A re-evaluation of the role of killer whales *Orcinus orca* in a population decline of sea otters *Enhydra lutris* in the Aleutian Islands and a review of alternative hypotheses

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ABSTRACT

1. During the past 15–20 years, sea otters *Enhydra lutris* in the Aleutian Islands, Alaska, USA, experienced a drastic decrease in population size. It has been hypothesized that an increase in killer whale *Orcinus orca* predation was the primary cause of this decline.

2. Causation of the decline by increased killer whale predation is now considered a textbook case of top-down predator control. The purpose of this review is to re-evaluate the evidence for killer whale predation and to review evidence for alternative causes.

3. The killer whale predation hypothesis is based on three lines of evidence: (i) there was an increase in the number of observed killer whale attacks on sea otters during the 1990s, coincident with a decline in sea otters, (ii) sea otter populations did not decline in areas considered inaccessible to killer whales, while they declined in adjacent areas considered accessible to killer whales, and (iii) the estimated number of attacks necessary to account for the rate of decline is similar to the observed number of attacks. Our re-evaluation indicates that although the killer whale hypothesis is by no means disproved, the supporting data are limited and inconclusive.

4. Increases in shark populations in the Aleutian Islands concurrent with the sea otter population declines indicate the need for further research into the role of alternative marine predators in the population decline.

5. High contaminant levels observed in sea otters in the Aleutian Islands warrant further investigation into the impact of these toxins on sea otter health and vital rates, and their possible role on the population decline.

6. Disease has not been ruled out as a significant contributor to the population decline, particularly in the early stages of the decline.

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INTRODUCTION

Identifying the causes of population declines is a persistent challenge for ecologists (e.g. Caughley 1994). One of the difficulties in determining causality is that population declines generally are not identified until the late stages, by which time the agent of decline may have diminished or disappeared. In the Aleutian Islands, Alaska, USA, the number of sea otters *Enhydra lutris kenyoni* in what is referred to as the 'Southwest distinct population segment' (DPS; US Endangered Species Act; Fig. 1), has declined substantially (Estes et al. 1998, Doroff et al. 2003, Estes et al. 2005). It is generally thought that the decline began during the late 1980s or early 1990s (Estes et al. 1998, Doroff et al. 2003, Estes et al. 2005); however, there is considerable uncertainty around the timing of the onset (Wade et al. 2009). Spatially, the western extent of the decline is Attu Island (Fig. 1), at the western end of the Aleutian archipelago, as numbers of sea otters in the Komandorskiye Ostrova, Russian Federation (west of Attu Island) appear to have remained stable (Kornev & Korneva 2006). The eastern extent of the decline, however, remains uncertain, but it has been suggested that it extends to populations in the Alaska Peninsula (Burn & Doroff 2005). The magnitude of the decline throughout the range was approximately 70% between 1992 and 2000 (Doroff et al. 2003), culminating in a loss of approximately 65000 otters over this time (Burn et al. 2003). This dramatic change is one of the largest marine mammal population declines observed in recent history and, as such, is a major conservation issue. Furthermore, such a pronounced decrease in a keystone predator population could signal larger, hitherto unrecognized ecosystem changes (Caughley & Gunn 1996).
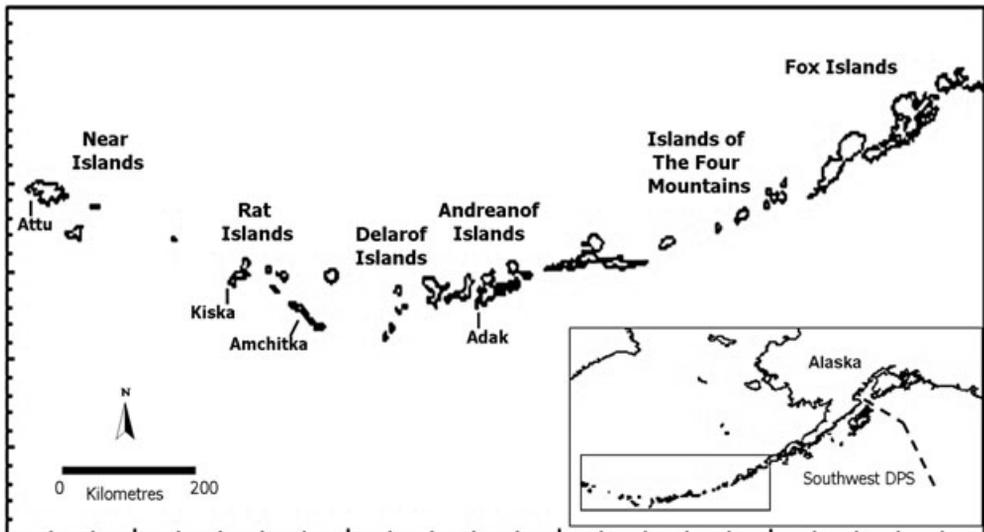

Fig. 1. Map of the Aleutian Islands, Alaska, USA, showing the six major island groups. The dotted line (- - -) illustrates the eastern extent of the declining southwest distinct population segment (DPS) of the sea otter.

Population declines are associated with decreased reproduction, emigration and/or increased mortality. It has been proposed that sea otter declines in the Aleutian Islands are the result of increased mortality, due to predation by North Pacific killer whales (Estes et al. 1998). Despite the compelling case put forth by Estes et al., the killer whale predation hypothesis is primarily inferential and based on limited empirical data. Sample sizes and data sets are small because of the challenges of studying marine mammals in a remote area, and because mortality events are inherently rare. Here, we re-evaluate the evidence for killer whale predation and assess the evidence for alternative causes (e.g. starvation, disease and toxins) first considered by Estes et al. (1998).

Why would killer whales have only recently included sea otters in their diet, as proposed by Estes et al. (1998)? As a broad explanation, Springer et al. (2003) suggested that a pattern of 'sequential megafaunal collapse' was caused by top-down ecological cascades mediated by transient killer whales (mammal-eating ecotype), whose prey-switching resulted in a pattern of consecutive declines of populations of several species of marine mammals. They posit that overexploitation of great whales by industrial-scale whaling from the 1940s to the 1960s caused killer whales to switch from preying primarily on the great whales to preying on more abundant marine mammal prey, first by targeting harbour seals *Phoca vitulina*, then fur seals *Callorhinus ursinus*, then Steller sea lions *Eumetopias jubatus*, and finally, the species with the lowest caloric value, sea otters. Subsequently, Whitehead and Reeves (2005) and Springer et al. (2008) have proposed an alternative mechanism by which industrial whaling caused an increase in killer whale numbers by provisioning them with carcasses, and Wade et al. (2007) and Mizroch and Rice (2006) have questioned whether killer whales ever preyed heavily on large whales.

The sequential megafaunal collapse hypothesis remains controversial; detractors focus on whether the declines were in fact sequential throughout the range of sea otters (e.g. DeMaster et al. 2006, Mizroch & Rice 2006, Wade et al. 2009). Others discount the mechanism and propose that nutritional stress (e.g. Trites & Larkin 1992) or climate change (e.g. Trites et al. 2007) caused the declines of species at various trophic levels, thus driving ecosystem-wide changes. However, the hypothesis that killer whales were responsible for the declines of sea otter populations has not been challenged, and in at least one textbook (Krebs 2001) it is referred to as established fact.

In Alaska, conservation and management of the southwest DPS of the northern sea otter is underway. In 2005, the DPS was listed as 'threatened' under the US Endangered Species Act (Anonymous 2005a). A recovery outline was published by the US Fish and Wildlife Service (Anonymous 2005b) listing predation by killer whales as a primary threat, and increased vulnerability to catastrophic events such as disease epidemics and oil spills as other possible threats to the viability of this population. However, there remains considerable uncertainty regarding the cause of the declines (Anonymous 2005b).

The overall objective of this review is to take a fresh look at the existing hypotheses on the population decline, 12 years after the original analysis by Estes et al. (1998). Specifically, we reviewed the published literature to (i) re-evaluate previously postulated hypotheses explaining the sea otter population decreases, as outlined by Estes et al. (1998), and (ii) suggest directions for future research to understand the declines.

INCREASED MORTALITY VS. DECREASED REPRODUCTION

Estes et al. (1998) concluded that the sea otter population decline was caused by increased mortality. Redistribution and reduced fertility were excluded as causes because: (i) radio telemetry studies indicated that there was no evidence of otter movement between islands, and (ii) birth rates and pup survival rates from birth to weaning were similar in the declining population and in stable populations. However, pre-weaning pup survival in the high-density, but declining Amchitka Island (see Fig. 1) population in 1992 was lower than in the lower-density, expanding population at Kodiak Island, Alaska, in 1986 and 1987 (Monson et al. 2000). Weaning success (pup surviving ≥120 days) was almost 50% lower at Amchitka than at Kodiak. The majority of pups (83%) born to marked females at Kodiak survived to weaning, whereas only 47% (24 of 51) of the pups born at Amchitka survived to weaning age. In addition, 40% of beach-cast carcasses (*n* = 143), collected between 1992 and 1994 at Amchitka were comprised of young animals of ≤2 years old (Monson et al. 2000). Data are inadequate to conclude that a decline in pup survival played a role during all stages of the decline at Amchitka, as there are several years during the 1980s and 1990s for which information is not available. However, given the evidence cited previously, it cannot be ruled out as a significant factor in at least the early stage of the decline.

KILLER WHALE PREDATION

The generally favoured hypothesis that predation by killer whales caused the sea otter population to decline is based on three lines of evidence: (i) there was an increase in the number of observed attacks by killer whales on sea otters during the 1990s, coincident with the decline, (ii) sea otter populations did not decline in areas considered inaccessible to killer whales while populations declined in adjacent areas accessible to killer whales, and (iii) the estimated number of attacks necessary to account for the rate of decline is similar to the observed number of attacks (Estes et al. 1998). Here, we evaluate each line of evidence independently.

Increase in observed attacks

The first recorded attack by a killer whale on a sea otter in the Aleutian Islands occurred in 1991 (Estes et al. 1998). Nine more were to follow between 1992 and 1996 in Alaska, all described in detail by Hatfield et al. (1998). Estes et al. (1998) suggested that the timing of the population decline coincided with the onset and subsequent increase of observed attacks. However, there is insufficient information to determine the onset of the decline, as no population surveys were conducted between 1965 and 1992 (Doroff et al. 2003, Wade et al. 2009).

Of the nine attacks described by Hatfield et al. (1998), six occurred in the Aleutian Islands between 1993 and 1996. The other three occurred in 1992 and 1993 in Prince William Sound, Alaska (east of the Aleutian Islands), where the number of sea otters increased between 1993 and 2000 (Bodkin et al. 2002). Before we evaluate the six reported incidents in the Aleutian Islands, the use of terminology should be clarified for consistency with other killer whale predation studies. Ford et al. (1998) defined a kill as an incident in which evidence was obtained indicating that a prey individual was killed and consumed. According to these authors, evidence of such an event includes: '. . . sighting portions of a prey species in the mouth of a whale, or finding the remains of a kill, such as flesh, blood, or oil, floating in the water following an

attack'. Because potential prey often become extremely cryptic when harassed or approached by killer whales, the simple failure to re-sight an individual after it has been pursued is not evidence of a kill. This definition is consistent with observations by Baird & Dill (1995) and Saulitis et al. (2000) who noted that prey handling often occurs just below the surface and observations of blood and/or pieces of blubber are common after kills. Moreover, killer whales often surface with prey in their jaws after making a kill (Baird & Dill 1995). Active pursuits in an apparently predatory manner but where the potential prey animal was not killed are referred to as harassments (Ford et al. 1998). Harassments by killer whales are common and if the fate of a pursued animal is unknown – that is, if a kill or mortal injury is not confirmed – the event is assumed to be a harassment. By these criteria, only one of the six killer whale-sea otter interactions in the Aleutian Islands described by Hatfield et al. (1998) was a confirmed kill, two probably resulted in mortal injuries and are presumed kills, while the other three were harassments. Consumption of a sea otter was only confirmed in a single case.

The first two accounts reported by Hatfield et al. (1998) occurred at Amchitka Island (see Fig. 1) in 1993 involving one adult male killer whale and three smaller whales. The two observations occurred within half an hour of each other, and both involved a sea otter moving away from a killer whale and into a kelp bed or a shallow rocky area. Both of these encounters ended with the sea otters swimming away and the killer whales abandoning their pursuit. In one of the cases, however, the otter's rear appendages were seriously injured, which presumably resulted in its death. The third and fourth accounts (Hatfield et al. 1998) occurred in 1994, also at Amchitka Island, and involved two adult female killer whales and one calf. An observer positioned 300m away observed all three whales circling a solitary otter followed by one of the adult females breaching on the otter. Physical contact between the killer whale and sea otter was thought to have been made and the otter was not seen again. The authors state that the otter 'unlikely escaped uninjured or unobserved' and that it was 'likely killed'. No evidence was reported indicating that the animal was consumed. The fourth account occurred a few minutes later and was described as an identical interaction to the previous one; however, this time the otter dove before contact and was not seen again. By the criteria presented previously, the first incident was a presumed kill and the latter a harassment event.

The only confirmed kill and consumption of a sea otter observed in the Aleutians was the fifth account (Hatfield et al. 1998), which describes a lone male killer whale engulfing a sea otter at the surface at Adak Island in 1995. The sixth and last account (Hatfield et al. 1998) was a harassment event that occurred the following year, also at Adak, and again involving a lone male killer whale. Two sea otters resting in a kelp bed were approached by the whale. When the whale was approximately one metre away from the otters, the otters dove for 10–20s, surfacing closer to shore in the same kelp bed. The killer whale did not pursue the sea otters and left the vicinity, while the otters began foraging within 5 min.

Like many other predators, transient killer whales sometimes demonstrate 'surplus killing', killing greater numbers of prey than they consume (DelGiudice 1998, Wobeser 2000, Short et al. 2002). In surplus killing incidents, the whale plays with animals, such as sea birds (Stacey et al. 1990) and harbour seal pups (Gaydos et al. 2005). The whales may breach on the victim or toss and ram it until it dies, but it is not consumed. This behaviour could be part of the process of learning to hunt, in

which adults are training young to capture and handle prey, or it could be simply play behaviour (Ford et al. 1998, Gaydos et al. 2005). Either way, surplus killing may be responsible for substantial mortality in some marine mammal and seabird populations. Mammal-eating killer whales have also been observed harassing North American river otters *Lontra canadensis* in British Columbia, Canada, but no kills or consumption have been documented (Ford et al. 1998). In Glacier Bay, Alaska, four juvenile transient killer whales harassed a sea otter by attempting to hit it with their tail flukes. After an hour, the whales left the otter alive (Matkin et al. 2007). In two of Hatfield et al.'s observations of harassments, the otters were injured and may have died. Despite the lack of supporting data, it is therefore at least theoretically possible that an increase in such surplus killing, as opposed to predatory killing, contributed to the decline.

It is not known whether the killer whales observed during the interactions described above were of the 'transient' (mammal-eating) or 'resident' (fish-eating) form. Although resident killer whales have never been observed consuming mammal prey, they are known occasionally to harass marine mammals (Ford et al. 1998). Most of these reported harassment events have involved the chasing and ramming of porpoises or seals, with the victims either escaping or disappearing without confirmation that they were injured or killed. Such observations are similar to the non-consumptive sea otter-killer whale interactions described by Hatfield et al. (1998). The abundance of fish-eating killer whales is approximately four times greater than that of the mammal-eating ecotype in the Aleutian Islands and Bering Sea region (1000 resident killer whales, CI = 379–2585 compared to 250 transient killer whales, CI = 97–644; Zerbini et al. 2007), and therefore the possibility exists that harassments by resident killer whales contributed to the sea otter decline. There is no evidence, however, that harassment behavior has increased concomitant with the sea otter decline.

Refuge use

One of the lines of evidence in support of killer whale predation driving the sea otter decline in the Aleutian Islands that Estes et al. (1998) presented was a lower rate of decline of otters in a lagoon considered inaccessible to killer whales than in a nearby open bay. From 1995 to 1997, 65% of tagged (with flipper tags and surgically implanted radio transmitters) otters in Kuluk Bay, Adak Island, disappeared from the site, compared to only 12% that disappeared from the apparent refugium, Clam Lagoon (Fig. 2). Subsequent surveys of Clam Lagoon, however, showed that numbers had declined by 49% (16% per year) from 2000 to 2003 (Doroff et al. 2004). This is similar to the decline of ~19% per year in Kuluk Bay between 1993 and 1997, reported by Estes et al. (1998).

Other differences between Kuluk Bay and Clam Lagoon could account for the timing differences in the disappearance of the otters. For example, Kuluk Bay experienced the most intense military activity around Adak (see Contaminants section below for further discussion). The levels of polychlorinated biphenyl (PCB), various metals and petroleum products reported in blue mussels *Mytilus edulis*, an occasional prey source for sea otters, all posed ecological risks in Kuluk Bay, whereas the levels measured in adjacent Clam Lagoon were below the hazardous level (Anonymous 2000). The highest concentrations of PCBs that have been recorded in bald eagles *Haliaeetus leucocephalus* were found in those from Kuluk Bay (Anthony et al. 1999).
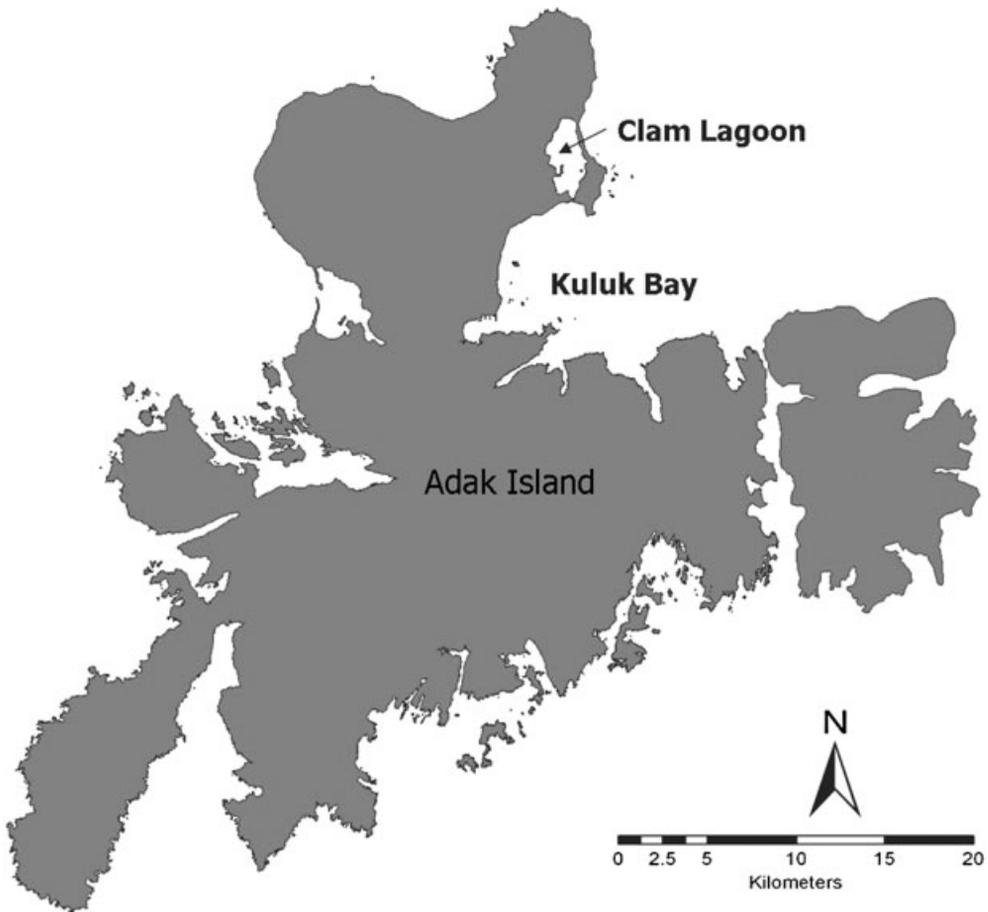
Fig. 2. Map of Adak Island, showing Kuluk Bay and Clam Lagoon. Kuluk Bay is an 'open' area where sea otters are vulnerable to predation, and the number of otters declined during the 1990s. Otter prey (i.e. fish and shellfish) in the Bay contain harmful concentrations of contaminants. Clam Lagoon is an enclosed area that is considered a possible 'refuge' from predators, where sea otter numbers remained stable during the 1990s and then declined from 2000 to 2003, and where prey are not contaminated.

Furthermore, in 1989, 2 million litres of JP-5 aircraft fuel were dumped into Sweeper Cove, which opens into Kuluk Bay (Anonymous 1993). There is little known about the health effects of JP-5 on sea otters; however, fatigue, apparent intoxication, anorexia, depression, lack of initiative, sleep disturbance, cancer and neurological effects such as reductions in coordination and concentration have all been documented in humans exposed to JP-5 (Anonymous 1998).

More recent surveys of the southwest Alaska sea otter DPS (e.g. Burn & Dorroff 2005) continue to document low numbers of animals. Sightings are primarily concentrated in bays and lagoons, as would be expected if the species is experiencing consistent predation and the areas provide partial or complete refuge. However, there is at least one other plausible explanation for this general pattern. Sea otters are known to prefer sheltered areas during rough weather (Kenyon 1969, Rotterman & Simon-Jackson 1988). In the Aleutian Islands they generally occupy waters <40m

deep and ≤400m from the shoreline, and bays and fiords <6km across (Burn et al. 2003). If bays and sheltered inlets with abundant prey are optimal habitat, they are expected to be the first areas occupied by expanding populations, and the last ones inhabited by those in decline. This appears to have been the case in the Near Islands (see Fig. 1), where, during colonization of the islands by sea otters in the 1960s, the first animals observed were in harbours, coves and bays (Estes 1990). As numbers increased, otters dispersed to more open habitat around the coastline, probably in response to intraspecific resource competition. Now that the population is very low and intraspecific competition for preferred habitat is reduced, the remaining sea otters are once again primarily found in sheltered areas. Although this mechanism does not rule out predation as a cause of the decline, it does not require it.

Observed vs. estimated attacks
Using life-tables, Estes et al. (1998) estimated the number of otters that killer whales would have needed to eat in order to reduce the population by the observed rate at Adak Island between 1991 and 1997, and used data on observer effort to predict that 5.05 predation events would have been observed during their study to match the observed population decline. This estimate compared favourably with the six actually observed attacks between 1991 and 1997. The fact that at least half of the interactions were harassments rather than kills, as described previously, weakens this line of evidence.

Sea otters as killer whale prey?
Interactions between killer whales and sea otters have been observed in the past, but there are very few reports of predation by the whales (e.g. Kenyon 1969). If killer whales changed their behaviour and are responsible for the decline of the otters (Estes et al. 1998), it could be because of either surplus killing or predation. Distinguishing between these mechanisms is unimportant if one is solely interested in the consequences to otters of increased killing. However, from a killer whale perspective, it does matter. There are two scenarios under the hypothesis suggested by Estes et al. (1998), both triggered by collapses in sea lion and harbour seal abundance: (i) a small group – possibly as few as four – killer whales switched to an exclusive or primary diet of sea otters, or (ii) larger numbers of killer whales expanded their diet to include sea otters while still feeding primarily on other prey.

   If the first scenario is correct, killer whales subsisting entirely or largely on sea otters should have shown a functional or a numerical response when sea otter numbers were greatly reduced, switching to other prey, moving to areas with higher prey densities, or declining themselves (Holling 1959). The expected long-term consequence of prey-switching by predators is stabilization of declining populations (Mills et al. 1995), and in either case, killing of sea otters in the Aleutian Islands should have decreased, allowing otter numbers to stabilize. Under the second scenario – diet expansion – predation pressure would not be expected to track prey numbers (Georgiadis et al. 2007) and a functional or numerical response to sea otter declines would not necessarily occur. This scenario is more consistent with the observed patterns in the Aleutians, where sea otters continued to decline by 29% per year between 2000 and 2003 (Estes et al. 2005).

   Incidental predation, which is common among generalist predators (Schmidt et al. 2001), predicts that predation on secondary prey should increase as primary prey

abundance increases. When the abundance of primary prey increases, predators consequently increase and severely deplete secondary prey species as bycatch (apparent competition; Holt 1977, 1984). Because reductions in secondary prey do not cause corresponding reductions in predator abundance, secondary prey may be more severely affected by predation than primary prey (Jones 2003). Therefore, we would only expect sea otters to continue to decline if the killer whales' primary prey (e.g. harbour seals or Steller sea lions) are abundant. To date, there have been no reports of significant rebounds in pinniped populations in the western or central Aleutian Islands (Fritz et al. 2006, Angliss & Outlaw 2008), and we therefore consider this mechanism unlikely.

In summary of this section, we find little empirical evidence for killer whale predation as a primary cause of the sea otter decline. However, hypotheses are not disproved by absence of data and we observe that the pattern of the sea otter decline is consistent with prey expansion by killer whales or other predators, and with behavioural changes in killer whales causing increased non-predatory killing.

ALTERNATIVE CAUSES OF THE SEA OTTER DECLINES

In their examination of the sea otter population decline, Estes et al. (1998) rejected starvation, disease and toxins as possible explanations. Here, we re-evaluate these causes, along with other possibilities that have not yet been considered.

Nutritional limitation and disease

Estes et al. (1998) reported that sea urchins *Strongylocentrotus* spp., a preferred sea otter prey, increased in biomass at Adak Island over the course of the sea otter declines, providing some evidence against nutritional limitation as the cause for the decline of otters in the same area. Because sea otter diet at the population level is diverse (Estes et al. 2003a), the publication of data from surveys of the abundance of other potential sea otter prey species, if available, would strengthen this argument.

Increased sea otter body length and mass at six of the Aleutian Islands (specifically at Adak, Amchitka, Attu, Kanaga, Kiska and the Semichi islands) during the 1990s, compared with sea otter body condition from the same area in the 1960s, also provides evidence against bottom-up forces causing the decline (Laidre et al. 2006). However, an early 1990s comparison of sea otter body condition between animals at Amchitka Island and animals at Kodiak Island revealed that females captured in 1992 at Amchitka were in significantly poorer condition than those captured at Kodiak in 1986 and 1987 (Monson et al. 2000). The authors observed an improvement in female body condition at Amchitka the following year (1993) and suggest that Amchitka otters may have been recently released from food-limitation at the time of their study (Monson et al. 2000).

Nutritional stress has been suggested as an explanation for the decline of Steller sea lions (Alverson 1992, Trites & Donnelly 2003) and other marine predators (Österblom et al. 2008) in the North Pacific and Bering Sea. Information on the quality of sea otter prey during the estimated time of the decline is not available. Sea otter numbers have been far below pre-decline numbers for close to two decades and it is unlikely the surviving animals are currently suppressing their prey base to an extent that would prevent a recovery. However, the possibility that nutritional stress arising from changes in the quality rather than quantity of sea otter prey has not been evaluated.

Several instances of sea otter populations being impacted by disease outbreaks have been documented along the North American coasts. For example, the population of southern sea otters in California has been in decline, and infectious disease was identified as a major cause of death (Estes et al. 2003b). Second, between June and October 1987, 60 sea otter carcasses were reported to have beached at Kodiak Island, and disease was the only possible cause for the die-off that could not be ruled out (DeGange & Vacca 1989). Finally, a large number of sea otter deaths in 2006 in south central Alaska were attributed to a phocine distemper virus outbreak in an area adjacent to the southwest DPS (Goldstein et al. 2009).

Estes et al. (1998) discount the hypothesis that disease was the primary factor driving declines of the southwest DPS because there was no evidence of disease in 66 sea otters captured in 1997 at Adak, Amchitka, Kiska and Kanaga Islands. However, the decline was well underway when these samples were taken, and as the animals captured were alive, they may have in fact represented a sample of healthy individuals that did not succumb to previous disease outbreaks.

Both nutritional limitation and disease were also rejected by Estes et al. (1998) as potential causes of the sea otter decline because they predicted that these factors would result in increased numbers of beach-cast carcasses, few of which were found during surveys. They argued that the number of carcasses collected during beach surveys in the Aleutians in the 1950s and 1960s was much higher (approximately 30 to 40 carcasses per month in March and April) than the number of carcasses observed during the recent otter population decline, providing evidence against nutritional stress or disease as a cause for the decline. Weather conditions and poor logistical support hinder regular monitoring in the Aleutian Islands and make accurate surveys of the coastline challenging. As a result, survey effort for carcasses has been variable and limited. Estes et al. (1997) collected seven carcasses at Adak Island in 1991 and 1992. Monson et al. (2000) reported 156 beach-cast carcasses collected at Amchitka Island between 1992 and 1994, while Watt et al. (2000) report only 26 carcasses, also at Amchitka Island and over the same time period. In 2003, beach surveys were conducted opportunistically over a total length of 37km in four islands (Attu, Kiska, Amchitka and Adak) between 28 August and 3 September, and only some disarticulated remains were discovered (Doroff et al. 2004). Surveys for beach-cast carcasses are typically done in the spring, as a large proportion of sea otter mortality occurs during the winter months (Kenyon 1969), while the 2003 surveys were conducted in late summer or autumn, a time of year when carcasses are not expected to be found. Overall, the temporal and spatial distribution of efforts in beach-cast carcass surveys conducted during the sea otter population decline do not encompass the spatial and temporal extent of the decline of otters.

In addition to the lack of survey effort conducted in the Aleutian Islands, climatic conditions influence carcass deposition rates. Wind, in conjunction with current, largely determines how many carcasses are deposited on beaches (Hyrenbach et al. 2001), making deposition rates highly variable. There is no literature on the drift patterns of sea otter carcasses, but examples exist for other marine species. For example, carcass drift experiments with sea birds (Bibby & Lloyd 1977, Bibby 1981) and sea turtles (Hart et al. 2006) have revealed that relatively few birds (0–59%) and turtles (20%) that die at sea ever reach shore; most are lost to scavenging or advection.

Changes in the atmospheric and oceanic circulation patterns can determine where and when carcasses wash up on shore. In the 1970s and throughout the 1980s, the

North Pacific Ocean experienced an abrupt climatic change resulting in altered wind patterns and intensity, and changes in depth of ocean current patterns (Hirons et al. 2001). The Pacific decadal oscillation (a climate shift in the north Pacific lasting 10–30 years) has two phases: warm and cool (Mantua & Hare 2002). There was a shift to the warm phase in 1977, lasting until at least the mid-1990s (Mantua et al. 1997), resulting in a change in wind patterns from clockwise winds (during cold phases) to anti-clockwise winds between 1977 and the mid 1990s (Mantua & Hare 2002). Changes in these wind patterns could change the location of beach-cast carcasses and the probability of them washing ashore at all. As a result, inferences of the causes of mortality before and after the decline was underway, based solely on beach-cast carcasses, are not reliable (Piatt & Van Pelt 1997).

The small percentages of carcasses that do reach the shore are vulnerable to terrestrial scavengers once they are beached (Bibby 1981). Beached sea otter carcasses could be scavenged and lost prior to the surveys. The Arctic fox *Alopex lagopus* for example, introduced on many of the Aleutian Islands, is a known marine mammal scavenger; remains of carrion from pinnipeds make up a substantial portion of stomach contents, and sea otter remains were found in fox scats (West 1987). Similarly, marine scavengers, such as some shark species, could consume carcasses before the carcasses reach the shore. Changes in the abundance or distribution of these scavenger species or in the alternative food resources available to them could significantly affect carcass counts.

Given the information evaluated from the published literature, the data on beach-cast carcasses are inconclusive with respect to the role that nutritional limitation and disease have played in the decline of the southwest DPS of sea otters. To be clear, we agree with Estes et al. (1998) that there is little direct support for the hypothesis that nutritional stress or disease were major contributors to the decline of sea otters in western Alaska, but note that these factors have not been comprehensively studied, and that little weight should be placed on existing sea otter carcass count data.

Contaminant exposure
Contaminants in Aleutian Island species
When persistent organic pollutants (POPs), such as PCBs or dichloro-diphenyl-trichloroethane (DDT), or heavy metals, such as mercury, enter the food web, their toxicity may impact survival and reproduction of organisms at higher trophic levels through biomagnification – the progressive accumulation of persistent substances by successive trophic levels (Connell 1990). There is evidence for contaminant bio-uptake and biomagnification affecting many species in the North Pacific and Bering Sea, including sea lions (Lee et al. 1996), sea otters (Estes et al. 1997), killer whales (Herman et al. 2005), birds (Estes et al. 1997, Anthony et al. 1999, Bustnes et al. 2000) and sea urchins (Sokolova et al. 1995). Effects of such contaminants on animals in the wild can rarely be assessed directly, but laboratory studies indicate that they can cause impaired reproduction and neurological function, behavioural alterations affecting survival, and suppression of immune system function (Macdonald et al. 2003a). Even trace quantities of certain chemicals are known to produce subtle disruption to endocrine systems with severe fitness-reducing consequences (Macdonald et al. 2003a). In California, high prevalence of diseases in sea otters has been hypothesized to reflect reduced immunocompetence resulting from exposure to toxic contaminants (Kannan et al. 1998, 2004, 2006a,b, 2007, Nakata et al. 1998).

Estes et al. (1997) reported high levels of PCB and DDT in seven beach-cast sea otter carcasses collected in 1991 and 1992 at Adak in the Aleutian Islands, and in bald eagle eggs from throughout the Aleutian chain at Adak, Amchitka (Rat Islands), Kiska (Rat Islands) and Tanaga (Delarof Islands), demonstrating the widespread occurrence of these contaminants. Sea otter livers tested at Adak had higher concentrations of PCBs (ΣPCB = 309ug kg^{-1}) than those of a threatened population of sea otters in California (ΣPCB = 185ug kg^{-1}, Estes et al. 2003b). The California population, from a highly industrialized region, experienced a decline from approximately 1994 to at least 1999 (Estes et al. 2003b). Levels in both locations were much higher than in southeast Alaska (ΣPCB = 8ug kg^{-1}) where sea otters are increasing (Estes et al. 1997).

Susceptibility of sea otters to PCB toxicity is unknown; however, the levels found in the otters at Adak are similar to levels associated with population declines and local extinctions of European otters *Lutra lutra* (Mason 1989, Mason & Ratford 1994, Lopez-Martin & Ruiz-Olmo 1996). The PCB concentrations observed by Estes et al. (1997) were also similar to those causing reproductive failure in the mink *Mustela vision*, a close relative of the sea otter (Aulerich & Ringer 1977) which (Wren 1991) identified as a useful surrogate for extrapolating sea otter susceptibility to PCBs.

Substantial evidence exists for high levels of contaminants in other species that co-occur with this population of sea otters in the Aleutian Islands. For example, cormorants *Phalacrorcorax spp.*, which share similar habitats and trophic levels with sea otters, have high concentrations of PCBs in the Near Islands, Rat Islands and Andreanof Islands (Rocque & Winker 2004). Other species in the area with known high levels of contaminants include the green-winged teal *Anas carolinensis* (Scharf 1995), bald eagle (Anthony et al. 1999, Stout & Trust 2002, Anthony et al. 2007), glaucous-winged gull *Larus glaucescens* (Burger et al. 2007a), common eider *Somateria mollissima* (Burger et al. 2008), tufted puffin *Fratercula cirrhata* (Burger & Gochfeld 2008), guillemot *Cepphus columba* (Burger et al. 2007b), North Pacific albatross *Phoebastria spp.* (Guruge et al. 2001), northern fur seal *Callorhinus ursinus* (Loughlin et al. 2002) and Steller sea lion (Lee et al. 1996). The finding of high contaminant levels in sea otters at Adak and high levels in other species throughout the Aleutian Islands highlights the need to examine further the potential role of contaminants in the sea otter decline.

Sources of contaminants

The Aleutian Islands have a history of extensive military occupation from the 1940s until the late 1980s, followed by clean-up activities at some of the sites beginning in the 1990s (Anonymous 2000, Stout 2001). Many of the islands surveyed for sea otters by Doroff et al. (2003) had some form of military occupation over the years, while the remaining islands surveyed were within approximately 30km (range of approximately 2–30km) of one of these sites. Figure 3 illustrates the spatial extent of sea otter population surveys (based on 1992 and 2000 surveys in Doroff et al. 2003) in the Aleutian archipelago, highlighting islands that also had some form of military occupation between the 1940s and the 1990s. Only sites where a minimum of 25 sea otters were counted in 1992 or 2000 are included, as population changes at islands with fewer animals might be strongly influenced by chance events.

Many of these sites have significant PCB contamination, fuel spills, harmful wastes including solvents, pesticides, heavy metals, chemical weapons waste, radioactive
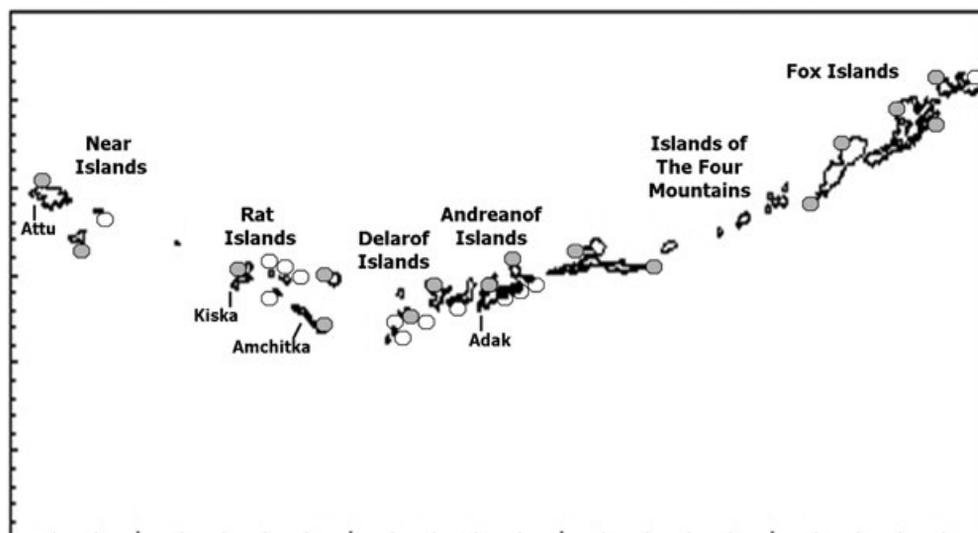
Fig. 3. Map of the Aleutian Islands showing the locations where population assessment surveys were conducted. The open circles (○) indicate locations where surveys were conducted, and there is no history of military occupation. The closed circles (●) indicate locations where surveys were conducted, and there is a history of military occupation.

waste, unexploded ordnances, military ship wrecks, nuclear testing sites, petroleum products, toxic metals and abandoned and leaking drums of various chemicals and fuels (Stout 2001). Over a 40-year period, hazardous substances, such as transformer oils containing PCBs, petroleum, chlorinated solvents and batteries were disposed of on or around Adak Island (Aydin et al. 2007). Several hundred one-ton containers of chemical warfare material were also disposed of 15km north of Adak Island, approximately 1000m below the sea surface sometime after the 1950s (Anonymous 2002a). There is also evidence that wastes were improperly disposed of during some 'clean-up' activities. For example, a US Navy employee on Adak Island was convicted in 1993 of dumping 2 million litres of jet fuel (JP-5) into Sweeper Cove, which opens into Kuluk Bay (see Fig. 2; Anonymous 1993).

Contaminants can accumulate at lower trophic levels and be ingested by sea otters. The primary prey of sea otters at Adak Island is sea urchins, but throughout the Aleutian Islands their diet also includes bivalves, crabs, worms, sea cucumbers and fish (Watt et al. 2000). In 1996, blue mussel and rock sole *Pleuronectes bilineatus* samples collected for contaminant analysis from areas around Adak Island had levels of arsenic, cadmium, chromium, copper, lead, nickel, selenium, zinc, chlorinated pesticides, PCBs, polycyclic aromatic hydrocarbons and petroleum products sufficient to pose ecological risks (Anonymous 2000). Moreover, human seafood harvesters consuming fish and shellfish from Kuluk Bay at Adak were found to have elevated risks of cancer (Anonymous 2000), which could suggest similar risks for sea otters in the area.

Long-distance transport is a second means by which contaminants enter the Aleutian's ocean environment. During the winter months, a large low pressure system draws air bearing contaminants from industrial sources in Southeast Asia along the Aleutian Archipelago (Simonich and Hites 1995, Stabeno et al. 1999). Some propor-

tion of these contaminants are deposited in the area by precipitation (Bailey et al. 2000, Macdonald et al. 2003b). Killer whales in the area bear high levels of POPs with patterns of congeners characteristic of such sources (Herman et al. 2005, Krahn et al. 2007).

In summary, contaminant exposure cannot be entirely disregarded as a potential contributor to the sea otter population decline in some parts of their range in the Aleutian Islands. However, the wide variety of contaminants in the Aleutians, the paucity of information on the synergistic effects of combinations of contaminants on sea otter health, the extensive geographic range of the decline, and the fact that contaminant concentrations in prey are dynamic, make a retrospective analysis of their role in the decline extremely challenging. We believe that the best approach to this problem would be a spatial one, involving sampling the prey of sea otters throughout the decline area and in adjacent areas.

Other predators

A potential agent of decline not yet considered in relation to sea otters is predation by species other than killer whales. Terrestrial predators, such as bears and larger canids, are known to prey on sea otters in some parts of their range, but these predators are not present in most of the Aleutian Islands. Bald eagles are common in the Aleutian Islands and are known to prey on otter pups. During surveys on Amchitka Island in 1969 to 1973, 9–21% of prey remains found in bald eagle nests were from sea otters (Sherrod et al. 1975). Such predation appears to be limited to young pups (Krog 1953, Sherrod et al. 1975) and has the potential to decrease sea otter recruitment significantly when sea otter popula-tions are at low densities. In one study in the Aleutian Islands (Anthony et al. 2008), the percentage of sea otter remains in eagle nests and sea otter abundance declined by similar proportions, suggesting a type 2 functional response (Holling 1959).

Sharks are another potential predator of sea otters. Like killer whales, sharks are apex predators and fluctuations in their populations may have significant effects on nearshore and pelagic community structure. White sharks *Carcharodon carcharias* are known to attack sea otters in California (Ames & Morejohn 1980) but are relatively rare in the Aleutian Islands (Martin 2004). In contrast, Pacific sleeper sharks *Somniosus pacificus* and salmon sharks *Lamna ditropis* are relatively common in the Aleutians Islands (Gaichas 2002). There is no direct evidence that either species preys on sea otters, but, as explained later on, there has been little effort to collect such evidence and it is plausible that predation does in fact occur.

Surveys by the International Pacific Halibut Commission and bycatch data from halibut and sablefish fisheries indicate that, during the 1990s and early 2000s, Pacific sleeper shark abundance increased in the northern Gulf of Alaska (Courteney & Sigler 2007), the central Gulf of Alaska (Mueter & Norcross 2002) and the Bering Sea and Aleutian Island region (Gaichas 2002, Courteney & Sigler 2007). Salmon sharks also increased during this time period, forming huge aggregations of hundreds of animals in bays and inlets (Gaichas 2002, Okey et al. 2007). In 2003, fishermen from six Aleut communities reported increasing densities of salmon sharks and other shark species along the Aleutian Archipelago (Okey et al. 2007). The reasons for these increases are not known, but it has been postulated that populations are rebounding following a 1992 moratorium on a high seas driftnet fishery that caused high

incidental mortality, or are responding to increased availability of prey resulting from changes in oceanic conditions associated with the Pacific decadal oscillation (Anonymous 2002b, Okey et al. 2007).

Sleeper shark and sea otter habitats overlap during the night, when sharks ascend above 100m, occasionally to depths of 2m (Hulbert et al. 2006). Sleeper sharks were once thought to be lethargic, bottom-dwelling predators, but are now known to move continuously in the water column and to be stealth predators of fast moving prey (Cherel & Duhamel 2004, Taggart et al. 2005, Sigler et al. 2006, Van den Hoff & Morrice 2008). The stomachs of 14% of 165 Pacific sleeper sharks from Alaskan waters contained marine mammal tissue, comprising one-third of the mass of items in the diet (Sigler et al. 2006). There is uncertainty about whether most or all of this material resulted from scavenging as opposed to predation, however, the diets of Pacific sleeper sharks and the closely-related species *Somniosus antarcticus* and *Somniosus microcephalis* have been shown to include living marine mammals (Crovetto et al. 1992, Lucas & Stobo 2000, Van den Hoff & Morrice 2008). Moreover, Frid et al. (2006) argued that the behaviour of harbour seals in Prince William Sound is consistent with heavier predation from sleeper sharks than from killer whales. Salmon sharks are believed to feed primarily on salmon and cephalopods (Hulbert et al. 2005) and are not known to prey on marine mammals. Nevertheless, they are highly energetic and reach weights fivefold greater than sea otters, and predation should not be ruled out.

Shark predation on sea otters could occur undetected, simply because it is very difficult to observe, as predation often occurs at night and underwater. In California, for example, most of the evidence of shark attacks on sea otters comes from characteristic lacerations on beach-cast carcasses, which were apparently killed incidentally by white sharks hunting pinnipeds (Ames & Morejohn 1980). If sleeper sharks or, less likely, salmon sharks in the Aleutians did in fact target sea otters as primary prey, carcasses would be expected to be entirely or largely consumed, leaving little, if any, evidence. However, even if predation on sea otters by sleeper or salmon sharks was relatively common, there has been no direct research on the topic in relation to the sea otter decline.

Overall, comparing sharks and killer whales as potential predators of sea otters, there is direct evidence that members of at least one population of killer whales feed on sea otters (the AT1 population of Prince William Sound, Vos et al. 2006), but no indication that the abundance or distribution of killer whales changed in the Aleutian Islands concurrent with the sea otter decline. In contrast, in the case of sharks, there is evidence of an increase in numbers, as described previously, but no direct evidence of predation on sea otters. One factor common to both of these predators is that the density of potential predators postulated to be driving the decline is higher in some areas where sea otter populations are in fact stable or growing, than they are in the region of the decline. For example, transient killer whale densities are high in British Columbia and south east Alaska (Ford & Ellis 1999, Zerbini et al. 2007) where there is no evidence of sea otter population declines. Similarly, sleeper shark densities are higher in the northern Gulf of Alaska, particularly in the Shelikof Trough (Courteney & Sigler 2007), than in the Aleutians. However, other factors probably differ between these areas, such as the types and availability of alternative prey species and the availability of prey refugia; therefore, predator prey dynamics should not be expected to be the same at all sites.

Ocean regime shifts

The North Pacific Ocean has undergone an extreme oceanic regime shift in recent years (Mantua et al. 1997), resulting in cascading effects on biota (Oedekoven et al. 2001, Jones et al. 2002, Steneck et al. 2002) including increased variability in sea surface temperatures (Rodionov et al. 2005) and changes in salinity (Royer 2005), which are coincident with marked declines of Steller sea lions, whiskered auklets *Aethia pygmaea*, Pacific ocean perch *Sebastes alutus*, and red king crabs *Paralithodes camtschaticus* (Schumacher & Kruse 2005). Such concurrent declines imply one or more common underlying mechanism, but it is not possible to assign cause and effect relationships at this time. No research has been done to investigate the role that regime shifts may have played in the decline of sea otter populations in the Aleutian Islands; however, because possible links have been identified in several North Pacific Ocean species, the role of the regime shift should not be ignored for sea otters.

CONCLUSIONS

In this review, we re-evaluated the widely held hypothesis that killer whale predation caused the sea otter population in the Aleutian Islands to decline at a precipitous rate, proposed by Estes et al. (1998). The hypothesis has focused attention on the role of predators in the structuring of North Pacific ecosystems, and has stimulated many interesting and productive discussions and debates (e.g. Estes et al. 1998, Springer et al. 2003, DeMaster et al. 2006, Estes et al. 2006, Mizroch & Rice 2006, Trites et al. 2007, Springer et al. 2008). That said, we found little empirical support for the killer whale hypothesis, and weakness in all three lines of evidence presented by Estes et al. (1998). It appears that one of the reasons that the hypothesis has gained wide acceptance over the past 12 years is that no other substantially more convincing mechanisms were proposed or examined. The lack of empirical support by no means disproves the killer whale hypothesis, but does highlight the need to examine it further and to investigate alternative hypotheses. Here, we reviewed alternative hypotheses and found several worthy of further research. Our findings suggest that research priority should be placed on predation – by killer whales, sharks and other predators – and disease, as the most likely drivers of the decline. We also recommend that work should continue on the potential contributing role of contaminants. In the meantime, we recommend that conservation planning for sea otters in southwest Alaska should focus on current impediments to recovery, which may or may not turn out to be the same factors that initiated and drove the decline.

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