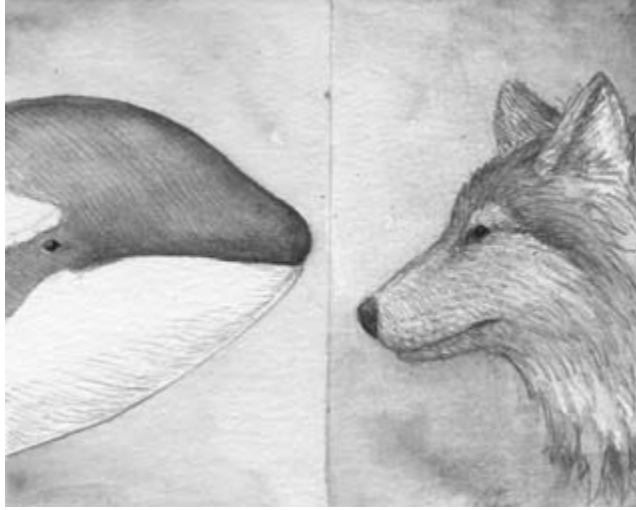


Killer Whales as Predators of Large Baleen Whales and Sperm Whales

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Three or four of these voracious animals do not hesitate to grapple with the largest baleen whales; and it is surprising to see those leviathans of the deep so completely paralyzed by the presence of their natural, although diminutive enemies. Frequently the terrified animal—comparatively of enormous size and superior strength—evinces no effort to escape, but lies in a helpless condition, or makes but little resistance to the assaults of its merciless destroyers.

CHARLES M. SCAMMON (1874), an American whaleman

The position of the killer whale (*Orcinus orca*) at the top of the marine trophic pyramid is unquestioned. It consumes a remarkable variety of organisms, ranging in size from small schooling fish to blue whales (*Balaenoptera musculus*) and as taxonomically diverse as seabirds (ducks and alcids; Bloch and Lockyer 1988), marine reptiles (leatherback turtles, *Dermochelys coriacea*; Caldwell and Caldwell 1969), elasmobranchs (Fertl et al. 1996; Visser 1999a), and terrestrial mammals as they swim across coastal channels (e.g., cervids; Dahlheim and Heyning 1999). If killer whales have any natural predators, these would be other killer whales, as there is some evidence to suggest “cannibalism” (Shevchenko 1975; but see Pitman and Ensor 2003).

The interactions of killer whales with other marine mammals range from predation to coexistence (Jefferson et al. 1991; Weller 2002). Foraging specialization is a typical feature:

The *transient* ecotype preys regularly, if not exclusively, on marine mammals, whereas the *resident* type preys mainly on fish (Ford and Ellis 1999; Baird 2000). In recent years, field observations of predatory behavior have led to several hypotheses concerning relationships between killer whales and the great whales—the large baleen whales and the sperm whale (*Physeter macrocephalus*). Corkeron and Connor (1999) argued that the low-latitude migrations of some baleen whales represent a strategy for avoiding killer whale predation on calves. Although Clapham (2001) forcefully contested that idea, citing the humpback whale (*Megaptera novaeangliae*) as an example, Pitman et al. (2001) subsequently proposed that “killer whales, through their predatory habits, represent a much more important selective force in shaping life history traits of individual marine mammal species, and in structuring their communities, than has generally been

acknowledged.” After witnessing several attacks on sperm whales off Mexico and California, Pitman et al. suggested that both the social organization and the sexually segregated distribution of sperm whales could be at least partly the result of predation pressure from killer whales. Earlier papers by Reeves and Mitchell (1988b) and Finley (1990) had argued that killer whale predation was likely an important factor in shaping the behavior, migration strategies, and life history of bowhead whales (*Balaena mysticetus*). There are many more first-hand descriptions of killer whale attacks on gray whales (*Eschrichtius robustus*) than on any other species of large whale (cf. Jefferson et al. 1991; Melnikov and Zagrebin 2005; and subsequently in this chapter), and young gray whale calves are considered “particularly vulnerable, even while under the watchful eye of their mothers” (Weller 2002; also see Black et al. 2003; Ternullo and Black 2003).

Our goal in this chapter is to add to the discussion of killer whales as primary predators of large baleen and sperm whales. If attacks by killer whales on these large cetaceans were common, a set of outcomes might be expected. These would include a relatively high incidence of witnessed attacks, detection of maimed bodies of victims and escapees, and clear evidence of specific antipredator behavior. Assessment is complicated, however, by the logistics of making field observations in oceanic systems, where much of the relevant behavior occurs underwater—in contrast to open terrestrial landscapes, where the interactions between large carnivorous mammals and their prey can be more readily observed. Hence, we are forced to rely on two less direct approaches.

First, given existing knowledge of large or medium-sized land carnivores, we consider whether inferences about *their* current roles in shaping ecological and prey dynamics would remain valid if based exclusively on historical observations. In other words, would historical anecdotes stretching back some 200 years, without the benefit of marked individuals and current study methods, have been sufficient to appraise a terrestrial predator’s ecological role? This question seems instructive, because we have little information apart from historical anecdotes with which to evaluate the importance of ecological interactions between killer whales and large whales in an earlier context when populations of the latter (if not also the former) were much greater than they are today.

Second, given the infrequency of witnessed predation by killer whales on large whales, we use indirect assessments of predation events and the antipredator behavior of prey to infer how killer whales might influence the spatial and population responses of other cetaceans. The following specific questions are addressed here:

1. Does predation occur sufficiently often to make it a major factor in regulating the populations of large whales?
2. What is the sex and age distribution of large whale prey taken by killer whales?

3. What can be inferred about the consumed:unconsumed ratio of the prey body mass when killer whales kill a large whale?

The observations and comparisons reported here span several centuries, stem from different parts of the world, and derive from accounts of scientists and hunters, whose astuteness and training have varied. Cumulatively, however, these diverse lines of evidence suggest that killer whales once played a role in determining the behavior and distribution of at least some populations of large cetaceans.

Historical Anecdotes about Terrestrial Carnivores: Were Past Insights Accurate?

While terrestrial and oceanic systems differ in important ways, the fundamental argument here is that predation as a selective force shapes the behavior of prey in similar fashion across systems. The primary issue, however, is not whether behavioral adaptations parallel species in respective systems, but whether sporadic, anecdotal observations of secretive or difficult-to-study species are likely to lead to accurate depictions of ecological dynamics. Before such tools as radio telemetry and biochemical analyses became available, speculations about prey choice on the part of hunting carnivores and about defense strategies of their prey were necessarily based on witnessed observations. Our understanding of the ecological dynamics of predators and prey, whether terrestrial or marine, large or small, will continue to be revised as new methods are applied and larger samples of observations become available. As a way of anticipating how views of killer whales in relation to their large whale prey may change in the future, we look back at what was once inferred about the ecological roles of three terrestrial carnivores and how understanding of them has been modified with studies involving improved techniques.

THE GRIZZLY BEAR: *Ursus arctos*, also called the brown bear in Europe and Asia, has been characterized ecologically in different ways through time. Early reports implied an ecological niche associated with herbivory and omnivory. During the 1830s and 1840s, Osborne Russell and John C. Fremont noted that bears in the Rocky Mountains fed in areas with willows and cherry trees, and William Kelly indicated that they dug for bulbs and roots in California (Bass 1996). Reports from as early as the 1600s also noted that grizzly bears fed on marine mammal carcasses along the California coast (Storer and Tevis 1955).

While grizzly bears are clearly omnivorous and subsist primarily on vegetation (Mattson et al. 1991), it is now clear that meat and fish are also important components of the diet (Hildebrand et al. 1999). Grizzlies have been shown to be capable predators of both juvenile and adult ungulates as large as elk (*Cervus elaphus*) and moose (*Alces alces*) (Gunther and Renkin 1990; Mattson 1997; Berger et al. 2001a). In fact, recent work with radio-collared neonatal moose in Alaska

TABLE 14.1
Chronologically Changing Insights or Speculations about Terrestrial Carnivore Ecology and Behavior

Species	Period	Insight	References
Grizzly bear	1830s–1880s	Primarily an omnivore and herbivore	Osborne and Fremont journals (Haines 1965; Schullery 1988; Clark and Casey 1996)
	Early 1990s–today	Effective (population-regulating?) predator; large effects on survival of neonatal caribou, moose, and elk	Gasaway et al. 1992; National Research Council 1997; Mech et al. 1998; P. J. White, personal communication
Wolverine	?–1980	Vicious scavenger and predator	Seton 1953
	1980–today	Uncertain	P. J. White, personal communication; Mech et al. 1998
Spotted hyena	1790–early 1960s	Scavenger	Kruuk 1972
	Mid 1960s–today	Effective predator	Kruuk 1972; Mills 1990

suggests that bear predation can limit population growth (Gasaway et al. 1992). In addition, grizzly bears were found to be more effective predators than wolves (*Canis lupus*) on 155 young radio-collared caribou (*Rangifer tarandus*), respectively accounting for 41% and 35% of the total mortality (Mech et al. 1998). Among 50 radio-collared Yellowstone elk fawns, bear (both grizzly and black, *Ursus americanus*) predation was responsible for 60% of the total mortality, with grizzly bears accounting for twice as much mortality as was caused by wolves (32% vs. 16%, respectively; P. J. White, personal communication).

Those findings (summarized in Table 14.1) illustrate how perceptions of bear ecology have changed over time and suggest that grizzly bears have played apex roles in ecological systems. Storer and Tevis (1955: 17) believed that grizzly bears shaped the “original native biota of California,” their food sources including bulbous plants, clovers, and grasses as well as berries, seasonally (e.g., elderberry, manzanita, and blackberry). Those same authors speculated that Native Americans avoided areas used by grizzly bears, just as some hunters of ungulates in the Yellowstone ecosystem today avoid areas with high densities of grizzlies (Berger, unpublished data). The loss of bears in at least parts of this ecosystem has led to a cascade of events that ultimately decreased avian diversity via the release of herbivores, followed by intensified herbivory in riparian plant communities (Berger et al. 2001b). The sometimes-subtle influences of bears at multiple trophic levels would not have been detected or recognized without detailed studies made possible, in part, by modern research tools and techniques (Hildebrand et al. 1999).

THE WOLVERINE: *Gulo gulo* remains a relatively understudied forest and sub-Arctic carnivore across North America, Europe, and Asia. An early account described it as exceeding the weasel (*Mustela* sp.) by 50 times in “courage . . . slaughter, sleeplessness . . . and demonic fury” (Seton 1953). Initially, wolverines were considered major predators of some native ungulates, but that view has been modified, at least to some extent, as more information on food habits has become available (Magoun 1985; Landa 1997; Persson 2003). For instance, wolverines have a far

smaller impact on neonate, let alone adult, mortality of ungulates than bears or wolves have: <1% for juvenile caribou (Mech et al. 1998); <1% for juvenile elk (Smith and Anderson 1996; P. J. White, personal communication); <1% for juvenile moose (Ballard et al. 1991; Testa et al. 2000). Although predation on adult ungulates may occur occasionally, it is very infrequent, judging by the number of radio-collared ungulates that die from other causes. Clearly, our view of the wolverine’s ecological role has changed during the past 50 years with the benefit of intensive research using modern tools and methods.

THE SPOTTED HYENA: *Crocuta crocuta* has been among the most misunderstood mammals, with misconceptions dating back to 1790 (Kruuk 1972). Early reports implied surprise when hyenas were observed to kill healthy prey. It was not until 1964 that Eloff (1964) inferred from tracks in the sand that hyenas hunted and killed more than just sickly prey. Subsequent study has confirmed that spotted hyenas in eastern and southern Africa are effective predators on large ungulates (Kruuk 1972; Mills 1990).

The three foregoing examples (see Table 14.1) show that reliance on anecdotal observations can cause us to misunderstand the relationships between carnivores and their prey. To be fair, anecdotes can also be highly informative. Indeed, ranchers had long insisted that coyotes (*Canis latrans*) were often responsible for low fawn recruitment in pronghorns (*Antilocapra americana*), a belief recently verified regionally by field work and explored by modeling (Byers 1997; Phillips and White 2003). Given our present knowledge about the ways that mammalian carnivores affect the dynamics of terrestrial and nearshore marine ecosystems (Estes et al. 1998; Soulé et al. 2003), however, it seems prudent to proceed cautiously in interpreting qualitative evidence dominated by historical anecdotes.

Observations by Whalemén

Jefferson et al. (1991) cautioned that reports from “whalers and other untrained observers” needed to be interpreted skeptically, yet at times biologists have been too eager to

dismiss such observations. For example, the description by whalers of a killer whale attack on a group of sperm whales off southern Africa (Best et al. 1984) was considered inconclusive by Jefferson et al. (1991), who neglected the statement by Best et al (1984: their Fig. 7) that “killer whales do occasionally prey on sperm whale calves,” a statement supported by photographs of a stranded animal. With the recent well-documented observations by biologists of successful attacks on sperm whales (Pitman et al. 2001; see later), historical reports by “untrained” whalers seem more credible.

Descriptions of killer whales attacking large whales are nevertheless remarkably rare in the first-hand narratives of whalers. One of us (Reeves) has examined many hundreds of whaling logbooks from the eighteenth and nineteenth centuries. Although sightings of killer whales were frequently recorded, often on whaling grounds (Reeves and Mitchell 1988a), descriptions of attacks or evidence of attacks (e.g., finding dead or wounded whales) were uncommon. Other whaling historians who have handled large numbers of logbooks and journals as well as published memoirs of whalers and explorers report similar experience (Michael Dyer, New Bedford Whaling Museum Library, New Bedford, MA, personal communication, October 2003; Klaus Barthelmess, Cologne, Germany, personal communication, October 2003). We emphasize, however, that lack of observations of whale behavior and natural history is the norm in whaling logbooks and first-hand narratives; few whalers had an interest in, or a knack for relating, such things.

While on a sperm whaling voyage to the Japan Ground, the ship *Phoenix* (1847–51MS) passed two right whales (*Eubalaena japonica*) and several humpbacks on February 28, 1849. The next day, at 35°52'N, 130°29'E, the ship's logbook recorded: “Saw a dead humpback surrounded by a school of killers.” No further mention of this event appears in the logbook, so it is impossible to be certain that the humpback was a victim of predation.

Another account is much more detailed. While at anchor in Magdalena Bay on the Pacific coast of Baja California (February 14, 1858), the crew of the whaleship *Saratoga* observed an attack on gray whales (*Saratoga* 1857–58MS):

saw 8 or 10 killers attacking a cow whale with her calf close in shore, the whale fighting bravely to protect her offspring, using . . . her flukes and fins, which were in constant motion, striking furiously . . . at her aggressors. . . . The battle had lasted about half an hour when we saw the water highly discolored with blood . . . when [a boat] arrived . . . both the whale and the killers had disappeared, they had no doubt killed the calf and taken it down.

The *Saratoga's* log further describes killer whales and their typical way of attacking large whales: “Their favorite morsel of food is the tongue, they attack the whale in concert, worrying him until they force his mouth open, when they seize upon the tongue and soon dispatch him.” Also, this logbook claims that whalers often took advantage of killer whales to

aid them in catching whales: “Whales are frequently taken by whalers, when attacked by killers, being nearly exhausted, a boat pulls up to him, fastens and he becomes an easy victim to the lance, the killers not daring to attack the boat.” This description, and others like it (e.g., Brown 1887: 284), anticipate the later accounts of “symbiosis-like” interactions between killer whales and shore whalers hunting right and humpback whales in Australia (Dakin 1934; Wellings 1964; Gaskin 1972; Mitchell and Baker 1980).

Killer whales often scavenged whales killed by whalers (see Whitehead and Reeves 2005). Charles Wilkes, commander of the U.S. Exploring Expedition, 1838–1842 (see Pond 1939), was told by whalers that killer whales sometimes dragged whales away from boats as they were being towed to the ship (also see Scammon 1874: 90). In modern industrial whaling, carcasses flagged for retrieval or fastened to the catcher boat were subject to scavenging (McLaughlin 1962: 130; Ash 1964: 56; Gaskin 1972; Mitchell and Reeves 1988). Heptner et al. (1996: 689–690) mentioned that killer whales “regularly tore out the tongues of dead and air-filled whales” in the Antarctic; these authors included a photograph, as did Gaskin (1972: 120), and noted the economic implications of the oil lost as a result of this scavenging. Interestingly, though, Heptner et al. had received no reports of killer whales tearing chunks of blubber from, or biting the fins and flukes of, whale carcasses. Gaskin, in contrast, claimed that in some areas near the South Shetland Islands, flagged carcasses of rorquals that were not recovered within 24 hours sometimes had their blubber stripped away by killers. He agreed with Heptner et al., however, that “usually” only the tongues were consumed. It was reportedly very difficult to deter the killers, “even by opening fire” on them (Heptner et al. 1996).

Gray Whales

Rice and Wolman (1971: 98–99) downplayed the significance of killer whale predation on gray whales despite the evidence adduced by Andrews (1914, 1916b) indicating that they were frequently preyed upon or scavenged by killer whales in Korean waters. Since the early 1970s, the evidence of predation along the North American coast has mounted. Jefferson et al. (1991) listed nine successful attacks, five apparently unsuccessful, and at least seven in which the outcome was uncertain or the evidence circumstantial. The lack of confirmation of a successful outcome (i.e., a dead prey), however, was sometimes due to interruption of observations. For example, an observation of killer whales closing on a pod of gray whales in the northern Bering Sea in May 1981 ended when the observers “had to leave the area because the aircraft was low on fuel” (Ljungblad and Moore 1983). Jefferson et al. (1991) classified this report as a “No” kill, but in fact the observation team had no opportunity to confirm the outcome one way or the other.

The relatively numerous accounts of attacks on gray whales establish several things. First, they show that killer whale

predation on gray whales is not new, dating at least as far back as the mid-1840s, when commercial whaling on gray whales began along the coast of Baja California (see the *Saratoga* event described in the preceding section; Scammon 1874: 90). Second, there is no basis for believing that such predation occurred only, or with greater frequency, when the gray whale population was especially large (i.e., before it was decimated by whaling). Attacks observed in about 1907 (Pond 1939), the 1940s (Walker 1949), and the early 1950s (Cummings and Thompson 1971) would have taken place when the eastern Pacific population of gray whales was well below its carrying capacity level. Third, predation is not limited to a particular segment or segments of the gray whale's annual distributional range; attacks have been observed in the calving/mating grounds off Baja California, at many points along the migration route between Mexico and Alaska, and on the feeding grounds in the Bering and Chukchi seas (Melnikov and Zagrebina 2005). Finally, even though calves and yearlings appear to be especially vulnerable, gray whales of any size are subject to attack.

Raymond M. Gilmore (1961) was an experienced gray whale watcher, having spent five field seasons in the lagoons of Baja California and many years observing the migration off San Diego, California. He had never seen killer whales in the lagoons, and although he saw them occasionally in California coastal waters during the gray whale migration, they usually "passed the gray whales without attack" or remained "at some distance without show of interest, or vice-versa" (Gilmore reported one unsuccessful attack by six killers on two grays off La Jolla in 1950). Theodore J. Walker (1975), Gilmore's contemporary with similarly long experience watching gray whales in Mexico and California, was aware of "isolated reports" of attacks that "occasionally" resulted in kills of gray whales, but he was, like Gilmore (and Rice and Wolman 1971), doubtful that killer whale predation was a significant feature in the lives of gray whales. Having spent six field seasons observing gray whales in Laguna San Ignacio (1977–1982), Jones and Swartz (1984: 342) reported that only one of the 32 stranded carcasses that they examined (an "immature") was the result of a killer whale attack. Swartz (1986) did not even mention killer whales in his review and analysis of the gray whale's migratory, social, and breeding behavior. Jorge Urbán-Ramírez (personal communication, December 2003), who had been studying gray whales in the lagoons and along the outer coast of Baja California annually for a decade (see Urbán Ramírez et al. 2003), had not seen killer whales in the lagoons, nor had his teams of researchers seen them close to gray whales during aerial and shipboard surveys outside the lagoons.

Jones and Swartz (2002) nevertheless referred to "frequent" reports of killers feeding on the tongues of gray whales and claimed that killer whale tooth rakes were "often" seen on the bodies of living gray whales. Those authors also speculated that avoidance of killer whale predation "might be a primary benefit to females leaving polar waters to give birth in the subtropics." Conversely, at the other end of the migration, Moore et al. (1986) suggested that the movement of

females and calves-of-the-year into the Chukchi Sea during the summer feeding season could represent a strategy to avoid killer whales, which were considered less common there than in the Bering Sea (cf. Forney and Wade, Chapter 12 of this volume). In fact, Moore et al. likened this situation to that on Isle Royale, Michigan, where moose cows with calves occupied suboptimal foraging areas that were "wolf-free," whereas solitary adult and yearling moose opted for prime foraging habitat and coexisted with wolves. Killer whale attacks on gray whales were said to be "fairly common" during the summer months in the Bering Strait region (George et al. 1994: 252; also see Melnikov and Zagrebina 2005). If gray whales migrate in part to reduce the risks of predation on calves, the long-range movements of killer whales can be seen as a counterstrategy. *Transient* killer whales from southeastern Alaska regularly appear in spring (April and May) in Monterey Bay (California), where they prey on northward-migrating gray whale calves, sometimes at least injuring, if not killing, mothers (Goley and Straley 1994; Black et al. 2003; Ternullo and Black 2003). Attacks on gray whales in Monterey Bay have occurred "on an almost predictable basis" since the late 1980s (Weller 2002: 993).

Although Jones and Swartz (2002: 533) concluded that "predation pressure does not appear to be a significant determinant in the gray whale's social organization," aspects of gray whale behavior have almost certainly been shaped by killer whale predation, as shown experimentally in playback experiments using recorded killer whale sounds (Cummings and Thompson 1971). Along the California coast, gray whales respond to the presence of killer whales by moving quickly and quietly into nearshore kelp beds and becoming quiescent; similar responsive behavior has been observed along the Korean coast (Andrews 1914, 1916b). When trying to avoid detection, gray whales typically "snorkel," meaning that they exhale underwater and barely expose their blowholes at the surface to inhale (Dahlheim and Heyning 1999). "Spyhopping," in which a whale stands vertically with the entire head exposed above the surface, is an oft-described feature of gray whale behavior, especially in the Mexican calving lagoons. Although gray whales spyhop under many circumstances when the threat of killer whale predation is not evident, one of the functions attributed to this behavior is visual scouting (Eberhardt and Evans 1962), including "looking for killer whales" (Cummings and Thompson 1971; Baldrige 1972). Cetaceans generally have good vision both in air and under water (Mass and Supin 2002). We are nevertheless skeptical of whether the eyes of a spyhopping gray whale would be far enough above the water surface to allow scanning at any but very close range, even in calm to moderate sea states.

Bowhead Whales

Most reports of killer whale attacks on bowhead whales are secondhand, having been described to biologists by Inuit hunters. Jefferson et al. (1991) listed 12 separate events, only two of which were witnessed by a biologist, both with an

uncertain outcome (Finley 1990). Relatively few reports have emanated from the western Arctic, where most modern research and monitoring of bowhead whales have taken place (only one of the 12 events listed by Jefferson et al. was from outside the eastern Arctic, and that was from the Sea of Okhotsk; also see George et al. 1994; Melnikov and Zagrebin 2005). One explanation could lie in the same reasoning as mentioned in the previous section in relation to gray whales: Killer whales are much less common in the Chukchi and Beaufort seas (where most western Arctic bowhead whales spend the open-water season) than in the Bering Sea (where bowheads occur mainly during the dark, ice-affected season). George et al. (1994) doubted that the bowhead migration out of the “rich feeding grounds” of the Bering Sea and into the Beaufort Sea during the spring and summer would represent a predator avoidance strategy, yet they offered no clear basis for such skepticism. In those authors’ view, the near absence of scarring on small bowheads taken by hunters was explained most plausibly by the fact that older bowheads have longer times to acquire scars (“greater exposure to killer whale attack”) and/or that few small bowheads survive attacks.

In contrast to the western Arctic, predation in the eastern Arctic is thought to be relatively common. Bowhead whales and other Arctic marine mammals are well known for behavior that Finley (2001) called “killer whale phobia.” Inuit of the eastern Canadian Arctic apply a specific word, *ardlungaijuq* or *aarlungajut*, to this fear of killer whales exhibited by whales and seals. Finley cited the belief of British whalers that differences in the summer distribution of bowheads of various sex and age classes reflected differences in their vulnerability to killer whale predation. Adult males were believed to remain in the “most exposed and open situations,” while females and juveniles penetrated farther into the ice. Finley (1990) interpreted the “coast-hugging” tendencies of autumn-migrating bowheads, “in the absence of protective ice cover,” as an adaptive response to killer whale predation (this may also be true of gray whales, especially during their spring migration, although alternative hypotheses are that they follow the coastline to facilitate navigation or to take advantage of sublittoral food resources; Braham 1984). In several instances summarized by Mitchell and Reeves (1982), bowheads came close to shore or wedged themselves into narrow ice cracks to avoid killers, making them easy targets of hunters.

Finley (1990: 151) considered predation to be significant for depleted bowhead whale populations, “particularly when killer whales have an abundant alternate food source, as they do in the Eastern Arctic (i.e., the killer whale population was not food limited when the bowhead population declined).” The alternative prey base that Finley had in mind would include phocid seals, narwhals (*Monodon monoceros*), belugas (*Delphinapterus leucas*), and possibly walrus (*Odobenus rosmarus*) (see also Reeves and Mitchell 1988b). His basic suggestion that bowhead whales in the eastern Arctic may be in a predator pit (Southwood 1975, as

cited by Bergerud and Elliot 1986) is consistent with the views expressed by Moshenko et al. (2003: 22), citing a published review of hunter knowledge (NWMB 2000) and the opinions of Canadian Inuit who regard killer whales as “possibly the greatest threat to bowhead recovery.” The idea that heavy ice confers protection from killer whale predation is implicitly supported by claims that in recent years with relatively light ice conditions in Foxe Basin (e.g., 1999), more killers were observed and unusually high numbers of bowheads were found dead (Moshenko et al. 2003: 24). It was reported that in western Greenland, during a four-day period in April 2002, “about 10 bowhead whales out of a pod of about 30 were killed by a large, uncounted pod of killer whales” (IWC 2003: 46). It has not been possible to verify that this event occurred, and we are very skeptical of its authenticity.

Sperm Whales

The infrequency of first-hand descriptions of attacks on sperm whales, which were the subjects of large-scale, worldwide whaling for approximately 200 years, is especially puzzling. Berzin (1972: 273) reported that remains of this species had not been found in the stomachs of killer whales and that Soviet scientists and whalers had reported “few cases of attack of killer whales on newborn sperms.” He concluded that killer whales should not be considered “serious enemies of the sperm whale” and that adult male sperm whales were “too strong for killer whales and thus immune to attack while a herd [of females and young] possesses a sufficiency of strong instinct of mutual aid to give them protection”—a view shared by Heptner et al. (1996: 833). Jefferson et al. (1991) mentioned only five specific records of attacks and one generalized account. The aforementioned observation off southern Africa of a group of sperm whales in a typical defensive formation (“rosette”; see later) being encircled by killer whales was designated a “No” kill by Jefferson et al., yet their source (Best et al. 1984) provided no indication of the outcome (i.e., it should have been classified as “[?]”). Furthermore, Best et al. (1984) illustrated “killer whale damage” on a sperm whale calf that stranded near Cape Town (not mentioned by Jefferson et al.). Jefferson et al. (1991) also dismissed as inconclusive and “second-hand” the reference by Yukhov et al. (1975) to a filmed attack on a group of sperm whale females and calves.

Several lethal attacks have been observed or otherwise documented in recent years. Visser (1999b) summarized interactions between killer whales and sperm whales off New Zealand, including the finding of a fresh carcass of a 9.8-m female sperm whale that bore clear evidence of having been attacked and mauled by killer whales. Visser and Bonoccorso (2003) reported an observation off Papua New Guinea in which at least 20 killer whales “appeared to be hunting” a group of about 12 sperms, including calves, but they considered this secondhand record to have been nonpredatory

(citing terminology of Jefferson et al. 1991). In Indonesian waters, Kahn (2003) witnessed the serious (probably lethal) wounding of a sperm whale calf and a subadult when five killers encountered a loosely associated pod of sperms. The attack did not appear to have been sustained to a point where either of the victims was killed outright, but the sperm whales were bleeding profusely and their mobility was seriously impaired before the killers moved slowly away from the area and beyond visual range of the observation vessel.

Pitman et al. (2001) provided the first well-documented record of a sustained, lethal attack. The first of three encounters (all in the eastern North Pacific) involved a group of eight sperm whales that formed a rosette—all animals huddled at the surface with their heads together and tails pointing outward—possibly in response to the presence of a group of about six killer whales. This event was confounded by the simultaneous presence of a school of short-finned pilot whales (*Globicephala macrorhynchus*), and there was no direct evidence of an attack by the killer whales before observations had to be terminated because of deteriorating weather. In the second encounter, observations began when an attack was already under way (with a large slick of blood and oil in the water) on a group of about nine female and subadult sperm whales in rosette formation. Up to about 35 killers were in the area, although only female and immature individuals were seen attacking the sperms, following what the authors called a “wound and withdraw” strategy (16 separate “attacks” took place during about four hours of observation). At least one of the sperm whales was killed and at least partially eaten and others were seriously injured. Pitman et al. concluded that at least three or four of the “survivors” were mortally wounded, “and it is quite possible that the entire herd died as a result of injuries from the attack.”

The third encounter described by Pitman et al. (2001) occurred only five days after the second one. During the course of a much less energetic and sustained attack, a series of small groups of sperm whales coalesced into an aggregation of about 50 individuals, apparently in response to the presence of five killer whales. The sperms formed a “spindle,” consisting of one to five animals abreast, 12 to 15 animals long, all facing the same direction. An adult female killer made several forays into the midst of the sperms and caused an oily slick to appear, “suggesting that one or more had been bitten, although no blood was visible.” This encounter ended with no apparently serious damage having been inflicted on the sperm whales. Whitehead (Chapter 25 of this volume) estimates that an average female sperm whale in the tropical Pacific might experience as many as 150 killer whale attacks in her lifetime.

Behavior of Killer Whales during Attacks

Some features of the specialized hunting behavior of killer whales were summarized by Jefferson et al. (1991): cooperation and coordination; biting the flukes and flippers to

impair the prey’s swimming ability; and swimming or “leaping” onto the whale’s back to impede its progress or prevent it from respiring normally. One feature that they did not mention explicitly, but implied by reference to internal injuries, is body ramming. Typically, when hunting gray whales in Monterey Bay, the killers chase and tire the female and calf, separate the calf from its mother, and then ram and “body slam” the calf repeatedly (Ternullo and Black 2003; also see Goley and Straley 1994). Body ramming has also been observed when killers are hunting gray whales on the northern feeding grounds (Melnikov and Zagrebin 2005).

Like other large pack-hunting predators, killer whales combine stealth with probing and testing of the prey. Judging by the fact that so many observed attacks end in no kill, or at least in an uncertain outcome (Jefferson et al. 1991: their Appendix I), together with the relatively high incidence of killer whale-inflicted scars and injuries in populations of large whales (see subsequent paragraphs), many attacks are probably unsuccessful. In fact, some attacks may be initiated primarily to provide learning opportunities for young killer whales.

Some specialization of roles has been noted. Adult females often appear to be the most active and effective individuals during the actual killing phase of an attack on a large whale (Silber et al. 1990; Finley 1990) although pairs of adult males have also been seen working together to kill gray whale calves (Ternullo and Black 2003). An adult male participated in the successful attack on sperm whales just described only to “finish off” a whale that had first been critically wounded by the females and immature killers. Pitman et al. (2001) considered this feature of the attack reminiscent of lions (*Panthera leo*), where adult males often use their larger size to move in and appropriate prey (Schaller 1972; Bertram 1979). Killer whales have been seen to continue feeding on a dead gray whale calf for up to 20 hours, with many more individuals participating than just those involved in the attack. Again, these features are in some respects reminiscent of lions.

Killer whales that prey on marine mammals usually stop vocalizing, or vocalize relatively little, while on the hunt (e.g., Cummings et al. 1974; Ljungblad and Moore 1983; Kahn 2003). Presumably, passive listening trumps active echolocation as a means of locating and tracking large prey that, like the killers themselves, must cross the air-water interface to breathe and that also depend on sound to communicate and echolocate. During a lethal attack on a female gray whale and calf in Monterey Bay, the killer whales reportedly “vocalized frequently during the entire episode” (Goley and Straley 1994). However, the attack had already been under way for about 40 minutes when Goley arrived on the scene and began audio recording. While silence may contribute to the stealth and prey-location phase of an attack, active sound processing presumably becomes allowable, and perhaps functionally important, once contact with the prey has been established. Although the sounds associated with an

attack may attract distant killer whales to the site, allowing them to benefit should a kill occur, this possibility has been judged unlikely (Deecke et al. 2005).

Size/Age Preferences

The question of whether killer whales hunt selectively for whales of particular age or sex classes is critical for evaluating the ecological significance of predation. Scammon (1874: 90) was equivocal about the intensity and significance of killer whale predation on whales, concluding on one hand that “the larger Cetaceans” were attacked “rarely,” but also that killers “chiefly prey with great rapacity” on the young of baleen whales. This latter suggestion appears largely consistent with the evidence amassed since his time (Dolphin 1987; Jefferson et al. 1991; Black et al. 2003; Melnikov and Zagrebina 2005). Also, however popular the notion may be that predators such as killer whales have a “purifying” effect on prey populations by selectively removing diseased, defective, and postreproductive individuals (cf. Bertram 1979: 231), the evidence of predation by killer whales provides little or no support for it.

The relatively frequent examples in the literature where killer whales attack and attempt to intimidate or debilitate large prey, but then abandon the hunt without making a kill, suggest that they are often wary of pressing beyond a certain threshold of energy investment, and perhaps of risk to their own health. We would expect there to be a gradation of some kind, from prey that can be attacked with little regard for the killer whales’ own safety and need to conserve energy to prey that represent both a safety risk and a questionable cost:benefit tradeoff in energy. On one side of this threshold could be animals that are smaller or only slightly larger than an adult killer whale (9 m), e.g. minke whales (*Balaenoptera acutorostrata* and *B. bonaerensis*) or young Bryde’s whales (*Balaenoptera brydei* and *B. edeni*). Attacks on such prey should represent little or no risk to the killers, and once contact has been made it is difficult to envision how these prey could avoid being killed (e.g., Hancock 1965; Wenzel and Sears 1988; Silber et al. 1990). On the opposite side of the size threshold, the outcome of an attack would be less certain, and the killers may be more tentative and cautious as they test their larger victims for speed, strength, and stamina (much as wolves do). Circumstances would, of course, play a large role. Groups of prey animals with the potential for mutual aid in defense presumably would be less vulnerable (e.g., unsuccessful attacks on right whales observed by Cummings et al. [1971, 1972; see the following section], on humpback whales by Whitehead and Glass [1985], and on sperm whales by Arnbom et al. [1987]). A chance encounter with a solitary large prey animal (e.g., the blue whale attack observed by Tarpay 1979) might give the killers an opportunity to obtain chunks of skin and meat while testing for weakness and vulnerability, thus deriving some energetic benefit even though the injured prey ultimately manages to escape. Calves of all large whale species would fall below the threshold of vulnerability. Although the

presence of mothers and other adults could tip the balance in the calf’s favor, it could also put the adults at risk of severe injury or death (e.g., Scammon 1874: 90; Goley and Straley 1994).

Resistance to Attack

Large whales (unlike minke whales) are clearly able to resist killer whale attacks. Weller (2002) singled out humpback whales in this regard, claiming that they were more aggressive than some other species in thrashing at the attackers with their flukes and flippers. This is consistent with the observations in Monterey Bay by Ternullo and Black (2003), who noted that although humpbacks there frequently have killer whale tooth rakes on their flukes, no lethal attacks have been observed. Dolphin’s (1987) observations of interactions between humpback whales and killer whales in Alaska, discussed subsequently, present a different picture, implying that attempts at predation are exceptional there.

Cummings et al. (1971, 1972) described a “full-fledged attack” by approximately five killer whales (four females and a calf) on two courting southern right whales (*Eubalaena australis*) in nearshore waters off Patagonia. At times during the attack, the right whales were entirely surrounded, but they kept close together and vigorously slashed at the attackers with their flukes and flippers. “Most of the time the killer whales were in a swimming frenzy that took them over, between, and under the two big right whales” (Cummings et al. 1971: 266). After 25 minutes the killers abandoned the effort and moved away, and the right whales relocated into shallower water and became quiescent. The observers saw no signs of blood or other evidence of physical harm to the right whales. Cummings et al. (1972) were told by local fishermen of a previous similar, but apparently lethal, attack. Miguel Iñiguez (personal communication, July 2003) and colleagues also have observed successful (i.e., lethal) attacks on right whales off Patagonia, but in all such instances adult male killers were involved. In their experience, when only females, juveniles, and calves took part, the attack invariably ended with the right whales (mainly mothers and dependent calves) escaping alive.

The gray whale—in spite of its reputation as a “devilfish,” dangerous to approach and difficult to kill (Scammon 1874)—has been described as exhibiting docile or submissive behavior on some occasions when under attack. A particularly graphic example was provided by Andrews (1916b: 200–201), in which a gray whale was delivered to a Korean whaling station after having been “shot in the breast between the fins.” The whaling captain reported that he had encountered the animal surrounded by killer whales, “lying at the surface, belly up, with the fins outspread . . . absolutely paralyzed by fright.” He was able to approach and fire the harpoon into its exposed chest region. This description is reminiscent of one by Norris and Prescott (1961: 358–359) of a female gray whale whose behavior changed abruptly after being chased by their capture vessel over “a considerable distance.” The whale

stopped trying to escape and rolled onto her back, exposing the ventral body surface with the flippers and lower jaw extended into the air. A possible explanation of this behavior is capture myopathy or capture stress, a syndrome often observed in ungulates (Chalmers and Barrett 1982).

There is also considerable evidence of nonresponsiveness, or at least lack of flight or avoidance responses, on the part of large whales to the presence of killer whales (Jefferson et al. 1991), as there is for savanna ungulates, which exhibit varying degrees of responsiveness to the presence of large predators. One explanation would be that the potential prey is somehow able to tell that the would-be predators are satiated or searching for easier targets (Dolphin 1987). Another explanation could be that the potential prey animals are aware of the food-preference differences between *resident* (fish-eating) and *transient* (mammal-eating) killer whales and that, therefore, the muted response or absence of response simply signifies an ability to distinguish between the two ecotypes, whether by visual, acoustic, or some other kind of cue.

Scarring and Mutilation as Evidence of Attack Frequency

Among the difficulties of interpreting scarring rates as indices of predation rates is that most predators fail in predation attempts much more often than they succeed (e.g., Mech 1970: 237). “Success rates” are difficult to measure accurately (Bertram 1979: 226). Hunter observations of attacks by killer whales on gray whales off Chukotka suggest a relatively high success rate, although it is difficult to judge whether the estimate of 80% success by Melnikov and Zagrebina (2005) is unbiased. Apart from the logistical challenges, high cost, and time requirements to obtain a representative sample of observations, predation by killer whales on whales is complicated by the fact that so much of the activity and evidence remains hidden below the sea surface and out of sight. Analyses of scarring and mutilation (e.g., bitten-off, frayed, or otherwise damaged appendages) are essentially studies of survivors. The timing of acquisition of scars, and the frequency of their occurrence on animals of different age classes, can nevertheless be instructive. Terrestrial mammals provide useful models in which scarring or maiming serves as an index for attacks by predators. Large herbivores such as elephants (*Loxodonta* sp.) and rhinoceroses were generally considered invulnerable to predation, but that conventional wisdom has changed. When tailless and earless black rhinoceros (*Diceros bicornis*) calves and adults were initially reported throughout sub-Saharan Africa, it was suggested that such anomalies reflected congenital problems (Goddard 1969). Later, the missing body parts (i.e., maiming) were tied to predation attempts by spotted hyenas (Hitchins 1986). Subsequent analyses of populations throughout Africa revealed an association between hyena density and degree of taillessness or earlessness in rhinos (Berger 1994). This idea was bolstered by the lack of maiming in regions where hyenas were absent (Berger and Cunningham 1994).

In populations of large whales, the percentages of individuals bearing rake-type scars (presumed to originate from killer whale attacks) vary by area, from a few percent to more than a third of the population (Mehta 2004; Mehta et al. in preparation). For example, 76 of 990 individually identified humpback whales from the Gulf of Maine population (about 7.5%) bear such scars. Seventy-four (97.4%) of the 76 had already acquired the scars prior to their first sighting on this feeding ground (Mehta 2004). Only two individuals that did not have such scars at first sighting were observed to have acquired them in a subsequent year. We recognize that Gulf of Maine humpback whales may not be representative of large whales in general, but the timing of scar acquisition in this population strongly suggests that the great majority of killer whale attacks target calves during the calves’ first migration to high latitudes from the species’ breeding grounds in tropical waters. Dolphin (1987) and Naessig and Lanyon (2004) reached similar conclusions from observations of humpback whales elsewhere, and analyses of scar acquisition in other mysticete populations indicate a similar pattern (Mehta 2004; Mehta et al. in preparation). As discussed in an earlier section of the present chapter, gray whale calves and yearlings appear to be more susceptible to predation than other cohorts in the eastern North Pacific population of that species.

The question of whether the rake-type scars on the bodies of large whales originate from killer whales has been debated. Other small or medium-sized odontocetes, particularly false killer whales (*Pseudorca crassidens*), short-finned pilot whales, and pygmy killer whales (*Feresa attenuata*), are known to associate with, and at least occasionally harass and bite, large whales (e.g., Earle and Giddings 1979; Palacios and Mate 1996; Weller et al. 1996). The “predatory advances” upon large whales by these smaller odontocetes, in combination with the “pronounced fear responses” exhibited by the larger animals (Weller 2002), imply that the potential for some kind of predator-prey interaction is at least perceived on both sides. However, comparison of rake marks on living whales with the dentition patterns of various potential predators (derived from examinations of museum specimens) strongly supports the belief that most rake-type scars do indeed originate with killer whales rather than other species (Mehta 2004; Mehta et al. in preparation). North Atlantic right whales (*Eubalaena glacialis*) appear to be an exception. They exhibit smaller and more narrowly spaced scars that are not consistent with killer whale dentition.

Consumption Patterns

Many descriptions of killer whale predation on large baleen whales stress that the killers were most interested in consuming the whale’s tongue (Jefferson et al. 1991; Weller 2002). Often only the tongue, lips, and portions of the ventrum were consumed before the prey was abandoned. In some instances, such incomplete consumption of the carcass might be explained by the fact that the killers were disturbed

or deliberately harassed by the observers. However, the frequent finding of beach-cast carcasses that have been bitten principally in the mouth and belly regions, with much of the rest of the body unmolested, implies that the killer whales routinely consume only certain portions of the large whales that they kill.

Silber et al. (1990) had the rare opportunity of watching an attack develop and conclude and then, two days later, locating the carcass of the Bryde's whale that had been killed. They noted that sections of the lower jaw had been removed, there was a large open wound on the abdomen, and parts of the viscera were extruded. Lowry et al. (1987) made similar observations on a 7-m gray whale killed and partially consumed by killer whales in Alaskan waters, and the observations of scavenging on whaler-killed carcasses (previously discussed) reinforce the finding that tongues are the killer whale's foremost interest.

However, in the observations by Pitman et al. (2001), the killer whales apparently fed heavily on the skin and blubber of the sperm whales, with no special attention given to the tongue or mouth area. A pod of approximately 30 killer whales observed attacking a young blue whale tore strips of skin, blubber, and muscle from its rostrum, sides, and back before abandoning their victim (Tarpy 1979). There was no opportunity to relocate the blue whale to see whether it survived or succumbed to its injuries, or to determine whether the killer whales obtained any additional nutrition for their efforts.

Discussion and Conclusions

Many biologists have expressed skepticism about the significance of killer whale predation on large whales. Heptner et al. (1996: 689), for example, claimed that even though killer whales were seen by Antarctic whalers in the vicinity of fin (*Balaenoptera physalus*), humpback, and other baleen whales, "no attempts by the killer whales to attack the others were ever recorded." According to those authors (p. 687), reports of attacks on baleen whales "have been copied from book to book" since the mid-nineteenth century, "without critical review." Dolphin (1987) claimed that reports of predation in the literature were "disproportionate to their frequency of occurrence." Andrews (1916a: 334), in contrast, was impressed by the frequency with which killer whale bite marks were found on the flippers and flukes of blue and fin whales (but not sei whales, *Balaenoptera borealis*) on the flensing decks of whaling stations in Asia. He considered killer whales "a menace" to the blue and fin whales around Japan, where killers were "very abundant." Andrews notwithstanding, Weller (2002) concluded that observed attacks on baleen whales were "not common." Until the 1990s, there was a fairly broad consensus among cetacean biologists that killer whale predation was an exceptional, rather than regular, feature in the lives of large whales, perhaps with two exceptions: gray whales on both sides of the Pacific and bowhead whales in the eastern Arctic.

Evidence of the last few decades has reinforced the impression that gray whales are common prey of killer whales and that calves, accompanied by their mothers, are particularly vulnerable as they move close along the west coast of North America from the winter breeding grounds in Mexico to the northern feeding areas. Recent observations on the feeding grounds near the Chukotka Peninsula suggest that young, perhaps recently weaned gray whales are similarly at risk of predation (Melnikov and Zagrebin 2005). Bowhead whales in the eastern Arctic, severely depleted by commercial whaling, are attacked at least occasionally even though killer whales do not appear to be particularly abundant there (suppressed in part by control hunting; Heide-Jørgensen 1988; Reeves and Mitchell 1988b). In contrast, there is little evidence of predation on bowhead whales in the western Arctic, where they were less severely reduced by whaling and where the ongoing hunt provides opportunities to examine carcasses for wounds and scars (George et al. 1994). With respect to sperm whales, remarkably little evidence of killer whale predation exists in whaling records, whereas recent field observations indicate that it occurs more frequently than was formerly assumed.

No definitive conclusions are possible concerning the scale and ecological significance of killer whale predation on large whales, whether viewed from a top-down or a bottom-up perspective. We can only speculate on the extent to which predation by killer whales helped regulate populations of large whales or, alternatively, killer whale populations were regulated by the availability of large whales as sources of nutrition. Killer whales definitely attack large whales, including adults, juveniles, and calves. For some species, such as the gray whale, attacks on calves are more likely to prove lethal, but adults are sometimes killed or seriously injured as well. The fact that killer whales have developed strategies for attacking, killing, and (often only partially) consuming large whales implies that these skills confer a selective advantage of some kind. Similarly, the fact that large whales have developed strategies for avoiding detection by, escaping from, and fighting off killer whales suggests that they have undergone selection pressure for these traits. However, Clapham (1993), noting that defense against predators is a major determinant of group size in a wide variety of taxa, suggested that the small, unstable groups typical of humpback whales could reflect (in part) a lack of need for large groups for communal defense or predator detection. In other words, predation events may not occur sufficiently often in the lives of humpback whales to warrant selection for large groups. Alternatively, other selective determinants of group size (e.g., foraging efficiency) may simply outweigh the risks of predation.

In assessing the importance of large whales in the diet of killer whales, it is important to consider two things in particular. First, calves and juveniles are probably substantially overrepresented in the class of animals removed from a population by killer whale predation. Second, consumption of large whale prey is often far from complete, with the tongues and ventral grooves of baleen whales clearly preferred over all

other body parts. Incomplete consumption is evident, both from direct observations of killer whales abandoning their prey prematurely and from the occurrence of stranded whales that have been mauled and mutilated but only partially eaten by killer whales.

In his comparative analysis of killer whale–baleen whale relations and the predator-prey relations between African predators and their ungulate prey, Dolphin (1987) implicitly assumed that large savanna ungulates (specifically, wildebeests, *Connochaetes* spp.; Cape buffalos, *Syncerus caffer*, and elephants, *Loxodonta africana*) lived in a state of “non-belligerent, if uneasy, coexistence” with their large, cooperatively hunting predators (specifically, lions, hyenas, and Cape hunting dogs, *Lycyaon pictus*). He posited a similar state of coexistence between baleen whales and killer whales, assuming that successful attacks on such large prey were “rare” (citing Leuthold 1977 to support this assumption for attacks by lions on buffalos and elephants). Carrying Dolphin’s reasoning further, we offer the hypothesis that before industrial hunting (particularly of elephants and whales), buffalos, elephants, and large whales were more filler fodder than staple fare for the big social predators. While some individual prides of lions, packs of canids, or pods of killer whales may have specialized in taking large prey and thus may have been, in some sense, obligate large-prey predators (and some prides, packs, and pods may still be), the essential condition of these species was to rely on small to moderate-sized prey as nutritional staples (e.g., pinnipeds, dolphins, porpoises, and minke whales in the case of mammal-eating killer whales) and to take large prey only opportunistically (facultatively) or in exceptional circumstances when their staple prey failed or the large prey were particularly susceptible (e.g., during migratory pulses). The concentrations of gray whale calves in the nursery lagoons and on their coast-hugging northbound migrations provide an example of the latter. Ice-edge aggregations of bowhead whales seeking access to their high-latitude summer feeding grounds might provide another example.

If the foregoing hypothesis were true, it would turn the argument by Springer et al. (2003) on its head. Thus, rather than the whaling-induced decline of large whales having a cascade of effects leading to the declines of pinnipeds, it would be the other way around. That is, declines of these formerly abundant and relatively catchable small to moderate-sized prey (e.g., harbor seals, *Phoca vitulina*, and sea lions, Otariidae) might help explain the recent surge in observations of attacks on large whales, including sperm whales. A number of considerations caution against that interpretation, however. The increase in human numbers, enhanced communication (reporting) opportunities, and growing interest in cetaceans, in combination, could explain the surge in reports of attacks on large whales. Also, California coastal waters, where many of the recently reported attacks occurred, host relatively large populations of the smaller prey species (at least California sea lions, *Zalophus californianus*, harbor seals, and elephant seals, *Mirounga angustirostris*), some of which may be more numerous now than they have been in decades, if not centuries. The

fact that killer whale predation on gray whales is not a recent innovation (as previously discussed) also could be interpreted as being inconsistent with our hypothesis. Finally, energetic/demographic analyses (Doak et al., Chapter 18 of this volume; Williams et al., in press) suggest that the smaller marine mammals, even at their estimated peaks of abundance, would not have been capable of sustaining the 300 or so *transient* killer whales estimated to inhabit the North Pacific today (Forney and Wade, Chapter 12 of this volume).

Acknowledgments

We are grateful to Michael Dyer, Librarian of the New Bedford Whaling Museum, for sharing his knowledge of old whaling manuscripts and providing the data from the nineteenth-century voyages of the *Phoenix* and *Saratoga*. We also thank Ameer Mehta and Jooke Robbins for sharing unpublished data on the frequency of scarring on large whales and on patterns of marks derived from examination of museum specimens. Tom Jefferson, Jorge Urbán-Ramirez, Miguel Iñíguez, and Klaus Barthelmess kindly shared various types of information relevant to this study. Jim Estes provided an insightful review. Partial financial support for this work was provided by the Pew Fellows Program in Marine Conservation, the National Marine Fisheries Service, and the U.S. Geological Survey.

Literature Cited

- Andrews, R.C. 1914. Monographs of the Pacific Cetacea, 1. The California gray whale (*Rhachianectes glaucus* Cope). *Memoirs of the American Museum of Natural History* New Series 1: 227–287.
- . 1916a. Monographs of the Pacific Cetacea, II. The sei whale (*Balaenoptera borealis* Lesson). *Memoirs of the American Museum of Natural History* New Series, 1: 289–388.
- . 1916b. *Whale hunting with gun and camera*. New York: D. Appleton and Co.
- Arnbom, T., V. Papastavrou, L.S. Weilgart, and H. Whitehead. 1987. Sperm whales react to an attack by killer whales. *Journal of Mammalogy* 68: 450–453.
- Ash, C. 1964. *Whaler's eye*. London: George Allen and Unwin.
- Baird, R.W. 2000. The killer whale: foraging specializations and group hunting, in *Cetacean societies: field studies of dolphins and whales*. J. Mann, R.C. Connor, P.L. Tyack, and H. Whitehead, eds. Chicago: University of Chicago Press, pp. 127–153.
- Baldrige, A. 1972. Killer whales attack and eat a gray whale. *Journal of Mammalogy* 53: 898–900.
- Ballard, W.B., J.S. Whitman, and D.J. Reed. 1991. Population dynamics of moose in south-central Alaska. *Wildlife Monographs* 114: 1–49.
- Bass, R. 1996. Foreword, in *California grizzly*. T.I. Storer and L.P. Tevis, eds. Berkeley: University of California Press, pp xii–xix.
- Berger, J. 1994. Science, conservation, and black rhinos. *Journal of Mammalogy* 75: 298–308.
- Berger, J. and C. Cunningham. 1994. Horns, hyenas, and black rhinos. *Research and Exploration* 10: 241–244.
- Berger, J., J.E. Swenson, and I. Persson. 2001a. Recolonizing carnivores and naïve prey: conservation lessons from Pleistocene extinctions. *Science* 291: 1036–1039.

- Berger, J., P.B. Stacey, L. Bellis, and M.P. Johnson. 2001b. A mammalian predator-prey imbalance: grizzly bears and wolf extinction affect avian neotropical migrants. *Ecological Applications* 11: 947–960.
- Bergerud, A.T., and J.P. Elliot. 1986. Dynamics of caribou and wolves in northern British Columbia. *Canadian Journal of Zoology* 64: 1515–1529.
- Bertram, B.C.R. 1979. Serengeti predators and their social systems, in *Serengeti: dynamics of an ecosystem*. A.R.E. Sinclair and M. Norton-Griffiths, eds. Chicago: University of Chicago Press, pp. 221–248.
- Berzin, A.A. 1972. *The sperm whale*. Jerusalem: Israel Program for Scientific Translations.
- Best, P.B., P.A.S. Canham, and N. MacLeod. 1984. Patterns of reproduction in sperm whales, *Physeter macrocephalus*. *Report of the International Whaling Commission* (Special Issue) 6: 51–79.
- Black, N., T. Ternullo, A. Schulman-Janiger, G. Ellis, M. Dahlheim, and P. Stap. 2003. Behavior and ecology of killer whales in Monterey Bay, California. Poster presentation, 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, North Carolina, December 14–19.
- Bloch, D. and C. Lockyer. 1988. Killer whales (*Orcinus orca*) in Faroese waters. *Rit Fiskideildar* 11: 55–64.
- Braham, H.W. 1984. Distribution and migration of gray whales in Alaska, in *The gray whale Eschrichtius robustus*. M.L. Jones, S.L. Swartz, and S. Leatherwood, eds. Orlando, FL: Academic Press, pp. 249–266.
- Brown, J.T. 1887. Whalers, vessels and boats, apparatus, and methods of the whale fishery, in *The fisheries and fishery industries of the United States, Section V. History and methods of the fisheries. Part XV. The whale fishery*. G.B. Goode, ed. Washington, DC: Government Printing Office, pp. 218–293.
- Byers, J.A. 1997. *American pronghorn: social adaptations and the ghosts of predators past*. Chicago: University of Chicago Press.
- Caldwell, D.K. and M.C. Caldwell. 1969. Addition of the leatherback sea turtle to the known prey of the killer whale, *Orcinus orca*. *Journal of Mammalogy* 50: 636.
- Chalmers, G.A., and M.W. Barrett. 1982. Capture myopathy, in *Non-infectious diseases in wildlife*. J.W. Davis and G. Hieff, eds. Ames: Iowa State University Press, pp.
- Clapham, P.J. 1993. Social organization of humpback whales on a North Atlantic feeding ground. *Symposia of the Zoological Society of London* 66: 131–149.
- . 2001. Why do baleen whales migrate? A response to Corkeron and Connor. *Marine Mammal Science* 17: 432–436.
- Clark T.W. and D. Casey. 1996. *Tales of the grizzly*. Moose, WY: Homestead Publishing.
- Corkeron, P.J. and R.C. Connor. 1999. Why do baleen whales migrate? *Marine Mammal Science* 15: 1228–1245.
- Cummings, W.C. and P.O. Thompson. 1971. Gray whales, *Eschrichtius robustus*, avoid the underwater sounds of killer whales, *Orcinus orca*. *Fishery Bulletin* 69: 525–530.
- Cummings, W.C., J.F. Fish, and P.O. Thompson. 1971. Bioacoustics of marine mammals off Argentina: R/V *Hero* cruise 71-3. *Antarctic Journal of the United States* 6: 266–268.
- . 1972. Sound production and other behavior of southern right whales, *Eubalaena glacialis*. *Transactions of the San Diego Society of Natural History* 17(1): 1–14.
- Cummings, W.C., P.O. Thompson, and J.F. Fish. 1974. Behavior of southern right whales: R/V *Hero* cruise 72-3. *Antarctic Journal of the United States* 9: 33–38.
- Dahlheim, M.E. and J.E. Heyning. 1999. Killer whale *Orcinus orca* (Linnaeus, 1758), in *Handbook of marine mammals, Vol. 6*. S.H. Ridgway and R. Harrison, eds. San Diego: Academic Press, pp. 281–322.
- Dakin, W.J. 1934. *Whalemen adventurers: the story of whaling in Australian waters and other southern seas related thereto, from the days of sails to modern times*. Sydney: Angus and Robertson.
- Deecke, V.B., J.K.B. Ford, and P.J.B. Slater. 2005. The vocal behaviour of mammal-eating killer whales: communicating with costly calls. *Animal Behaviour* 69: 395–405.
- Dolphin, W.F. 1987. Observations of humpback whale, *Megaptera novaeangliae*-killer whale, *Orcinus orca*, interactions in Alaska: comparison with terrestrial predator-prey relationships. *Canadian Field-Naturalist* 101: 70–75.
- Earle, S.A. and A. Giddings. 1979. Humpbacks: the gentle giants. *National Geographic* 155(1): 2–17.
- Eberhardt, R.L. and W.E. Evans. 1962. Sound activity of the California gray whale, *Eschrichtius robustus*. *Journal of the Audio Engineering Society* 10: 324–328.
- Eloff, F.C. 1964. On the predatory habits of lions and hyaenas. *Koedoe* 7: 105–112.
- Estes, J.A., M.T. Tinker, T.M. Williams, and D.F. Doak. 1998. Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* 282: 473–476.
- Fertl, D., A. Acevedo-Gutierrez, and F.L. Darby. 1996. A report of killer whales (*Orcinus orca*) feeding on a carcharhinid shark in Costa Rica. *Marine Mammal Science* 12: 606–611.
- Finley, K.J. 1990. Isabella Bay, Baffin Island: an important historical and present-day concentration area for the endangered bowhead whale (*Balaena mysticetus*) of the eastern Canadian Arctic. *Arctic* 43: 137–152.
- . 2001. Natural history and conservation of the Greenland whale, or bowhead, in the northwest Atlantic. *Arctic* 54: 55–76.
- Ford, J.K.B. and G.M. Ellis. 1999. *Transients: mammal-hunting killer whales of British Columbia, Washington, and southeastern Alaska*. Vancouver: University of British Columbia Press.
- Gasaway, W.C., R.D. Boertje, D.V. Grangaard, D.G. Kellyhouse, R.O. Stephenson, and D.G. Larsen. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120: 1–59.
- Gaskin, D.E. 1972. *Whales, dolphins and seals, with special reference to the New Zealand region*. London: Heinemann.
- George, J.C., L.M. Philo, K. Hazard, D. Withrow, G.M. Carroll, and R. Suydam. 1994. Frequency of killer whale (*Orcinus orca*) attacks and ship collisions based on scarring on bowhead whales (*Balaena mysticetus*) of the Bering-Chukchi-Beaufort seas stock. *Arctic* 47: 247–255.
- Gilmore, R.M. 1961. *The story of the gray whale*. 2nd edition. San Diego: American Cetacean Society.
- Goddard, J. 1969. A note on the absence of pinnae in the black rhinoceros. *East African Wildlife Journal* 7: 179–180.
- Goley, P.D. and J.M. Straley. 1994. Attack on gray whales (*Eschrichtius robustus*) in Monterey Bay, California, by killer whales (*Orcinus orca*) previously identified in Glacier Bay, Alaska. *Canadian Journal of Zoology* 72: 1528–1530.
- Gunther, K.A. and R.A. Renkin. 1990. Grizzly bear predation on elk calves and other fauna of Yellowstone National Park. *International Conference on Bear Research and Management* 8: 329–334.
- Haines, A.L. (editor). 1965. *Journal of a trapper 1834–1843*. Lincoln: University of Nebraska Press.

- Hancock, D. 1965. Killer whales kill and eat a minke whale. *Journal of Mammalogy* 46: 341–342.
- Heide-Jørgensen, M.P. 1988. Occurrence and hunting of killer whales in Greenland. *Rit Fiskideildar* 11: 115–135.
- Heptner, V.G., K.K. Chapskii, V.A. Arsen'ev, and V.E. Sokolov. 1996. *Mammals of the Soviet Union, Vol. 2, Part 3. Pinnipeds and toothed whales Pinnipedia and Odontoceti*. English-language edition. J.G. Mead, ed. Washington, DC: Smithsonian Institution Libraries and National Science Foundation (originally published in Russian by Vysshaya Shkola Publishers, Moscow, 1976).
- Hildebrand, G.V., C.C. Schwartz, C.T. Robbins, M.E. Jacoby, T.A. Hanley, S.M. Arthur, and C. Servheen. 1999. The importance of meat, particularly salmon, to body size, population productivity, and conservation of North American brown bears. *Canadian Journal of Zoology* 77: 132–138.
- Hitchins, P.A. 1986. Earlessness in the black rhinoceros—a warning. *Pachyderm* 7: 8–10.
- IWC. 2003. Report of the Scientific Committee. *Journal of Cetacean Research and Management* 5 (Suppl.): 1–488.
- Jefferson, T.A., P.J. Stacey, and R.W. Baird. 1991. A review of killer whale interactions with other marine mammals: predation to co-existence. *Mammal Review* 21: 151–180.
- Jones, M.L. and S.L. Swartz. 1984. Demography and phenology of gray whales and evaluation of whale-watching activities in Laguna San Ignacio, Baja California Sur, Mexico, in *The gray whale Eschrichtius robustus*. M.L. Jones, S.L. Swartz, and S. Leatherwood, eds. Orlando, FL: Academic Press, pp. 309–374.
- . 2002. Gray whale *Eschrichtius robustus*, in *Encyclopedia of marine mammals*. W.F. Perrin, B. Würsig, and J.G.M. Thewissen, eds. San Diego: Academic Press, pp. 524–436.
- Kahn, B. 2003. *Solor-Alor visual and acoustic cetacean surveys: interim report April–May 2003 survey period*. Sanur (Bali), Indonesia: The Nature Conservancy, Coral Triangle Center. Available at http://www.coraltrianglecenter.org/downloads/Alor3_Interim_Survey_Report_Final_150dpi.pdf. Accessed June 1, 2006.
- Kruuk, H. 1972. *The spotted hyena: a study of predation and social behavior*. Chicago: University of Chicago Press.
- Landa, A. 1997. *Wolverines in Scandinavia: ecology, sheep depredation, and conservation*. Trondheim: Norwegian University of Science and Technology.
- Leuthold, W. 1977. *African ungulates: a comparative review of their ethology and behavioral ecology*. New York: Springer Verlag.
- Ljungblad, D.K. and S.E. Moore. 1983. Killer whales (*Orcinus orca*) chasing gray whales (*Eschrichtius robustus*) in the northern Bering Sea. *Arctic* 36: 361–364.
- Lowry, L.F., R.R. Nelson, and K.J. Frost. 1987. Observations of killer whales, *Orcinus orca*, in Western Alaska: sightings, strandings, and predation on other marine mammals. *Canadian Field-Naturalist* 101: 6–12.
- Magoun, A.J. 1985. Population characteristics, ecology, and management of wolverines in north-western Alaska. Ph.D. Thesis, University of Alaska, Fairbanks.
- Mass, A.M. and A. Ya. Supin. 2002. Vision, in *Encyclopedia of marine mammals*. W.F. Perrin, B. Würsig, and J.G.M. Thewissen, eds. San Diego: Academic Press, pp. 1280–1293.
- Mattson, D.J. 1997. Use of ungulates by Yellowstone grizzly bears, *Ursus arctos*. *Biological Conservation* 81: 161–177.
- Mattson, D.J., B.M. Blanchard, and R.R. Knight. 1991. Food habits of Yellowstone grizzly bears, 1977–1987. *Canadian Journal of Zoology* 69: 1619–1629.
- McLaughlin, W.R.D. 1962. *Call to the south: a story of British whaling in Antarctica*. London: George G. Harrap and Co.
- Mech, L.D. 1970. *The wolf: the ecology and behavior of an endangered species*. Garden City, NY: Natural History Press.
- Mech, L.D., L.G. Adams, T.J. Meier, J.W. Burch, and B.W. Dale. 1998. *The wolves of Denali*. Minneapolis: University of Minnesota Press.
- Mehta, A.V. 2004. How important are baleen whales as prey for killer whales (*Orcinus orca*) in high latitudes? M.S. Thesis, Boston University.
- Melnikov, V.V., and I.A. Zagrebin. 2005. Killer whale predation in coastal waters of the Chukotka Peninsula. *Marine Mammal Science* 21: 550–556.
- Mills, M.G.L. 1990. *Kalahari hyaenas*. London: Unwin Hyman.
- Mitchell, E. and A.N. Baker. 1980. Age of reputedly old killer whale, *Orcinus orca*, “Old Tom” from Eden, Twofold Bay, Australia. *Report of the International Whaling Commission* (Special Issue) 3: 143–154.
- Mitchell, E. and R.R. Reeves. 1982. Factors affecting abundance of bowhead whales *Balaena mysticetus* in the eastern Arctic of North America, 1915–1980. *Biological Conservation* 22: 59–78.
- . 1988. Records of killer whales in the western North Atlantic, with emphasis on eastern Canadian waters. *Rit Fiskideildar* 11: 161–193.
- Moore, S.E., D.K. Ljungblad, and D.R. Van Schoik. 1986. Annual patterns of gray whale (*Eschrichtius robustus*) distribution, abundance, and behavior in the northern Bering and eastern Chukchi seas, July 1980–83. *Report of the International Whaling Commission* (Special Issue) 8: 231–242.
- Moshenko, R.W., S.E. Cosens, and T.A. Thomas. 2003. *Conservation strategy for bowhead whales (Balaena mysticetus) in the eastern Canadian Arctic*. National Recovery Plan No. 24. Ottawa: Recovery of Nationally Endangered Wildlife (RENEW).
- Naessig, P.J. and J.M. Lanyon. 2004. Levels and probable origin of predatory scarring on humpback whales (*Megaptera novaeangliae*) in east Australian waters. *Wildlife Research* 31: 163–170.
- National Research Council. 1997. *Wolves, bears, and their prey in Alaska*. Washington, DC: National Academies Press.
- Norris, K.S. and J.H. Prescott. 1961. Observations of Pacific cetaceans of Californian and Mexican waters. *University of California Publications in Zoology* 63: 291–402.
- NWMB. 2000. *Final report of the Inuit bowhead knowledge study*. Iqaluit: Nunavut Wildlife Management Board.
- Palacios, D.M. and B.R. Mate. 1996. Attack by false killer whales (*Pseudorca crassidens*) on sperm whales (*Physeter macrocephalus*) in the Galápagos Islands. *Marine Mammal Science* 12: 582–587.
- Persson, J. 2003. *Population ecology of Scandinavian wolverines*. Umea: Swedish Agricultural University.
- Phillips, G.E. and G.C. White. 2003. Pronghorn population response to coyote control: modeling and management. *Wildlife Society Bulletin* 31: 1162–1175.
- Phoenix. 1847–51MS. *Logbook of the ship Phoenix of New Bedford, Joseph McCleave, master. August 3, 1847–May 28, 1851*. New Bedford, MA: Kendall Institute, New Bedford Whaling Museum, log number KWM 399.
- Pitman, R.L., L.T. Ballance, S.L. Mesnick, and S.J. Chivers. 2001. Killer whale predation on sperm whales: observations and implications. *Marine Mammal Science* 17: 494–507.

- Pitman, R.L. and P. Ensor. 2003. Three forms of killer whales (*Orcinus orca*) in Antarctic waters. *Journal of Cetacean Research and Management* 5: 131–139.
- Pond, J.E. 1939. Truth stranger than fiction. *U.S. Naval Institute Proceedings* 65: 1309–1332.
- Reeves, R.R. and E. Mitchell. 1988a. Killer whale sightings and takes by American pelagic whalers in the North Atlantic. *Rit Fiskideildar* 11: 7–23.
- . 1988b. Distribution and seasonality of killer whales in the eastern Canadian Arctic. *Rit Fiskideildar* 11: 136–160.
- Rice, D.W. and A.A. Wolman. 1971. *The life history and ecology of the gray whale* (*Eschrichtius robustus*). American Society of Mammalogists, Special Publication No. 3. Lawrence, KS: American Society of Mammalogists.
- Saratoga*. 1857–58MS. *Logbook of the ship Saratoga of New Bedford, Frederick Slocum, master. April 23, 1857–December 12, 1858 (partial or incomplete voyage)*. New Bedford, MA: Kendall Institute, New Bedford Whaling Museum, log number KWM 180.
- Scammon, C.M. 1874. *The marine mammals of the north-western coast of North America, described and illustrated together with an account of the American whale-fishery*. San Francisco: John H. Carmany and Co.
- Schaller, G.B. 1972. *The Serengeti lion: a study of predator-prey relations*. Chicago: University of Chicago Press.
- Schullery, P. 1988. *The bear hunter's century: profiles from the golden age of bear hunting*. New York: Dodd, Mead, and Company.
- Seton, E.T. 1953. *Lives of game animals*. Vol. 2. Boston: Charles T. Branford.
- Shevchenko, V.I. 1975. Nature of correlations between killer whales and other cetaceans. *Morsk Mlekopitayushchie Chast' 2*: 173–174 (in Russian).
- Silber, G.K., M.W. Newcomer, and M. Hector Perez-Cortes. 1990. Killer whales (*Orcinus orca*) attack and kill a Bryde's whale (*Balaenoptera edeni*). *Canadian Journal of Zoology* 68: 1603–1606.
- Smith, B.L. and S.H. Anderson. 1996. Patterns of neonatal mortality of elk in northwestern Wyoming. *Canadian Journal of Zoology* 74: 1229–1237.
- Soulé, M.E., J.A. Estes, J. Berger, and C. Martinez del Rio. 2003. Ecological effectiveness: conservation goals for interactive species. *Conservation Biology* 17: 1238–1250.
- Southwood, T.R.E. 1975. The dynamics of insect population, in *Insects, science, and society*. D. Pimentel, ed. New York: Academic Press, pp. 151–199.
- Springer, A.M., J.A. Estes, G.B. van Vliet, T.M. Williams, D.F. Doak, E.M. Danner, K.A. Forney, and B. Pfister. 2003. Sequential megafaunal collapse in the North Pacific Ocean: an ongoing legacy of industrial whaling? *Proceedings of the National Academy of Sciences* 100: 12223–12228.
- Storer, T.I. and L.P. Tevis. 1955. *California grizzly*. Berkeley: University of California Press.
- Swartz, S.L. 1986. Gray whale migratory, social and breeding behavior. *Report of the International Whaling Commission* (Special Issue) 8: 207–229.
- Tarpy, C. 1979. Killer whale attack. *National Geographic* 155: 542–545.
- Ternullo, R. and N. Black. 2003. Predation behavior of transient killer whales in Monterey Bay, California. Poster presentation, 15th Biennial Conference on the Biology of Marine Mammals, Greensboro, North Carolina, December 14–19.
- Testa, J.W., E.F. Becker, and G.R. Lee. 2000. Temporal patterns in the survival of twin and single moose calves (*Alces alces*) in southcentral Alaska. *Journal of Mammalogy* 81: 162–168.
- Urbán Ramirez, J., L. Rojas-Bracho, H. Pérez-Cortés, A. Gómez-Gallardo, S.L. Swartz, S. Ludwig, and R.L. Brownell, Jr. 2003. A review of gray whales (*Eschrichtius robustus*) on their wintering grounds in Mexican waters. *Journal of Cetacean Research and Management* 5: 281–295.
- Visser, I.N. 1999a. Benthic foraging on stingrays by killer whales (*Orcinus orca*) in New Zealand waters. *Marine Mammal Science* 15: 220–227.
- . 1999b. A summary of interactions between orca (*Orcinus orca*) and other cetaceans in New Zealand. *New Zealand Natural Sciences* 24: 101–112.
- Visser, I.N. and F.J. Bonaccorso. 2003. New observations and a review of killer whale (*Orcinus orca*) sightings in Papua New Guinea waters. *Aquatic Mammals* 29: 150–172.
- Walker, L.W. 1949. Nursery of the gray whales. *Natural History* 58(6): 248–256.
- Walker, T.J. 1975. *Whale primer, with special attention to the California gray whale*. San Diego: Cabrillo Historical Association.
- Weller, D.W. 2002. Predation on marine mammals, in *Encyclopedia of marine mammals*. W.F. Perrin, B. Würsig, and J.G.M. Thewissen, eds. San Diego: Academic Press, pp. 985–994.
- Weller, D.W., B. Würsig, H. Whitehead, J.C. Norris, S.K. Lynn, R.W. Davis, N. Clauss, and P. Brown. 1996. Observations of an interaction between sperm whales and short-finned pilot whales in the Gulf of Mexico. *Marine Mammal Science* 12: 588–594.
- Wellings, H.P. 1964. *Shore whaling at Twofold Bay assisted by the renowned killer whales: an important industry now defunct*. Privately published, printed at The Magnet-Voice, Eden, Australia.
- Wenzel, F. and R. Sears. 1988. A note on killer whales in the Gulf of St. Lawrence, including an account of an attack on a minke whale. *Rit Fiskideildar* 11: 202–204.
- Whitehead, H. and C. Glass. 1985. The significance of the Southeast Shoal of the Grand Bank to humpback whales and other cetacean species. *Canadian Journal of Zoology* 63: 2617–2625.
- Whitehead, H. and R.R. Reeves. 2005. Killer whales and whaling: the scavenging hypothesis. *Biology Letters* 1(4): 415–418.
- Williams, T.M., J.A. Estes, D.F. Doak, and A.M. Springer. 2004. Killer appetites: assessing the role of predators in ecological communities. *Ecology* 85: 3373–3384.
- Yukhov, V.L., Ye. K. Vinogradova, and L.P. Medvedev. 1975. Diet of killer whales (*Orcinus orca* L.) in Antarctic and adjacent waters. *Morsk Mlekopitayushchie Chast' 2*: 183–185 (in Russian).