warm airflow from the North Pacific. In summer, storms generally move eastward and curve northward into the Bering Sea, with a frequency of only about two to three per month. Spatial variations of El Niño can cause an eastward shift in the Aleutian Low, resulting in increased air and seawater temperatures in the eastern half of the Bering Sea, but during La Niña the Aleutian Low appears to become less intense and shifts westward, resulting in cooling. Additionally, the Pacific Decadal Oscillation (PDO) affects shifts between cold and warm regimes: i.e., a cycle of warm waters and mild winters occurs when the northeast Pacific experiences cold ocean waters and harsh winters. The presence of warming North Pacific waters affects sea-ice melting in the central and western Bering Sea, and the southern extent of sea ice in spring. However, explanation of the interplay of El Niño/La Niña, the Aleutian Low, and the PDO remains unresolved.

Biological production is also influenced by seasonal changes in light intensity and duration. Ambient light levels from late fall to mid-winter are too low to permit significant phytoplankton growth, and sea ice further limits production over the shelf. Differences in temperature, salinity, currents, freshwater runoff, seasonal heating and cooling, sedimentation, sea-ice dynamics, wind stress, and horizontal and vertical mixing interact to subdivide the Bering Sea into domains of differing productivities relevant to biotic distributions (Fig. 7.2; Cooney, 1981; Loughlin et al., 1999):

- **Alaska coastal domain**: shore to about 50 m depth; flow northerly at 1–5 cm s⁻¹; vertically well mixed and influenced by seasonal discharge of freshwater; summer surface temperatures to 14°C; winter water temperatures near freezing.
- **Mid-shelf domain**: approximately 50–100 m depth; little net circulation; surface layer wind-mixed; lower layer (≥30 m) tidally mixed; surface temperatures 3–10°C in summer to near freezing in winter; lower layer 1–9°C.
- **Gulf of Anadyr domain**: currents generally strong; influenced by the Anadyr River; summer surface layer to 8–9°C; lower layer 0–2°C.
- **Outer shelf domain**: approximately 100–200 m depth; dominated by north-northwest current flow at 1–5 cm s⁻¹; surface layer mixed by winds, temperatures to 9–10°C in summer; lower layer tidally mixed, winter temperatures 2–4°C. Bering deep domain: depth more than 200 m; greatly influenced by inflow from North Pacific; generally ice-free in winter; surface temperatures usually about 4–6°C.

In sum, the extraordinary abundance of birds and mammals is testimony to the high annual productivity of the Bering Sea. Factors affecting production and marine-mammal distribution are extraordinarily complex, and are also strongly affected by sea ice, which is examined in detail in Section 4.

### 7.3 Marine Mammals of the Southeastern Bering Sea

Three pinnipeds (Fig. 7.5) illustrate conservation issues of the southeastern Bering Sea: Steller sea lion (Eumetopias jubatus), northern fur seal (Callorhinus ursinus, family Otariidae, earless seals), and the harbor seal (Phoca vitulina, family Phocidae, “true” seals). Each species uses different portions of the sea to forage and each is affected by both natural and anthropogenic perturbations in contrasting ways.

#### 7.3.1 Natural history

Factors that determine these three species’ distributions include atmosphere and ocean climate, predator avoidance, prey distribution, reproductive strategy, and movement patterns among habitats. Avoidance of terrestrial predation might have been an important factor in determining present distributions since most rookeries (breeding areas) and haulouts (resting areas) are located at sites inaccessible to terrestrial predators.

All three species are opportunistic feeders, eating a wide variety of fishes and invertebrates. They are also “central-place foragers,” which places energetic constraints on foraging (Ch. 5, Section 5.4.2.5). Thus, distribution of prey and energetics probably determines the extents of dispersal during non-reproductive seasons. Choice of prey is influenced by prey biomass, availability, water depth, degree of association with the bottom, reproductive behavior, degree of aggregation (e.g., solitary vs. schooling), and temporal and spatial distribution patterns. BenFic feeding is a common pinniped strategy, perhaps because the bottom limits prey alternatives for escape. Schooling behavior of prey optimizes energetic costs associ-
ated with search and capture. All three species are the occasional prey of orcas (*Orcinus Orca*) and sharks. The likelihood of shark attack is probably greater for Steller sea lions off the Washington, Oregon, and California coasts because of the greater abundance and diversity of sharks than in waters farther north.

### 7.3.1.1 Steller sea lion

This is the largest eared seal (Fig. 7.5a). Males can attain 1120 kg in weight and 3.25 m in length and are two to three times larger than females (Loughlin, 2009). Steller sea lions range across the North Pacific Ocean rim, from the Kuril Islands to California (Burkanov and Loughlin, 2005), and occupy numerous rookery (Fig. 7.6) and haulout sites. They are not known to migrate. Recent genetic studies of DNA, cell proteins, and morphology have indicated that six groups occur through their range, and that at least two subspecies exist, an eastern and a western one (Fig. 7.7; Phillips et al., 2009).

Female sea lions may nurse their pups until they are four months to two years old, and are generally weaned just prior to the next breeding season. Individual sea lions may range widely. Individuals up to approximately four years of age tend to disperse farther than adults. As they approach breeding age, they have a propensity to stay in the general vicinity of breeding islands, and return to their island of birth to breed as adults. Principal prey of Steller sea lions includes a wide variety of fishes and invertebrates, and food preferences shift with positions along the coast (Sinclair and Zeppelin, 2002; Fig. 7.8). They tend to make relatively shallow foraging dives, with few dives recorded at greater than 250 m. Foraging-trip duration for females in summer is much less (about 24 hours) and covers less distance (average 17 km) than in winter (about 200 hours and 133 km, respectively). Yearling sea lions in winter exhibit foraging patterns intermediate between summer and winter females in trip distance (mean of 30 km), but shorter in duration (mean of 15 hours), with only an average of 1.9 hours per day spent diving (Loughlin et al., 2003).

### 7.3.1.2 Northern fur seal

Mature males of this moderately sized pinniped attain up to 200–250 kg in weight and 1.9 m in length; males are two to three times larger than females (Fig. 7.5b; Gentry, 2009). During winter, the southern limit of their range extends across the Pacific Ocean from southern California to the Okhotsk Sea and Honshu Island, Japan, north of about 35° N latitude. In spring, most seals migrate north to breeding colonies in the Bering Sea. The largest colonies are on the Pribilof Islands and compose approximately 74% of the world population. Other breeding colonies are on the Commander Islands in the western Bering Sea and on Robben Island in the Okhotsk Sea and support approximately 15 and 9% of the population, respectively. Smaller breeding colonies reside on the Kuril Islands in the western North Pacific, Bogenstof Island in the central Aleutian Islands, and San Miguel Island off the southern California coast.

Northern fur seals are highly migratory and the most pelagic of pinnipeds. From November to March they remain at
Fig. 7.6 Breeding range of Steller sea lions. The shaded area represents the approximate range of sea lions at sea. Arrows indicate breeding rookeries, some of which are too small to be shown on the map. Haulout areas are too numerous to be shown. The line separating the eastern and western subpopulations is at Cape Suckling, 144° W longitude. Phillips et al. (2009) has determined that the eastern and western "stocks" are subspecies.

dive to 200 m or more, for a maximum of 11 minutes (Gentry, 2009).

7.3.1.3 Pacific harbor seal

Both sexes of this relatively small seal weigh about 90–120 kg, but can weigh as much as 180 kg (Fig. 7.5c). Lengths range from 1.2–1.8 m; males tend to be slightly larger (Burns, 2009). In Alaska, they occur principally in the nearshore zone (Boveng et al., 2003). They use hundreds of sites to rest or haul out along coastal and inland waters, including intertidal sand bars and mudflats in estuaries, intertidal rocks and reefs, sandy, cobble, and rocky beaches, islands, ice floes in fjords and inlets, log-booms, docks, and floats in marine areas. Group sizes typically range from small numbers of animals on some intertidal rocks to several thousand animals that occur seasonally in coastal estuaries. Harbor seals breed and feed in the same area throughout the year and are considered non-migratory. Depending on the region, they typically give birth on shore during a two-week period in spring and nurse their single pup for four to five weeks. After pups are weaned, they disperse widely in search of food. Breeding usually occurs in the water shortly after pups are weaned. Harbor seals commonly prey on many species of fish, squid, octopus, and small crustaceans, usually diving to less than 100 m for about two minutes. However, they are known to dive to >400 m depth and stay submerged >20 minutes (Iguchi and Harvey, 2005).

7.3.1.4 Ecological partitioning

Sea lions, fur seals, and harbor seals overlap in distributions, times spent in the Bering Sea, and items consumed (Fig. 7.9) but do so in different ways, thereby limiting competition for food (e.g., Call and Loughlin, 2005; Robson et al., 2004). Fur seals reproduce on only one island group in the eastern Bering Sea where foraging locations for females often are >200 km from the islands. Time spent on land is only about two days for nursing, then back at sea for 4–10+ days foraging, amounting to approximately eight days a month, or approximately 35
Percent frequency of prey occurrence
P=Pollock; Sa=Salmon; At=Arrowtooth flounder; PC=Pacific cod; Sl=Sand lance; AM=Alka mackerel; H=Herring; C=Cephalopods

<table>
<thead>
<tr>
<th>Area</th>
<th>P</th>
<th>S</th>
<th>At</th>
<th>PC</th>
<th>Sl</th>
<th>AM</th>
<th>H</th>
<th>C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Marmot (64)</td>
<td>69</td>
<td>39</td>
<td>36</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>5</td>
</tr>
<tr>
<td>Chirikof (74)</td>
<td>69</td>
<td>43</td>
<td>19</td>
<td>9</td>
<td></td>
<td></td>
<td></td>
<td>9</td>
</tr>
<tr>
<td>Atkins (101)</td>
<td>86</td>
<td>46</td>
<td>6</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td>1</td>
</tr>
<tr>
<td>Pinnacle (79)</td>
<td>67</td>
<td>71</td>
<td>9</td>
<td>33</td>
<td></td>
<td></td>
<td></td>
<td>33</td>
</tr>
<tr>
<td>Bogoslof (74)</td>
<td>78</td>
<td>19</td>
<td>1</td>
<td>30</td>
<td></td>
<td></td>
<td></td>
<td>30</td>
</tr>
<tr>
<td>Clubbing (70)</td>
<td>87</td>
<td>33</td>
<td>26</td>
<td>16</td>
<td></td>
<td></td>
<td></td>
<td>33</td>
</tr>
<tr>
<td>Ugamak (155)</td>
<td>51</td>
<td>48</td>
<td>3</td>
<td>33</td>
<td></td>
<td></td>
<td></td>
<td>33</td>
</tr>
<tr>
<td>Akun (58)</td>
<td>36</td>
<td>33</td>
<td>19</td>
<td>55</td>
<td></td>
<td></td>
<td></td>
<td>55</td>
</tr>
<tr>
<td>Adugak (73)</td>
<td>9</td>
<td>24</td>
<td>73</td>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>55</td>
</tr>
<tr>
<td>Seguam (117)</td>
<td>10</td>
<td>3</td>
<td>90</td>
<td>11</td>
<td></td>
<td></td>
<td></td>
<td>11</td>
</tr>
<tr>
<td>Ulak (105)</td>
<td>10</td>
<td>100</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>100</td>
</tr>
<tr>
<td>Kiska (4</td>
<td>16</td>
<td>21</td>
<td>95</td>
<td>10</td>
<td>21</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

1 Sand lance also included
2 Cephalopods and deepsea smelts included
3 Cephalopods and herring included
4 Two sites

Fig. 7.8 Prey of the Steller sea lion. Percent frequency of occurrence of prey items collected from Steller sea-lion seals, June-August, 1990-8. Numbers in parenthesis, column 1, are sample sizes.

Days a year that the female spends on land. Adult reproductive males may be on land for more than two months, never leaving until the end of the breeding season, unless they lose their breeding territory to a competitor. Young animals may remain at sea for as long as two years.

Steller sea lions have shorter summer foraging trips than fur seals (<10 km), but extend those trips in winter when not held to shore by a pup. Rookeries are numerous and seem to be far apart as the distance that females feed from the rookery, without overlapping with those from the nearest other rookery. This suggests that the distance between rookeries might be a result of competition among females. Sea lion pups have evolved to go without food for two days at most, compared to fur seal pups that may go days to weeks without milk. Harbor seals are on the opposite extreme, being more terrestrial, hauling out at each tidal cycle, and spending a large portion of their time resting or just languidly swimming near shore. Their rookeries are numerous and fairly close to one another (20–30 km apart). They do not venture far from shore to forage and tend to stay in the same general areas all year.

These three species also differ in their timing and duration in the Bering Sea. Fur seals are present there for only about six months (June to November). Sea lions are present all year, but are more dispersed in the non-breeding season, venturing farther offshore to feed and for longer periods than in summer and across hundreds of miles, rather than thousands of miles for fur seals. Harbor seals disperse only over small distances.
7.3.2 Status, trends, and implications of environmental change

All three southern Bering Sea pinnipeds can be counted reasonably accurately while on land, and assessments indicate that all have recently declined overall, although some population segments of each species may be stable or slightly increasing (Pitcher et al., 2007; Simpkins et al., 2003; Small et al., 2003). Steller sea lion numbers in western Alaska are now only a small portion of those a few decades ago (Fig. 7.10). The western subspecies declined about 70% from the late 1950s to the 1990s in some areas; the rate of decline reached about 15% per year during 1985–89, but decreased in the 1990s to 5% annually. Between 2000 and 2004, this subspecies increased at approximately 3% per year—the only period of increase since trend information began to be collected. Results from a 2008–9 survey show that the population is now stable or declining slightly, with considerable regional variability. Therefore, this subspecies is still considered to be at risk of extinction within the next 100 years. In 2010, the National Marine Fisheries Service (NMFS) curtailed commercial fishing for Atka mackerel and Pacific cod in the central and western Aleutian Islands, important sea lion prey in those areas. This ruling is being challenged by the fishermen; the courts will likely be forced to intervene.

Causes for this decline are difficult to determine. Computer modeling and mark-recapture experiments suggest that the likely factor is decreased juvenile survival; lower reproductive success may also contribute. In some Alaskan areas where the diet includes numerous prey species, as in the eastern Aleutian Island area, sea lion numbers have been stable or increasing slightly, but in areas where sea lions primarily depend on one prey item, the population is declining. However, whether population trends are closely associated with diet diversity is equivocal. Possible effects of a declining prey base on Steller sea lions could include increased juvenile mortality, prolonged weaning periods, stunted pup growth, and increased effort to find and capture prey (Fig. 7.11). Other possible causes include disease, pollution, effects of fisheries, and environmental change. Available evidence is insufficient to demonstrate that disease has played, or is playing, any significant role. The effects of fisheries and synergistic effects of environmental change are areas of intense research to determine causal effects.

Recent counts of eastern Pacific northern fur seals show that the population has declined by about 60% from a histori-
cal high of more than two million in the 1970s to about 655,500 in 2009. This decline is likely linked to both ecological and human causes. The Pribilof Islands portion of the population was designated as depleted pursuant to the Marine Mammal Protection Act on 17 June 1988 because the seals had declined >50% since the late 1950s; the population has continued to decline since this designation. There is no compelling evidence that northern fur seal carrying capacity has changed substantially since the late 1950s, and data on pup production are equivocal.

Genetic studies on Alaskan harbor seals suggest population subdivisions on a scale of 600–820 km between groups (Westlake and O’Corry-Crowe, 2002; O’Corry-Crowe et al., 2003). Based on these studies NMFS has designated 12 management subdivisions that they term “management stocks.” These 12 management stocks extend from the Pribilof Islands in the north, the Aleutian Islands in the west, and Clarence Strait (near British Columbia) in the south. The most current 2001–7 surveys indicate that numbers have declined in the Aleutian Islands and Bering Sea management units (about 9,000 seals total) while numbers elsewhere have increased slightly during the past two decades. The estimated number of harbor seals for all stocks is a little over 150,000, with over 90% of those in the Gulf of Alaska and Southeast Alaska management stocks.

In summary, none of these three pinniped populations is robust. Why these species are declining is unknown, but it is likely that many factors are working together. Eastern subpopulations of Steller sea lions in the central Gulf of Alaska and eastern Aleutian Islands may be slightly increasing, or stabilizing, but the decline in the western Aleutian Islands is severe. The fur seal story is complex in that they had been commercially exploited until the early 1980s, were subject to mortality in high seas salmon gill-net fisheries during the 1970s and 1980s, and for unknown reasons have declined to abundance at the Pribilof Islands. Very little attention has been given to harbor seals, but scientists and the public are noticing that there are not nearly as many as in the recent past.

These southern Bering Sea pinnipeds almost certainly have lived through many regime shifts in the two to three million years of their existence. What may be different about this most recent reduction in numbers of all three species is the coincident development of extensive fisheries targeting the same prey that sea lions, fur seals, and harbor seals depend on for food. Fisheries in the Bering Sea expanded enormously during the 1960s and 1970s. The existence of strong environmental influences, such as climate change, could also increase the sensitivity of sea lions, fur seals, and harbor seals to fisheries effects, or to changes in those ecosystems resulting from fisheries.

### 7.4 ICE-DEPENDENT PINNIPEDS OF THE NORTHERN BERING SEA

Unlike southern pinnipeds, five Beringian “pagophilic” (sea-ice dependent) pinnipeds depend on sea ice as habitat for reproduction, nursing, molt, and rest (Fig. 7.12): Pacific walrus (*Odobenus rosmarus divergens*), ribbon seal (*Histriophoca fasciata*), spotted seal (*Phoca largha*), bearded seal (*Erignathus barbatus*), and ringed seal (*Phoca hispida*). These species partition habitats during their winter-spring reproduction periods according to the character of the pack ice (Burns, 1970; Burns, 1981; Fay, 1974; Braham et al., 1984; Lentfer, 1988; Ray and Huford, 1989; Ray et al., 2010). Reproduction in winter-spring depends on the synchronous timing, structure, and extent of sea ice. However, climate change is altering these sea-ice characteristics, making interpretation of sea-ice/habitat relationships difficult, particularly with respect to the phenological relationships of reproductive behavior.

#### 7.4.1 Natural history

Natural history is key to understanding the importance of sea ice to all species of pagophilic pinnipeds for at least three reasons. First and foremost, sea ice provides reproductive habitat. Second, moving ice enlarges the ocean area over which these species feed. Third, all species are adapted to specific sea-ice “seascape” structure (ice associations, thickness, ridge formation, etc.). Critical to these is phenology (Ch. 5, Section 5.4.2.5): the time of the animals’ birthing and mating must match sea ice formation and growth to be successful. That is, the duration of sea ice must be long enough to support walrus mothers and their calves during their northerly migration, and for pup seals to nurse and molt before taking to the water to feed.

##### 7.4.1.1 Pacific walrus

Walruses (Fig. 7.12a,b) are circumpolar in distribution. Two subspecies are differentiated (Fay, 1982). The Atlantic walrus (*O. r. rosmarus*) ranges from the northwest Atlantic to the seas off central Siberia; the Pacific walrus is Beringian (shelf areas of the Bering, Chukchi, and East Siberian seas; Fig. 7.13). Pacific walruses historically occurred as far south as Unimak Pass, east to Southeast Alaska, and west to the tip of the Kamchatka Peninsula. Presently, they are confined to seasonal sea ice in winter and coastal haulouts (males in summer). Field observations indicate that they mainly occupy areas dominated by thick, ancient, ridged, and moderately sized ice separated by intersecting leads (long openings) and lake-like openings called “polynyas” (Ray and Huford, 1989; Ray et al., 2010). New ice in leads and polynyas is tolerated as walruses can break ice up to 20 cm thick.

Walruses are among the most gregarious of mammals. Herds are composed of many groups that may collectively number in the thousands (Fig. 7.14). Typically, walruses are concentrated in two subpopulations in the north-central and southeastern Bering Sea from January through April to reproduce (Fig. 7.13). As sea ice disintegrates and retreats northward, walruses generally migrate with it, but should the ice reverse direction they may leave it periodically and swim north. By July, almost all females with newborn young, juveniles, and a few mature males occupy the marginal-ice zone of the eastern and western Chukchi Sea. Most mature males, however, move to coastal haulouts for the summer. From October through December, the entire population migrates
back to Bering Sea ice as it is forming. The sequence of ice formation (Section 7.4.2.1) is critical to this migratory pattern. Should sea ice vary in distribution, walruses would be expected to vary with it; therefore, due to varying ice conditions from year to year, their general distribution could potentially span most of the Bering Sea shelf area.

Male walruses reach 350 cm in length and 1700 kg in weight; females are a third smaller. Both sexes have formidable tusks, which help protect them from predation, principally by polar bears. Tusks also are used to assist hauling out on ice, as an anchor while resting (Fig. 7.15), and for sexual, dominance display, but not for digging for food, as has sometimes been assumed. Mating occurs in January through March in sea-ice environments. Mature males in the water engage in ritualized "song," displays that appear to establish male acoustic territories (Fig. 7.16). Walruses have among the lowest of mammalian reproductive rates. Delayed egg implantation and gestation occupy about 15 months; thus, the maximum reproductive rate is only one calf every two years per adult female at most (Fay, 1982). Maternal care is intensive; females provide body warmth to vulnerable calves (Fig. 7.12b) and closely guard them; calves may remain with their mothers for up to two years. Natural mortality of individuals more than one year old is very low, probably around 1% per year. Polar bears and orcas are their only natural predators at sea, but on the Alaska Peninsula brown bears are predators.

Walruses forage on and in sediments, in water depths rarely greater than 100 m. Their diet consists of a wide variety of benthic invertebrates. They appear to favor large, deeply buried clams (Fay et al., 1984a); they detect food with their vibrissae and lips as they move forward along the bottom powered by their rear flippers (Fig. 7.15). Organisms in the sediment are rooted out, much in the manner of pigs rooting in soil. Biomass consumption indicates that walrus feeding may also have substantial ecological effects through bioturbation (Section 7.5), which may qualify them as a "key" foundation species (Ch. 5: Fay et al., 1984b; Ray et al., 2006).

7.4.1.2 Bearded seal
The bearded seal occurs widely in the Arctic and is the largest Arctic, ice-dependent seal (Kovacs, 2009: Fig. 7.1.2c). It occurs singly or in small groups in pack ice during winter and spring, but most frequently occurs in similar areas as do walruses (Ray
**Fig. 7.13** Seasonal distribution of Pacific walruses prior to the 21st century. Two breeding concentrations occur in the Bering Sea in winter, west-central and southeast. The sexes then disperse differently in spring: females and young to the Chukchi Sea, males mostly to land haulout areas in the Bering and Chukchi seas. Diminishment of sea ice is changing these patterns. See text for explanation. From Fay (1982).

**Fig. 7.14** On-ice walrus concentration in broken pack in the south-central Bering Sea, recorded April 1975 from NASA flights at 300-450 m altitude. Arrows indicate directions of flight lines. Box 1 encloses the bulk of the herd and Box 2 encloses two particularly large groups. Sizes of filled circles represent estimated numbers of animals visually observed. From Ray and Watkaik (1980).
7.4.1.3 Spotted seal

The spotted seal is a coastal species except when breeding (Burns, 2009; Fig. 7.12d). It is superficially similar to the harbor seal, but is larger and generally paler with a spotted pelage. Males reach about 135 kg in weight and 170 cm in length; females are slightly smaller. Mating pairs form in March and stay together as a ‘family’ (Fig. 7.23) through pup birth in March to early April and until the pup is weaned; they then mate. They spend much of their time at sea, particularly in the farthest east of the Aleutian Islands, where the population is greatest. They seldom enter the Bering Sea, and are not found in the Okhotsk Sea or the Sea of Okhotsk.

7.4.1.4 Ringed seal

This smallest of Beringian seals is distinguished by its distinctive ringed pattern (Fig. 7.12e). Females attain 50–100 kg and 115–40 cm in length; males are slightly larger. Ringed seals occur throughout the Arctic and into adjacent icy seas (Hammill, 2009). They commonly occur in a heavy continuous sea ice (Ray et al., 2010), being uniquely able to maintain breathing holes in ice of up to 2 m thick. Ringed seals are generally solitary, except when with a pup. Individuals are most concentrated in nearshore ice, but are most numerous over large areas of offshore, thick, semi-continuous sea ice (Fig. 7.23). They take advantage of large, flat, ice floes in spring and construct submarine birth lairs in shorefast ice and pres-
7.4.1.5 Ribbon seal

This most unmistakable and strikingly patterned seal is among the least known of all pinnipeds (Lowry and Boveng, 2009; Fig. 7.12f,g). Males reach 140 kg in weight and 180 cm in length; females are slightly smaller. Ribbon seals occupy loose pack, often with spotted seals, but are most abundant from a bit east of St. Matthew, westward into the Gulf of Anadyr and south along the Kamchatka coast. They are pelagic for most of the year, almost never coming onto land. In winter-spring, ribbon seals occupy the inner loose pack (Ray et al., 2010) on laces of varying thickness, concentration, shape, and size; they appear to prefer fairly thick, often-ridged, snow-covered laces (Burns, 1981; Fedoseev, 2002). Their life history is similar to spotted seals during reproduction, but they do not form family groups. During March, ribbon seals gather in loose aggregations on sea ice to reproduce. They frequently occur on heavy laces of remnant ice (Box 7.1), where the marginal-ice seascape shows evidence of wave action and collisions. Pups are born from mid-March through early April. Nursing lasts for about three weeks and molting is complete by early July, at which time they become exclusively pelagic. Ribbon seals primarily consume fishes, small crustaceans, and cephalopods.

7.4.2 "Seascape" and habitat partitioning

Sea ice is most critical for pagophilic pinnipeds during their winter-spring reproductive periods. Habitat partitioning at that time has been strikingly illustrated by Braham et al. (1984; Fig. 7.17). Although those authors did not specifically refer to sea ice, the different patterns shown by walruses and seals strongly suggest that sea ice may be differentiated as habitat "seascapes" (Ray et al., 2010) following principles of landscape ecology (Wu and Hobbs, 2007). Significantly, natural scaling properties of sea ice have also become better understood, and appear closely to match the interacting scales that determine pinniped-sea-ice habitat relationships (McNutt and Overland, 2003).

7.4.2.1 Sea-ice formation and habitat relationships

Arctic sea ice occurs across the Arctic as two major types: seasonal ice that forms each year and melts in summer, and multi-year ice that persists for more than one year. In winter,
seasonal sea ice normally covers about 75% of the Bering Sea shelf. Multi-year ice only occasionally occurs south of Bering Strait as intrusions from the Chukchi Sea. In summer, sea ice retreats into the Chukchi Sea, leaving the Bering Sea typically ice-free. This seasonal ice advance and retreat is the most extensive for any Arctic region.

Beringian sea ice is first formed along the coasts of the Chukchi and Bering seas in late October and extends farthest south by mid-March (the “climatological norm,” see Fig. 7.24a,c,e). New ice is formed in a southward-moving “conveyor belt” over the shelf, where it meets warmer water and melts near the shelf-break (Pease, 1980). By April, dominant northeasterly winds decrease and atmospheric and oceanic temperatures begin to rise. Ocean surface currents, solar insolation, and winds then force the melting ice slowly northward through the Bering Strait. By the end of June only remnant ice remains in the northern portions of the Bering Sea.

Sea-ice formation and dynamics are best understood at multiple scales (McNutt and Overland, 2003; Fig. 7.18), each of which reflect sea-ice properties specific to marine-mammal natural histories. At local scales, individual floes coincide with species’ ice preferences, characterized by such adjectives as “closed” vs. “open” pack, or “new,” “ridged,” or “heavy” ice. At intermediate (meso-) scales, sea ice behaves more as a plastic continuum, governed primarily by fracture mechanics and resulting in larger-scale “seascape” patterns equivalent to marine-mammal habitats; seascapes move more slowly and can move as larger units according to how closely floes may be associated together. At the regional scale, sea ice responds to internal atmospheric and ocean forcing on weekly and longer time scales, and is characterized by extent (how far north or south the ice extends), cover (how much of the region is covered), roughness (e.g., ridges), and mean thickness (mass). The regional scale coincides with the “range” over which each species may occur.

More precisely, at the seascape-scale, variable wind and current conditions result in six distinct seascape formations in winter-spring that have, until recently, been observed to be relatively consistent and predictable in timing and location (Fig. 7.19). “Broken pack” occurs in the central Bering Sea where thick, continuous ice is broken by oceanic swells that penetrate far into the pack and where leads and polynyas are frequent. “Loose pack” occurs at the southern extent of the pack and is particularly affected by atmospheric and oceanic conditions at the sea-ice margin. “Pack-ice-with-leads” occurs to the northwest and into Gulf of Anadyr, an area constrained by the land basin, and characterized by parallel leads. “Rounded pack” occurs where northward-moving currents confront southward-moving ice, resulting in very thick, heavily ridged, convergent floes. “Continuous pack” occurs near the Bering Strait region where the narrow strait concentrates floes and causes continuous stresses that form large pressure ridges. “Large polynyas” occur both within the pack and adjacent to land masses, according to wind conditions, which can rapidly change their extent. These six seascape types define potential winter-spring habitats within which pinniped species may be patchily distributed in time and space, or conversely, unfavorably areas that they avoid. That walruses mostly occur in the same area as “broken pack” is indicated by historical records (Fay, 1982; Fig. 7.20). A principal component analysis of
Bering Sea seals and walruses: responses to environmental change

**Fig. 7.18** A hierarchical relationship of regional sea-ice cover, sea-ice type, and local walrus natural history. The regional scale reflects the general range of the species; the seascape scale is specific to habitat options, i.e., sea-ice "seascapes" (Fig. 7.19); and the local scale is appropriate for species' floe-type preferences.

**Fig. 7.19** Historical winter-spring seascape types exhibit distinct characteristics important to sea-ice dependent mammals in the Bering Sea. NOAA AVHRR (Advanced Very High Resolution Radiometer) infrared image of 30 March 1988: (1) broken pack; (2) bone pack; (3) pack ice with leads; (4) rounded pack; (5) continuous le; (6) polynyas. See text for explanation. From Ray and Huford (1989).

Walrus winter distributions is consistent with this broken-pack association (Fig. 7.21). The extensive, north–south occurrence of rounded pack seems to divide St. Lawrence from Bristol Bay walruses (see Fig. 7.13). Observations of walruses on ice from icebreakers add additional support for these two subpopulations (Fig. 7.22). These findings agree with Native hunters' observation of "two waves" of walruses passing St. Lawrence Island during spring migration.

As for seals, repeated field observations confirm that spotted seals and ribbon seals consistently occupy loose pack. However, bearded and ringed seals seem not to be strongly associated with any particular seascape, but rather are more sensitive to local conditions within various seasapes. A combination of ship observations combined with regional satellite imagery enables "scaling up" from local field observations to the seascape-scale and allows testing of species/seascape relationships during critical reproductive periods (Fig. 7.23) and particularly under future scenarios of climate change.

### 7.4.2.2 Seascape trends and the "mixing bowl"

Changing climate (Fig. 7.1) is currently causing highly variable sea-ice conditions. Later onset of winter ice formation and earlier spring breakup have shortened the sea-ice season by 6–8 weeks (Walsh, 2008). Although sea-ice cover (the total area covered by sea ice) has diminished, regional sea-ice extent (how far north or south the sea ice occurs) seems not to be a significant factor in overall sea-ice cover. Variable wind conditions can create large polynyas due to southerly shifts of sea ice, but with little significant change of cover, i.e., total sea-ice habitat available (Fig. 7.24).

Sea-ice changes are further exacerbated by increased spring freeze-thaw episodes that create greater open-water areas, where winds can shift seascape patterns into a complicated "mixing bowl" of sea-ice types (Box 7.1). Thus, floes become disassociated and seasapes become less cohesive and consistent. Floes have been observed to accelerate one day and move little the next without a clear triggering mechanism. What is clear, however, is that floes can move more independently when floes are dispersed than when they are concentrated. This is because, when floes are closely packed, they are forced to move together, but when disassociated, their movements depend on their different amounts of above-water "sail" or submerged.
"keel" that cause each floe to react independently to currents and/or winds. This mixing bowl effect on habitat is not predictable at present because it is very difficult to measure individual impacts of various stresses on sea-ice floes—wind, ocean currents, water and air temperature, ice pack internal interactions, shoreline boundaries, and bathymetry.

The consequences of the combined effects of the mixing bowl and rapid melt-out in spring on marine-mammal habitat are, first, that climate change is now resulting in a less well-structured seascape. The Bering Sea is slowly becoming ice-free earlier than the climatological norm of 1 July. Some floes are melting in place or melting before being advected very far into the southern Chukchi Sea. Thus, the consistent pattern of sea-ice types as observed in the past (Fig. 7.19) seems now less evident. Second, although the southerly extent of the ice seems not to influence the rapidity of melt-out, it may have a very significant effect on migration. Ice-dependent pinnipeds that rely on ice floes to "ride" into the Chukchi Sea must do so earlier in the spring and on more dispersed ice or be forced to undergo an energy-demanding swim.

7.5 DO LARGE MARINE MAMMALS MATTER?

The eight species of Bering Sea pinnipeds considered here clearly demonstrate both food and habitat partitioning, thus reducing competition for food and space while also maximizing fitness, i.e., their ability to perpetuate future generations. Reduction in their populations would be expected to have a cascading effect on lower levels of the food web and potentially higher entropy of the Bering Sea ecosystem as a whole.
Fig. 7.21 Principal component analysis illustrates an association of walrus winter distributions (crosshatched, Fig. 7.13) with sea-ice types. The north-central Bering Sea subpopulation appears to co-occur with (a) broken pack, but not with (b) rounded pack. The Bristol Bay subpopulation appears not to be associated with either sea-ice type, but is probably due to the occurrence of suitable floes. Distributions of ice types result from statistical analyses of NOAA AVHRR imagery for March in 10 consecutive years, 1973–82; the darker-blue shading indicates greatest probability of occurrence. The rounded pack is suggestive of a strong barrier separating the two walrus subpopulations. From Ray and Huflord (1989).

Fig. 7.22 Walrus observations from cruises of the icebreaker Healy. (a) 2006 spring migration and (b) 2007 late winter distribution after the reproductive season. Both years’ distributions suggest two “waves” of walruses passing north, first from the west-central subpopulation, followed by lesser numbers from the southeast subpopulation. Observations are in accord with patterns from Ray (1982).

Although the southern and northern sections of the Bering Sea are fundamentally different ecologically, in common they share large populations of pinnipeds. Thus, the ecological consequences common to both regions would be expected to relate significantly to the depletion of these large consumers.

Pinniped consumption of Beringian biomass is extensive in species consumed (Fig. 7.9) and also massive in quantity. Ray (1982) calculated Pacific walrus total biomass consumption alone, assuming a population of 200,000 animals, to be approximately 8900 metric tons (mt) day⁻¹, or 3.25 × 10⁴ mt per year. This represents a net rate of consumption, as walruses consume only soft parts of prey; if all organic matter was included, the gross “consumption” (i.e., amount of organic matter redistributed) reaches 9.5–12.6 × 10⁴ mt a year. If annual consumption by all Beringian pinnipeds—walruses plus several hundred thousand bearded seals, spotted seals, ribbon seals, and ringed seals (NOAA, 2010)—were to be included, biomass removal would be enormous, substantially
Fig. 7.23 Seascape and local scales of sea-ice types and pinnipeds. (a) Pacific walrus on ice floes observed within broken pack southwest of St. Lawrence Island. 20 April 2007. The sharp-edged character of individual floes and the intersecting leads separating floes are characteristic of broken pack. (b) Spotted seal "family" on outer fringes of loose pack. 15 March 2010. Areas enclosed by dashed yellow lines illustrate cover of broken pack (a) and loose pack (b), as determined by helicopter flights and interpretation of MODIS imagery. Environmental images from MODIS satellite imagery. From Ray et al. (2010). Reproduced with permission of John Wiley & Sons. Walrus and seal photographs © Ray & McCormick-Ray.
Fig. 7.24 Regional sea-ice cover from MODIS satellite imagery (resolution 250 m) for March, May, July, and late summer 2006 and 2007, showing change in northern Bering and Chukchi seas. White lines on (a), (c), and (e) represent the climatological norm for March at the time that ice extent is maximal. The sea-ice extents for 2006 and 2007 are very different. Arrows on (b) and (c) indicate areas of polynyas, which must be taken into account when estimating total ice cover. Again, 2006 and 2007 are strikingly different. Yellow lines on (d) and (b) indicate the 100 m depth contour in the Chukchi Sea during late summer, north of which walruses rarely feed; in both years, sea ice was near or north of that line, forcing walruses to occupy small areas of remnant pack (2006) or to retreat to haulouts (2007). The arrow on (c) indicates the location of ice with ribbon seals that was tracked (Fig. B7.1.1, 2006, red line); arrows on (f, g) indicate tracked movement of a very large congested floe (Fig. B7.1.1, 2007, red line).

Exceeding all fisheries removals. Significantly, pinniped consumption constitutes recycling within the ecosystem, whereas fisheries represents biomass removal from the system; that is, the former would be expected to increase productivity due to increased turnover of resources, whereas fisheries depletes resources and thereby energy.

Furthermore, with respect to benthic consumption, walrus and bearded seal predation on in- and epifauna would be expected to exert top-down effects on benthic community composition and production (Ray et al., 2006). In this respect, benthic community composition is of particular interest, as different species assemblages, whether resulting from predation or not, would contribute differentially to ecosystem performance (McCormick-Ray et al., 2011). Biophysical effects of pinniped feeding are no less significant. For example, Johnson and Nelson (1984) estimated that feeding by walruses and gray whales—bioturbation—suspends approximately $120 \times 10^8 \text{m}^2 \text{yr}^{-1}$ of sediment in the north Bering and south-central Chukchi seas—twice the yearly sediment load of the Yukon River. Feeding bioturbation also has the potential to increase nutrient flux from the benthos to the water column by two orders of magnitude (Ray et al., 2006), and thereby for productivity. Patchy patterns of benthic production have been observed by oceanographers and have been presumed to result
Box 7.1 The Bering Sea “mixing bowl”

Tracking individual floes from satellite imagery implies a “mixing-bowl effect.” A combination of satellite imagery corresponded with ship (USCGC Healy) observations during 2006, 2007, 2008, and 2009. The first two years are illustrated here (Fig. B7.1.1). Thirteen floes tracked from 8 May to 11 June 2006 indicate general sea-ice movement. In April and early May, a major sea-ice melt left large expanses of open water. Consequently, 12 floes moved northward mainly in response to ocean circulation, with short perturbations in direction due to the winds. When winds were greater than 7.6 ms⁻¹, floes moved significant distances, especially through loose pack ice and open water. Floes in the central and western Bering Sea generally moved 9–50 km day⁻¹, which dispersed them over a much larger area. They accelerated with increased current speed as they moved toward and through the constricted Bering Strait. Two rounded floes (#9 and #12) in the eastern Bering Sea moved northward as they became entrained into the Alaska Coastal Current, their movements ranged from 10–74 km day⁻¹ south of 64° N and greater than 92 km day⁻¹ north of 64° N. A concentration of floes in remnant ice containing many ribbon seals was observed from the ship near the international dateline (Fig. 7.24c). The ice appeared to be a large concentration of shorefast and nearshore floes covered in places with sediment. Exceptionally clear weather and the size of the concentration allowed tracking for 33 days. High-resolution imagery showed the floe concentration to be >1 km in size. Prior imagery allowed backtracking to the origin off the mouth of the Anadyr River on 9 May in the Gulf of Anadyr. Storm winds superimposed on ocean currents on 12 May rapidly pushed the floe from near the Anadyr River southeast. The floe then lingered southeast of Cape Navarin for 14 days where the ocean current exerted sufficient stress on the floe to balance any wind stress. The result was that the floe became quasi-stationary and/or meandered near one location. Ocean currents then apparently pushed the floe northeastward slowly. Another wind event on 2 June rapidly pushed the floe farther northeast toward St. Lawrence Island, grounding it near the southwest tip of the Island where it melted in place. Overall the floe moved a total of 674 km. The track of this floe is an excellent example of the combined effects of winds and currents moving ice and associated seals.

In comparison, a major melt-out of sea ice occurred in the Bering Sea in early May 2007, despite its greater southerly extent (Fig. 7.24e). Strong northerly winds that typify winter conditions, and normally cease in early April, continued into May. The result was that nine floes were pushed southeastward by the winds, some south of the marginal ice. These floes melted, eliminating them as potential habitat by mid-May. A very large, unique, and unmistakable congealed floe was observed in satellite imagery on 10 April (Fig. 7.24f, g) and backtracked into the central Gulf of Anadyr to 14 March. This floe was pushed eastward by storm winds on 14 April toward the mouth of the Gulf of Anadyr. After a few days, the floe then drifted northeastward. Storm winds again pushed the floe east-southeast. The floe continued to slowly drift eastward, reaching St. Lawrence Island on 5 June where it broke up and melted in place. It is of interest that this floe track differed considerably from the large floe track in 2006.

The two years contrast sharply with respect to extent and cover of the pack. However, the sequences of events are similar. They also have in common a less concentrated pack than, for example, is shown historically in Fig. 7.19, leading to the observation that floe mixing is occurring and seascapes are becoming less organized.

![Fig. B7.1.1 Tracked floes. 2006–7. Floes are shown to vary by change direction as forced by winds and currents, causing a mixing of floes and disruption of seascapes especially under conditions of sea-ice diminishement, as is presently occurring. Long red lines indicate large floe associations tracked for long distances (See also Fig. 7.24c, f, g). See text for explanation.](image-url)
from primary production (e.g., Grebmeier et al., 2006), but it seems possible that these patterns may also result from the feeding bioturbation by walruses, bearded seals, and gray whales, among others. The consequences of the combined effects of bioturbation have yet to be tested.

Spatio-temporal effects of pinniped feeding on production may originate in at least three ways. First, widely distributed species, such as those considered here, are likely to be distributed as metapopulations (Ch. 5), as is known for Steller sea lions and fur seals, and suggested for walruses (Jay et al., 2008). In this circumstance, spatio-temporal differences in feeding might be expressed. Second, all southern Bering Sea pinnipeds are "central-place foragers" (Ch. 5), that is, they leave rookeries or haulouts to feed, and return to the same general location afterwards. However, among the pagophiles, only the walrus may demonstrate this behavior. Field observations indicate that walruses remain within circumscribed areas of the broken pack when feeding, although they may not return to exactly the same ice area following feeding bouts (Jay et al., 2008). In doing so, walruses would avoid the negative energetic trade-offs of central-place foraging (Ch. 5, Section 5.4.2.4), as their "central place" is in constant motion, allowing new food patches to be exploited. This situation changes for walruses on land, where local depletion of food resources would be likely. The 2007 sea-ice retreat north in summer (Fig. 7.24h) forced thousands of walruses to aggregate on terrestrial haulout sites on U.S. and Russian Chukchi Sea shores, a circumstance that has been repeated in subsequent years. In such cases, depletion of local resources would have been likely. Third, loss and structural changes of sea-ice habitat would likely result in walrus population depletion. Landscape population models suggest that loss and structural change of habitat, as would likely result from the "mixing bowl" effect, increase the proportion of time that the population spends in the portion of the habitat where reproduction may not be possible and/or where mortality is higher. This situation theoretically leads to a downward spiral toward regional extirpation or even extinction (Fabrig, 2007; Fig. 7.26). In this case, an uncertain future is predictable for walruses, and possibly for all Beringian ice-dependent pinnipeds. Ecological effects are to be expected.

The various effects of marine mammals on Bering Sea ecology are difficult to predict and may occur separately by species, or more likely to some degree, simultaneously. How marine mammals affect communities and production processes is fundamental for determining ecosystem change, and will also affect future management. However, present states of knowledge are not adequate for projections to be made.

7.6 THE CONFLICT ARENA

Resource conflicts are fundamentally different for the southern and northern portions of the Bering Sea. For the former, uncertainties about fisheries’ effects on marine mammals presently dominate. For the latter, prospective oil and gas development, increased ship traffic, possibly including cruise liners, and northern fisheries expansion resulting from diminishing sea ice pose significant challenges. In addition, the Bering and Chukchi seas are divided almost equally between the U.S. and Russia. For that reason, marine-mammal studies under the

![Fig. 7.25](image-url) Cartoon representing ice floe/benthic relationship hypothesized for walrus as due to "central place foraging." Hauled-out groups of walruses (white circles) rest on sea ice (blue "seascape" areas). Vertical arrows indicate walrus movements from their sea-ice floes to forage on the benthos then return to the same general area of the pack. The sea ice is moving with time (horizontal arrows). The continuous brown area below represents the benthos where patches of food are variably distributed. Black circles indicate areas where walruses have fed; open circles represent patches not fed upon. The result is a very patchy feeding distribution. See text for further explanation, From Ray et al. (2006). Pacific walrus: benthic bioturbator of Beringia. *Journal of Experimental Marine Biology and Ecology* 330, 403–419.
U.S.-Russia Agreement on Cooperation in the Field of Protection of the Environment and Natural Resources have been essential and close cooperation continues (Box 7.2).

After World War II, high seas fisheries developed rapidly throughout the Bering Sea. Fisheries in Alaska were transformed by the passage of the Magnuson Fishery Conservation and Management Act (MFCMA, Ch. 3) and the Marine Mammal Protection Act (Ray and Potter, 2011). One of MFCMA’s principal objectives was to restrict foreign fishing fleets so as to encourage development of the domestic fishing industry. As a result, the temporal and spatial distribution of the catch, especially of pollock, changed. Between 1963 and 1997 in both the Bering Sea/Aleutian Islands and Gulf of Alaska regions, pollock were fished increasingly in fall and winter in areas designated in 1993 as critical for Steller sea lions (Fig. 7.27). Commercial fisheries target several other important prey species eaten by sea lions, fur seals, and harbor seals and remove millions of metric tons of fish from the sea each year, potentially affecting their food supply. These pinnipeds are further affected directly by incidental catch in nets, entanglement in derelict debris (Fig. 2.14a), and shooting, or indirectly through competition for prey, disturbance, or disruption of prey schools. Incidental catches probably contributed to the early sea lion declines in the Aleutian Islands and western Gulf of Alaska, but are not presently considered to be an important component. However, the complexity of ecosystem interactions and limitations of data and models make it difficult to determine the extent to which pinnipeds are affected by fishing. For example, their primary prey (pollock) has continued to be abundant. Therefore, the declines seem not to be because of prey removal by fisheries, but may be due to the spatial or temporal availability of fish to predators. Biologists argue that fisheries cause “localized depletion” when trawlers take fish from small areas where dense fish schools occur in the same areas where sea lions and harbor seals feed (Fritz and Hinckley, 2005; Hennen, 2004).

The general conclusion is that no single factor, but a combination of factors, may be causing these declines. Therefore, what can be done? Actions to conserve sea lions include prohibitions on shooting, reductions on allowable incidental take in fisheries, placement of zones around rookeries to restrict trawling, designation of critical habitat, development of a Steller Sea Lion Recovery Plan, and other measures. NMFS does not want to impose regulations that might needlessly stifle the fishing industry, yet the government is required to protect and conserve the sea lion. There seems to be little doubt that sea lions and commercial fishing efforts concentrate on the same prey, yet data are not available to conclude that the fishing fleet is totally responsible for the decline. Nevertheless, fishing bears the brunt of responsibility since management of fishing is the parsimonious way to facilitate recovery. Furthermore the federal government has implemented numerous measures for the conservation of Steller sea lions, but none have been proposed for fur seals or harbor seals.
Box 7.2 Marine mammal studies under U.S.-Russia Agreement on Cooperation in the Field of Protection of the Environment and Natural Resources

Steven Kohl
Department of the Interior, Fish and Wildlife Service, Washington, D.C., USA

In 1972 the United States and Soviet Union signed an Agreement on Cooperation in the Field of Protection of the Environment and Natural Resources ("Environmental Agreement") to provide a framework under which the two nations could collaborate on issues of mutual interest. The Agreement was renegotiated in 1994 to replace the U.S.S.R. with the Russian Federation as signatory. Prior to 1972 there had been little joint marine mammal research or management activity between American and Russian scientists, with the exception of implementation of the 1911 North Pacific Fur Seal Treaty and occasional exchanges sponsored by the Academies of Sciences of the two nations. When the Environmental Agreement took effect, bilateral contacts increased considerably with the creation of a Marine Mammals Project under its auspices. A U.S.-Russia Working Group was set up to meet periodically in alternating countries to review the results of studies of shared cetacean and pinnipeds species and to adopt a program of joint activities for the following 18–24 months. The Working Group has continued uninterrupted to the present day; its 21st meeting was convened in Moscow in March 2010; the 22nd meeting was held in March 2013 in Seattle.

Federal and state government agencies, non-governmental organizations, major research institutions, and universities of both countries take part in the Marine Mammals Project. In the U.S. these include the National Marine Fisheries Service, Fish and Wildlife Service, U.S. Geological Survey Biological Resources Division, Alaska Department of Fish and Game, Alaska SeaLife Center, Monterey Bay Aquarium, and others. Among the Russian participants are the Russian Federal Fisheries and Oceans Research Institute (VNIRO) in Moscow, several branches of the Russian Pacific Federal Fisheries Research Center (TINRO), Academy of Sciences, Kamchatka Northeast Fisheries Agency (Sevvostrybyvod), and the Federal Fleet Development and Research Institute (Giproybflot) in St. Petersburg. Joint activities range from aerial surveys and shipboard studies to satellite tagging and shore-based work on haulouts.

In the years since 2005, cetacean studies have centered on gray, bowhead, beluga, and orca whales. Concern over western gray whale has resulted in several research cruises to monitor their feeding activities and reproductive success in the Sea of Okhotsk off Sakhalin Island. Deployment of satellite tags on large cetaceans is an annual U.S.-Russia effort, permitting studies of their movements, wintering areas, and degree of population discreteness. Intensive photography of gray and right whales has allowed American and Russian scientists to verify annual sightings with accuracy. Stepped-up collection of biopsy samples from beluga, gray, and orca whales has resulted in a corresponding increase in genetic research.

Pinnipeds continue to be the major focus of bilateral collaboration under the Marine Mammal Project. For walrus, a major current activity was the analysis and reporting of data collected during a 2006 comprehensive U.S.-Russian aerial and vessel-based survey of Pacific walrus throughout the Bering-Chukchi Seas region. Technological advances, including thermal scanning of walrus "hot spots" from aircraft and infrared photography, have been paired with more traditional survey methods such as visual observation to produce the first count of Pacific walruses since 1990. Recent joint studies of true seals (harbor, ribbon, spotted, ringed, bearded) have been carried out on their abundance, haulout spatial structure, feeding habits, genetics and mortality, with monitoring of Native subsistence harvests and ice conditions. For eared seals (fur seals, Steller sea lions), there has been intensive tagging and branding of newborn pups, analysis of telemetric data for survival rates and reproductive potential, and studies of diet composition, foraging behavior, and diseases.

Sea otters are a species of particular concern for American and Russian scientists. A reported 70% decline in sea otter populations in the northern Kuril Islands between 2004 and 2008 caused alarm, and mirrors a similar decrease in the Aleutian Islands that occurred at the end of the 1990s (Box 13.3). Joint studies seek to explain the reasons for such sharp drops in abundance, with diminished habitat carrying capacity leading to overexploitation of food resources suspected as a possible cause. At the same time, the Commander Islands and Kamchatka coastal populations of sea otters have been stable; Marine Mammal Project scientists are examining the comparative ecology of declining and stable populations.

All the species of marine mammals studied by American and Russian scientists are subject to increasing effects of climate change on their spatial and temporal distributions and alterations in the physical characteristics of their habitats. Joint work is underway to conduct Arctic marine ice-cover modeling at various times of the year and to determine key sea-ice habitat parameters affected by climate, through collection of remotely sensed and optical data, analysis of telemetric information provided by satellite downlinks, and examination of seasonal atmospheric circulation patterns. In the future, climate change and its ramifications will figure large in bilateral activities carried out under the Marine Mammal Project.
In the north, detailed management plans have been developed only for walruses. From the passage of the MMPA in 1972 to the late 1980s, lack of management regulations and increasing demand for ivory for the cottage industry led to increased take, which was poorly recorded. In 1997, the U.S. Fish and Wildlife Service (FWS) and the Eskimo Walrus Commission established a cooperative agreement, including Russian counterparts, with two major components: a Marking, Tagging, and Reporting Program and a Walrus Harvest Monitoring Project. Together, these are intended to reduce waste, monitor subsistence take, collect biological information, and help control illegal take, trade, and transport. Presently, the total reported annual catch in 30 Native communities in Alaska and Russian Chukotka is estimated to be in the order of approximately 3000 animals; the presumed struck-and-lost rate is 40%, bringing the total take to approximately 4000–5000 animals per year. On the Russian side, subsistence hunting is currently regulated via agreements between Native communities and local district authorities that issue annual village catch quotas and collect harvest statistics. In Alaska, Native communities are not limited by federal law to the number of walruses that can be taken. Taking only the head for ivory is considered wasteful and is illegal. Current policy requires hunters to retrieve tusks (tagged for identification), heart, liver, "coak" (brisket), flippers, and "some red meat." The ivory, hides, and penis bone can be sold, but only if transformed into Native handicrafts or clothing. Non-Native catch is forbidden in both countries, and accidental kills, net entanglement, and boat collision losses are low. Shore haulout sites are strongly protected, but poaching and ship, air, and tourist disturbance are common.

A major problem concerns population assessment. Under the MMPA, an "optimum sustainable population" is an objective for all marine mammals. This is particularly difficult in the case of walruses and ice seals due to highly variable seasonal population shifts, inaccessibility, patchy distributions, time spent in water, and logistics in carrying out the assessment. In 2006, the FWS, in collaboration with Russian counterparts, conducted the most ambitious assessment to date, but with uncertain results: i.e., an estimated total of 129,000 animals, with a confidence range of 50,000–507,000 (Speckman et al., 2010). Efforts are currently underway to assess ice seals. Problems of assessment leave management agencies in a difficult position under scenarios of climate change and loss of sea ice. Perhaps most importantly, very little research is being conducted on the ecological consequences of loss of marine mammals. Thus, the effects of rapid economic exploitation and sea-ice diminishment will remain highly speculative.

### 7.7 CULTURAL FACTORS: SUBSISTENCE HUNTING, TRADITIONAL KNOWLEDGE, AND COMMUNITY WELL-BEING

The pinnipeds of Beringia, particularly Pacific walrus, bearded seal, ringed seal, and, to a lesser extent, spotted seal, Steller sea lion, and fur seal, have been actively exploited as food, domestic, and commercial resources by aboriginal communities of the Bering and Chukchi Sea shores of Alaska and Siberia. Hence, the projected changes in pinniped distribution, abundance, and life cycle would certainly act as drivers of socioeconomic change. Understanding the nature of these changes is made urgent by growing evidence of shifts in climate, sea ice, and other physical-ecological parameters that may trigger dramatic restructuring of marine ecosystems of Beringia. Concerns have already been raised about negative impacts of these changes on the area’s indigenous people, their economy, and well-being.

#### 7.7.1 Historical factors

Archaeology offers solid evidence for an established human use of marine ecosystems of the coastal-shelf zone of the
North Pacific as early as 10,000 years ago. The earliest dated record within the Bering Sea proper from the Anungulua Blade site in the eastern Aleutian Islands, dated 8750–8250 BP, suggests a marine economy with diversified use of resources. It is no accident that such an economy first emerged in the richer and more ecologically diverse southern portion of the Bering Sea. Along its southern margins on Kodiak Island and the Alaska Peninsula, several sites of about 6000 BP yield bones of harbor seal, porpoise, sea otter, Steller sea lion, waterfowl, albatrosses, salmon, cod, and halibut. Indigenous marine hunting economies developed somewhat later in the northern Bering and southern Chukchi seas. The earliest evidence of indigenous marine hunting comes from Wrangel Island in the western Chukchi Sea and from the southern Chukchi Peninsula in the northern Bering Sea at about 3500–3800 BP, including middens pits with fractured bones of walrus, seals, and birds, artifacts made of walrus ivory, and engravings featuring scenes of walrus and whale hunting. These offer the earliest proof of human use of the Pacific walrus. In Alaska, a slightly later cultural complex of about 3300 years ago from Cape Krusenstern, southern Chukchi Sea, produced tools for maritime hunting as well as a litter of whale bones. All later coastal cultures of western and northwestern Alaska possessed sophisticated seal-hunting equipment and used walrus ivory for hunting tools, house implements, art, and decorated ritual objects, such as masks.

The first maritime hunters of Beringia were succeeded around 2200–1500 BP by people who were direct ancestors of the historic Inuit (Iñupiat and Yupik) and maritime Chukchi in Siberia. They lived in year-round coastal villages and possessed technology for effective year-round hunting of walrus, seals, and, later, whales—including large skin-covered boats. They also had dogs, used marine-mammal oil for heating and cooking, and stored large supplies of sea-mammal meat and blubber in underground ice cells for use in wintertime. They built their villages at the best walrus- and seal-hunting locations—on cliffs, spits, and offshore islands in the midst of the sea, such as St. Lawrence, and Big and Little Diomede—for efficient open-water and sea-ice hunting.

The peak of the northern Bering Sea economy came with the development of whaling for bowhead whales from large skin boats, presumably around 1000 years ago. Whale hunting triggered population growth and the establishment of permanent villages at sites facing spring ice leads and polynyas along whale and walrus migration routes. The largest coastal villages housed several hundred residents with dozens of skin boat crews engaged in cooperative hunting.

The latest technological breakthrough came with European contacts. Russians introduced iron weapons, nets, and commercial hunting for fur seals and sea otters in the southern Bering Sea: they also exterminated the Steller sea cow (Hippodamalis gigas) on the Commander Islands. The Americans after the 1840s brought firearms, wooden boats, whaling darting- and shoulder-guns, and later outboard motors. They also depleted northern Bering Sea stocks of bowhead and gray whales and Pacific walrus.

The newly introduced technologies made a dramatic impact on the efficiency of Native marine hunting, but Native tactics for hunting in ice leads, on ice floes, and in open water have not been altered profoundly. In many ways, present-day subsistence hunting in the northern Bering Sea remains a direct descendant of indigenous coastal cultures of the region. In the southern Bering Sea, local humans largely shifted towards fur seals, other small seals, and sea otter. Also, abundant local fish, shellfish, and migrating bird resources continued to be actively exploited in both areas.

7.7.2 The walrus in Native subsistence economies

The Pacific walrus population has been exploited by indigenous hunters throughout its entire biological range in the Bering and southern Chukchi Sea for at least the past 2000 years. The area with the heaviest indigenous reliance on walrus is the junction of the Bering and the Chukchi seas, including the mainland shores of Northeast Asia and North America and the islands in between (St. Lawrence, Diomede, Sledge, and King Islands). Local Eskimo (Iñupiat and Yupik) and Chukchi may rightly be called the "walrus people." Traditionally, walruses provided 50–80% of their annual need for human and dog food, depending upon how well the hunting proceeded each year.

Aboriginal hunting equipment might seem "primitive" compared to modern rifles and motorboats. Nonetheless it was sophisticated and quite efficient (Fig. 7.28). Also, Native hunting, particularly of larger animals, tended to single out easier prey, such as juveniles, yearlings, pregnant females, and nursing cows because they were smaller, moved slowly, and were easier to catch. Furthermore, the number taken was not trivial and might have been at least several thousand animals per year. For example, Alaskan Iñupiat hunters of Wales in the Bering Strait killed 322 walruses, 32 white whales, 80 bearded seals, and 4000–5000 other seals in 1890, for a village population of 539 (Thornton, 1931). On the Chukchi Peninsula, Siberia, the reported number of walruses killed by Native hunters in the early 1920s was about 2000–2500 animals per year, with at least a 30–50% loss rate of wounded and uncovered animals. Native catch on the Alaskan side could have been a half of this, making a total of 3000–4000, or up to 5000 per year if killed and lost or wounded animals were included. In the late 1800s, Native catch was substantially higher, perhaps up to 8000–10,000, due to higher commercial demand for walrus ivory.

Those early data do not support a common assumption, namely, that Native subsistence hunting included some sort of "intuitive management" and was done strictly to cover for daily needs. Quite to the contrary, reported annual catches fluctuated dramatically from village to village, often by factors of two to three among years. The reasons for these oscillations were primarily natural. Local ice and weather conditions differed from year to year, thus affecting the position of advancing or retreating ice pack, and the availability of walrus within reach of hunters in small boats. More generally, resources available to Arctic subsistence hunters, either marine or terrestrial, are highly seasonal, and the seasons of "abundance" are usually brief. Also, resource availability is difficult to predict from year to year. These contingencies highlight the crucial significance of surplus catch and surplus food storage. Thus,
huge amounts of fresh meat and blubber were laid in storage or air-dried on open racks each year. The objective was to store more than enough food to last at least until the next season. In sum, walruses provided the most reliable local resource and offered the best return per hunting effort in terms of high-quality food that may be also stored in sufficient quantities. 

The economic contribution in terms of meat, blubber, hides for boat covers, and other products served as the major determinant of the size of human populations. When walrus hunting failed on St. Lawrence Island for two years (1878/9 and 1879/80), more than two-thirds of the island population died of starvation, hypothermia, and related accidents triggered by weakness and a desperate search for food. Presently in both Alaska and Russian Chukotka, only Native people are allowed to hunt for walruses and seals (Fig. 7.29a) and to make full use of their products, including for commercial purposes such as ivory carving and souvenir production. Hunting is done with rifles from small motor-powered boats, but harpoons with floats and lances are still widely used. Walrus meat is actively consumed and stored for lean seasons (Fig. 7.29b), though it is rarely used for dog food, as dog teams are few in modern coastal villages, especially in Alaska, where people use snowmobiles and four-wheelers for traveling. Also, walrus skins are now hardly used for boat covers, except in a few communities, the reason being the adoption of faster aluminum boats. The economic value of ivory, walrus teeth, and skeletal bone for carving and souvenir production is extremely high, particularly on the Alaskan side, where it remains an important source of income.

7.7.3 Indigenous knowledge, co-management, and current environmental threats

Biologists working in the Bering Sea region have long experience in partnering with local hunters, studying the distribution, biology, and annual cycles of marine mammals. Nonetheless, traditional subsistence knowledge was largely treated as “anecdotal evidence,” compared to systematic, natural-science research. Also, interests of local subsistence users were often ignored in biological assessments of marine mammal population health, and even more so in governmental efforts to protect depleted stocks and to establish legally binding management regimes. This situation started to change in the 1970s, with the establishment of the first indigenous marine-mammal management organizations, such as the Alaskan Eskimo Whaling Commission (1976), Eskimo Walrus Commission (1978), Alaska Beluga Whale Committee (1988), Alaska Nanuq (Polar bear) Commission (1994), Pribilof Islands Marine Mammal Commission (1998), and others. In 1992, a new umbrella organization, Alaska Indigenous People’s Council for Marine Mammals (IPCoMM) was established, presently including 18 local marine-mammal commissions and regional groups. Also, a new term, “co-management,” was brought into practice during the 1980s, assuming shared responsibility for the preservation, management, and scientific research on individual species, even local stocks. The actual level of partnership and data sharing varies for different marine-mammal species, being the strongest for the bowhead whale and the weakest for ice seals, with Pacific walrus somewhere in between.

Since the 1990s, indigenous management organizations, anthropologists, and marine biologists initiated a series of special programs for documentation of indigenous and traditional ecological knowledge (TEK) and subsistence hunting practices for many marine-mammal species. The main purpose was to document aboriginal management and conservation practices; an impressive amount of local ecological knowledge has been documented as well. Subsistence hunters helped identify certain morphological stocks at subspecies and/or metapopulation levels, specifically for bowhead whale and Pacific walrus, a feature that had not yet been recognized by marine biologists. Their knowledge was also instrumental in establishing local ranges and groupings for walrus, white whale, ice seals, and polar bear, and in documenting the specifics of seasonal migrations, reproductive cycles, and associations with sea ice. Substantial amounts of new publications have resulted from this cooperative work, both as gray literature and in academic publications (e.g., Bogoslovskaya, 2003; Bogoslovskaya et al., 2007; Freeman et al., 1995; Huntington et al., 1999;
7.8 ARE BERINGIAN PINNIPEDS AND THE BERING SEA ECOSYSTEM AT RISK?

The looming issue for the Bering Sea ecosystem, its species, and its Native people concerns emergent conditions and lag effects caused by climate change. Pinnipeds respond to environmental changes and human activities in ways that are poorly understood, and only uncertain hypotheses can be posed about their resiliency to rapid ecosystem shifts. Changes in abundances of large, slow-growing animals with low reproductive rates may lag behind projected environmental transitions, thereby making timely management measures difficult to implement. Therefore, current population assessments may reflect species' adjustments to past conditions, and trends may not become evident until some time after density-dependent responses are initiated. In addition, both the animal species and indigenous people of Beringia have been long subjected to recurring environmental shifts, often dramatic in time and scale, and thus have developed certain mechanisms for both short-term rapid response and long-term adjustment. Unfortunately, sufficient population or environmental baselines against which to measure change are insufficient for making future projections (Jackson et al., 2011).

The result of changing conditions on Bering Sea pinnipeds is not necessarily extinction, but extirpation throughout much of their ranges, remnant populations for some of them, accompanied by expected ecosystem consequences. With respect to sea-ice-dependent pinnipeds, similarities between the hierarchical structure of sea ice and scaled habitat associations may be functional and evolutionary. Recent trends towards high inter- and intra-annual variability of sea-ice conditions at multiple scales and towards reduction and structural changes of seascapes may play reinforcing roles in shifting marine-mammal habitats and abundances. Consequently, it is highly

Krupnik and Ray, 2007; Metcalf and Krupnik, 2003; Noongwook et al., 2007; Ossewa et al., 2004; Salomon et al., 2011)

Certain indigenous organisations, like the Alaskan Eskimo Whaling Commission and the Nanuq (Polar bear) Commission, accepted responsibility for enforcing community hunting quotas, conducting periodic game counts, imposing guidelines for non-wasteful catch, and training young hunters in effective traditional practices. The current trend, particularly in Alaska, is towards more collaboration, or at least consultation, among subsistence users and federal and state agencies in policy and management decisions concerning Beringian marine mammals.

The recently completed International Polar Year (IPY) 2007–8 featured several collaborative projects that combined efforts by scientists and indigenous residents in observation and knowledge documentation related to marine mammals and environmental change in Beringia and other polar regions (Krupnik et al., 2011). Hunters, particularly in the communities adjacent to Bering Strait, report earlier spring migration of walruses and bowhead whales; more rapid retreat of the ice pack, which shortens the spring hunting season; and later fall advance of pack ice and associated marine species. As a result of IPY 2007–8, new collaborative observational efforts have been introduced, such as long-term ice monitoring in several communities (Krupnik et al., 2010) and the Sea Ice for Walrus Outlook program since 2010 (SIWO online). The latter combines sea ice and walrus observations from scientists, local villages, satellites, and ships, and reports directly to walrus hunters in indigenous communities.

As a result of these recent developments, any future debates about the health of Beringian marine mammals and of their prospective listing as endangered or threatened species due to climate change and ice diminishment will most likely include substantial components of local biological and ecological knowledge, and observations by indigenous stakeholders.
likely that the variable conditions of the recent past will become more pronounced in the future, with implications for pinnipeds, other ice-dependent biota, the ecology of polar regions, and lifeways of many of its indigenous peoples.

In this context, a new, expanded research agenda is required, more directed toward ecosystem/habitat relationships and less toward numerical population assessments. Management agencies are forced to spend a majority of their resources on uncertain population enumeration, ironically a consequence of requirements of the the Marine Mammal Protection and Endangered Species acts' requirements for population assessment upon which management is presumed to be based. However, the major needs are for vastly improved knowledge of species' natural history, behavior, demographics, and ecological functions as these may be directly or indirectly related to scenarios of environmental change. Lacking that, the result may be to "miss the signal by focusing intensely on what is all too commonly statistical noise" (Jackson et al., 2011).

REFERENCES


Call KA, Ream RR (2012) Prey selection of subadult male northern fur seals (Callorhinus ursinus) and evidence of dietary niche overlap with adult females during the breeding season. Marine Mammal Science 28, 1–15.


