THE ECOLOGICAL ROLE OF MARINE MAMMAL-EATING KILLER WHALES IN THE NORTH PACIFIC OCEAN SURROUNDING ALASKA

REPORT OF
THE MARINE MAMMAL COMMISSION
April 2016

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CITATION
Suggested format for citation of this report: Andersen Garcia, M., L. Barre, and M. Simpkins. 2016. The Ecological Role of Marine Mammal Killer Whales in the North Pacific Ocean Surrounding Alaska. Marine Mammal Commission, Bethesda, MD 20814. 40 pages.

REPORT AVAILABILITY
This report is available at www.mmc.gov.

PHOTOGRAPHS AND FIGURES
Figure 1: High Latitudes of the North Pacific Ocean, including the Bering Sea and Gulf of Alaska. Source: NMFS Alaska Fisheries Science Center.

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Executive Summary

High latitudes of the North Pacific Ocean surrounding Alaska have long been a source of bountiful living marine resources. Historically, the North Pacific waters around Alaska have supported commercial enterprises including whaling, hunting of sea otters and seals for the fur trade, and fishing. Over the past 30 to 50 years, harbor seals, Steller sea lions, northern fur seals, and sea otters have declined markedly in large portions of both the Gulf of Alaska and the Bering Sea, raising concerns about the current status and long-term stability of North Pacific ecosystems. In recent years, some populations of harbor seals and Steller sea lions have stabilized or even begun to grow, but fur seal and sea otter populations continue to decline as do other harbor seal and Steller sea lion populations. Several hypotheses have been proposed regarding the causes of these declines, including diminished or altered food resources caused by commercial fishing or environmental changes, effects of contaminants, disease epidemics, increased mortality due to entanglement in marine debris, and increased predation by killer whales. Research to investigate several of these hypotheses has focused primarily on Steller sea lions because of their interactions with commercial fisheries.

Hypotheses regarding the impact of killer whale predation on pinnipeds and sea otters in the North Pacific Ocean were proposed beginning in the early 2000s. In 2004, Congress asked the Marine Mammal Commission to "*review available evidence regarding the theory that rogue packs of killer whales are wiping out discrete populations of the most endangered marine mammals*." An adequate response requires consideration of multiple factors that have affected the Gulf of Alaska and Bering Sea over the past several decades and that may have contributed to the declines of pinnipeds and sea otters or to changes in killer whale ecology and behavior.

The complexity of ecosystem-scale processes that may affect the interactions between killer whales and their marine mammal prey in the North Pacific Ocean illustrates the importance of long-term research and monitoring to better understand the status and dynamics of marine mammals and ecosystems. The primary anthropogenic threats facing marine mammal stocks often include indirect impacts such as those resulting from the destruction of habitat and competition with fisheries. Understanding these indirect impacts require additional information on ecosystem interactions that is not commonly collected as part of the current marine mammal stock assessment process.

In response to the above-referenced Congressional question, the Commission considered three key questions: (1) Did killer whale predation contribute to the decline of pinnipeds and sea otters in the North Pacific Ocean around Alaska? (2) Is killer whale predation currently contributing to the decline or impeding the recovery of pinnipeds and sea otters North Pacific Ocean around Alaska? and (3) Has the decline in pinnipeds and sea otters had an impact on killer whale population(s) in the North Pacific Ocean around Alaska?

To address these questions, the Commission initiated a review of the ecological role of so-called "transient" (i.e., mammal-eating) killer whales (also known as Bigg's killer whales) in the North Pacific Ocean. In 2005, the Commission convened a workshop of experts to assess existing knowledge on this subject and to identify important information gaps. It convened a second workshop later in 2005 to develop a long-term, ecosystem-scale research program required to fill the information gaps identified in the first workshop. Further, the Commission funded several research projects relevant to specific information needs identified in the workshops. This report summarizes the Commission's analysis and findings regarding the ecological role of transient killer whales in the North Pacific Ocean surrounding Alaska.

Did killer whale predation contribute to the decline of pinnipeds and sea otters in the North Pacific Ocean surrounding Alaska?

Transient killer whales in the North Pacific are known to prey on whales, seals, sea lions and sea otters. For this report, we are interested in transient killer whales preying on harbor seals, Steller sea lions, northern fur seals, and sea otters. As large predators with large energetic needs, killer whales could kill and consume a substantial number of those prey items. Therefore, it is possible that transient killer whales contributed to the declines of those prey species; however, without estimates of transient killer whale predation rates on pinnipeds and sea otters before and during the periods when the populations were declining, it is not possible to confirm or refute such a hypothesis. Although current and future predation rates can be estimated based on observational studies and energetic models, it is not clear how historical predation rates could be estimated reliably, and without such estimates the question cannot be answered conclusively.

Is killer whale predation currently contributing to the decline or impeding the recovery of pinnipeds and sea otters in the North Pacific Ocean surrounding Alaska?

As is the case for historical declines, it is possible that transient killer whale predation affects prey population dynamics because (1) transient killer whales are known to prey on harbor seals, Steller sea lions, northern fur seals, and sea otters, and (2) as large predators with large energetic needs, transient killer whales could kill and consume a substantial number of those prey items. On the other hand, it is not possible to answer this question conclusively because no estimates of current predation rates are available that take into account seasonal changes in distribution, density, and behavior of killer whales and their prey. That being said, such estimates could be derived from long-term research efforts and used to evaluate whether and to what extent killer whales are likely to affect the dynamics of prey populations in the future.

Has the decline in pinnipeds and sea otters had an impact on killer whale population(s) in the North Pacific Ocean surrounding Alaska?

Harbor seals, Steller sea lions, and northern fur seals are known to be important prey of transient killer whales in the North Pacific Ocean surrounding Alaska, as are various other marine mammal species. It appears that sea otters were not important prey until the 1990s. The declines of harbor seals and Steller sea lions from the 1970s and into the 1990s were quite large and likely reduced the availability of those species as prey for killer whales. The even more dramatic decline of sea otters in the 1990s and early 2000s likely reduced their availability to killer whales. The decline of northern fur seals has also been large and the population is continuing to decline; however, the fur seal population is still quite large and, therefore, the species is potentially able to contribute significantly to meeting the energetic needs of killer whales.

Additional research is required before conclusions can be drawn. The principal research questions that remain to be answered regarding the ecological role of transient killer whales in the North Pacific Ocean are:

- How many transient killer whales are in the North Pacific Ocean surrounding Alaska and how has this changed over the past 50 years?
- What are their distribution and movement patterns?
- How does killer whale predation affect marine mammal prey populations?

Although some information exists to address each of these questions, further research is required to account for regional and seasonal variation in transient killer whale abundance, distribution, diet, and particularly predation rates. In order to answer these research questions in detail, a long-term, ecosystem-scale research program would be needed. General components of any research program designed to address ecosystem-scale issues would need to include:

- Long-term research at selected sites to study relevant components of the ecosystem and the processes that control the dynamics of interest (in this case the reproduction and survival rates of transient killer whales and their prey);
- Periodic, broad-scale research efforts (e.g., surveys) to provide context and information for extrapolating the findings from specific study sites; and
- Further development of technology and analytical techniques to collect data remotely (to reduce the need to physically follow specific animals or capture and handle them to gather the necessary observations and data).

Introduction

The Marine Mammal Commission (Commission) has been working for several years on its response to a question from Congress about whether killer whales are "wiping out" populations of endangered marine mammals in the North Pacific Ocean surrounding Alaska[1]. Specifically, in 2004 Congress asked the Commission to "*review available evidence regarding the theory that rogue packs of killer whales are wiping out discrete populations of the most endangered marine mammals*." Hypotheses regarding the ecological role of so-called "transient"[2] killer whale predation in the decline of seals, sea lions, and sea otters have been controversial in the scientific community and the potential ramifications for management of human activities, such as commercial fishing, are significant. We carefully considered the growing body of research to inform this report.

The Commission initiated a review of the ecological[3] role of killer whales in marine ecosystems of the North Pacific Ocean, focusing particularly on the relationship between transient killer whales and their marine mammal prey. As part of its review, in 2005 the Commission convened a workshop of leading killer whale researchers from the United States and Canada to assess existing knowledge regarding the ecological role of transient killer whales that prey on other marine mammals in the North Pacific and to identify important information gaps. The Commission convened a second workshop later in 2005 to develop a long-term, ecosystem-scale research program required to address the information gaps identified in the first workshop. In addition to these workshops, the Commission reviewed the relevant scientific literature, which grew rapidly in the 1990s and early 2000s in response to increased interest in the issues, as well to as a large pulse of research funding, particularly for Steller sea lion research, provided by Congress in the early 2000s.

In the course of its review, the Commission took advantage of the extensive published work by individual researchers and research groups. The book "Whales, Whaling, and Ocean Ecosystems" (Estes et al. 2006) provides a review of historical data and hypotheses on the roles whales play in food webs and the continuing ecological chain reactions as a result of the depletion of large whales by commercial whaling. Additional reviews and results of new studies have been published since the Commission-sponsored workshops in 2005 (Estes et al. 2005, Whitehead and Reeves 2005, Fritz and Hinckley 2005, DeMaster et al. 2006, Hennen 2006, Mizroch and Rice 2006, Maniscalco et al. 2007, Matkin et al. 2007, Schrope 2007, Trites et al. 2007a, Trites et al. 2007b, Wade et al. 2007, Zerbini et al. 2007, Springer et al. 2008, Estes et al. 2009, Wade et al. 2009, Durban et al. 2010, Kuker and Barrett-Lennard 2010, Dahlheim and White 2010, Barrett-Lennard et al. 2011). The Commission also funded several research projects

[1] For the purposes of this report, the "North Pacific Ocean" refers to Pacific Ocean waters surrounding the State of Alaska, including the Bering Sea and Gulf of Alaska, unless otherwise specified.
[2] For the purposes of this report, "transient killer whale" means killer whales that prey largely on marine mammals, also referred to as "Bigg's killer whales".
[3] For the purposes of this report, the term "ecosystem" is used to refer to the environment of the North Pacific Ocean waters surrounding Alaska, including the water, wildlife and climate. The "ecological role" of transient killer whales refers to the role those populations play in the food webs of the area, and the resulting ecological chain reactions from predation.

(Mock and Testa 2007, Straley 2007, London et al. 2012, Mehta et al. 2007). (Research summaries can be found in Appendix 1.)

We often fall short of our goals to achieve effective management that ensures the maintenance of resources as functioning elements in healthy ecosystems. The current monitoring for marine mammal stocks under the Marine Mammal Protection Act (MMPA) focuses almost exclusively on monitoring the stocks' population dynamics and the impacts of human-caused mortality or serious injury, with a focus on incidental mortality and injury ("bycatch") in commercial fisheries. For all stocks in U.S. waters, the level of monitoring has been insufficient to provide the information necessary to effectively manage even this single type of direct impact on many marine mammal stocks (NMFS 2004, Taylor et al. 2007). Some populations of marine mammals are declining in spite of protection, yet the causes of the declines and the consequences for food webs, ecosystems, and human activities are often poorly understood.

To address Congress's specific question, it is necessary to consider three key questions: (1) Did killer whale predation contribute to the decline of pinnipeds and sea otters in the North Pacific Ocean surrounding Alaska? (2) Is killer whale predation currently contributing to the decline or impeding the recovery of pinnipeds and sea otters in the North Pacific Ocean surrounding Alaska? and (3) Has the decline in pinnipeds and sea otters had an impact on killer whale population(s) in the North Pacific Ocean surrounding Alaska?

Killer Whales in the North Pacific

The killer whale is the largest member of the family Delphinidae and a top predator in marine ecosystems of all oceans. Killer whales have distinctive black and white markings and are sexually dimorphic, with adult males growing larger than females. One global species of killer whales is currently recognized; however, variation in morphology (Baird and Stacey 1988, Ford et al. 2000, Dahlheim et al. 2008), social structure (Bigg 1990, Baird and Whitehead 2000, Parsons et al. 2009), vocalizations (Ford 1989, Barrett-Lennard et al. 1996, Deecke et al. 2005, Filatova et al. 2012, Riesch et al. 2012), diet (Ford et al. 1998, Ford et al. 2000, Hanson et al. 2010, Ford and Ellis 2014), and genetic characteristics (Leduc and Taylor 2004, Hoelzel et al. 2007, Morin et al. 2010, Pilot et al. 2010, Foote et al. 2011, Ford et al. 2011a, Parsons et al. 2013) has led cetacean taxonomists to suggest revisions to the single species description (Reeves et al. 2004).

Three types of killer whales, termed "residents," "transients," and "offshores," occur in the temperate coastal North Pacific Ocean. While the ranges of these types of killer whales overlap, they are reproductively isolated, genetically distinct, and vary in their social dynamics, vocal behavior, and foraging strategy (Ford et al. 1998, Ford et al. 2000, Dahlheim et al. 2008). So-called resident killer whales live in stable social groups and feed primarily on fish and squid, particularly salmon (Ford et al. 1998, Saulitis et al. 2000, Ford and Ellis 2006, Hanson et al. 2010, Ford et al. 2016). So-called transient killer whales travel in small groups and are acoustically quiet, using stealth to hunt marine mammal prey. Based on direct observations, analysis of stomach contents, and chemical tissue analyses, transient killer whales are known to prey on marine mammals and occasionally birds, but generally not fish (Baird and Dill 1995, Ford et al. 1998, Ford and Ellis 1999, Herman et al. 2005, Dahlheim and White 2010). Recent information suggests that squid is a larger component of the diet of transients than previously recognized (Hanson and Walker 2014). So-called offshore killer whales tend to be found in outer continental shelf waters (Dahlheim et al. 2008). Chemical analyses indicate that the diet of offshore killer whales differs from those of other killer whales (Herman et al. 2005). They have been observed to eat sharks (Ford et al. 2011b), but more information is needed to characterize the natural history and diet of offshore killer whales.

Because of the differences in prey preferences among the different types of killer whales, this review focuses on the ecological role of marine mammal-eating ("transient") killer whales in the North Pacific and provides additional background on transient killer whales more generally. Transient killer whales live in small groups of one to six animals, but can join into larger groups to kill or feed on large baleen whales. The U.S. National Marine Fisheries Service (NMFS) recognizes three stocks of transient killer whales in the North Pacific: the West Coast transient stock (California to southeast Alaska), the AT1 transient stock (Prince William Sound, Alaska), and the Gulf of Alaska, Aleutian Islands and Bering Sea transient stock. Current population estimates in the most recent U.S. Stock Assessment Reports (SARs) are 243 West Coast transients (Allen and Angliss 2015), 7 AT1s (Muto and Angliss 2016), and 587 Gulf of Alaska, Aleutian Islands, and Bering Sea transients (Allen and Angliss 2015). Predation by the AT1 stock and the Gulf of Alaska, Aleutian Islands, and Bering Sea stock are reviewed in this report.

Matkin et al. (2007) studied transient killer whale predation off the eastern Aleutian Islands including Unimak Pass, where a high percentage of kills were gray whales. Those authors contrast the eastern Aleutians with other areas and emphasize the need to further examine transient movements and predation regionally and seasonally. Harbor seals are the primary prey of transient killer whales in Washington state and British Columbia (Baird and Dill 1995, Ford et al. 1998), and harbor seals and harbor porpoises are primary prey in northern Glacier Bay and the Icy Strait region of southeast Alaska (Matkin et al. 2007). In Prince William Sound and Kenai Fjords the dominant prey of AT1 transients are harbor seals and Dall's porpoises (Saulitis et al. 2000), and sea lions are the focus of predation in the Gulf of Alaska. Wade et al. (2007) summarized predation in several regions based on observations of confirmed kills and stomach contents from the eastern North Pacific since 1950. In the Gulf of Alaska more than half of the documented predation events involved harbor seals and Steller sea lions, over 30 percent involved small odontocetes (Dall's porpoises, harbor porpoises, belugas), 8 percent involved minke whales, and 3 percent involved sea otters. In the Gulf of Alaska a fin whale was observed as prey on one occasion. Wade et al. (2007) reported 41 percent of predation events involved pinnipeds (northern fur seals, walruses, harbor seals, and Steller sea lions), 24 percent small odontocetes, 18 percent large baleen whales (all gray whales), 12 percent minke whales, and a single sea otter. Dahlheim and White (2010) observed transients in coastal waters of southeast Alaska year-round and reported primary prey of killer whales to be Dall's porpoises, Pacific white-sided dolphins, harbor porpoises, and minke whales. They also noted that several potential prey species were common and abundant, but not targeted, including humpback whales, elephant seals, and sea otters. Based on observations of 138 attacks on marine mammals in southern British Columbia and Washington State (Baird and Dill 1996), individual transient killer whales were estimated to eat approximately 1.5 harbor seals per 24-hour period (Baird 2002). Food intake rates varied both seasonally (Baird and Dill 1995) and with group size (Baird and Dill 1996).

Several researchers have noted that they have seen no signs of individual specialization for transient killer whales and have observed the same individuals or groups consuming a variety of prey species (Ford et al. 1998, Dahlheim and White 2010), indicating that transient killer whales can master the predatory tactics for several marine mammal prey (Heise et al. 2003). Lack of focus on a particular species of marine mammal and wide-ranging movements allow transient killer whales to capitalize on seasonally or locally abundant prey. The ease with which killer whales can adapt to foraging on different prey species, however, is not known and is likely to vary between killer whale pods because foraging tactics appear to be culturally transmitted from mothers to their offspring within pods (Guinet and Bouvier 1995, Baird 2000, Rendell and Whitehead 2001). Barrett-Lennard et al. (2011) reported seasonally concentrated predation on gray whales for extended periods, presumably a response to the high-density available of migrating gray whales near the Aleutian passes. They also described transient killer whales leaving uneaten portions of prey and later returning to resume feeding (Barrett-Lennard et al. 2011).

Declines of Marine Mammals in the North Pacific Ocean Surrounding Alaska

Historically, the North Pacific Ocean waters around Alaska have supported commercial enterprises including whaling, hunting of sea otters and seals for the fur trade, and fishing. Currently, the marine ecosystems of the Gulf of Alaska and Bering Sea (Figure 1) continue to support a diverse marine mammal fauna as well as some of the world's largest fisheries in terms of both biomass landed and market value.

Several marine mammal species in this area have declined in the last several decades. These include northern fur seals, sea otters, and Steller sea lions, among others. The causes of these declines are not known and, in many cases, studies focus on local populations that may not represent the entire ecosystem. Over the past 30 to 50 years, however, harbor seals, Steller sea lions, northern fur seals, and sea otters have declined markedly in large portions of both the Gulf of Alaska and Bering Sea, raising concerns about the current status and long-term stability of North Pacific Ocean ecosystems. In particular, concerns regarding the decline of Steller sea lions and potential conflicts with commercial fishing have led to substantial changes in the implementation of commercial groundfish fisheries along the Aleutian Islands and Alaskan Peninsula.

Generally, declines in wild populations can be caused either by increased mortality or decreased reproduction and recruitment. Researchers have proposed hypotheses to explain the pinniped and sea otter declines around Alaska, pointing to (1) diminished or altered food resources caused by commercial fishing or (2) environmental changes, particularly oceanic regime shifts, (3) excessive predation by killer whales, or (4) some combination of factors. Hypotheses regarding the impact of killer whale predation on pinnipeds and sea otters have been particularly controversial. In 2003, Springer et al. hypothesized that transient killer whales sequentially depleted the populations of harbor seals, northern fur seals, Steller sea lions, and sea otters after commercial whaling from the 1950s to the 1970s had drastically reduced the biomass of large whales available as prey to transient killer whales. This hypothesis was contested immediately by other scientists, and alternate hypotheses were proposed regarding the ecological interactions among killer whales, large whales and whaling, and how these could have driven the declines of pinnipeds and sea otters.

Figure 1. High Latitudes of the North Pacific Ocean, including the Bering Sea and Gulf of Alaska. Source: NMFS Alaska Fisheries Science Center.

Killer Whales

Long-term studies have provided information on the population status, feeding behavior, and life history traits of some transient killer whale stocks. Trend data are available for more thoroughly studied populations of fish-eating killer whales in Puget Sound, Washington, and British Columbia, Canada, and the remnant population of marine mammal-eating killer whales in Prince William Sound, Alaska. Matkin et al. (2012) analyzed photographic data since 1984 and determined Gulf of Alaska transient killer whale populations in the northern Gulf are stable; however, reliable data on trends in the population in the Aleutian Islands and Bering Sea are not available (Allen and Angliss 2015). The counts for AT1 transient killer whales declined from 22 whales in 1989 to 7 whales in 2014, although most of the deaths responsible for the decline apparently occurred in 1989-1990 (Muto and Angliss 2016).

Northern Fur Seals

Northern fur seals declined from the 1950s to early 1980s (York 1987). The initial decline was due largely to a directed effort to reduce the population, ostensibly to facilitate a density-dependent increase in reproduction and thus boost the number of young males available for the commercial harvest. The intentional reduction was stopped in 1968 and the population showed signs of recovery, but began to decline again in the mid-1970s. The larger population on St. Paul Island stabilized during the 1980s and 1990s, but recently has begun to decline further. The smaller population at St. George Island has continued a relatively steady decline since the mid to late 1970s. As a result of the population declining to less than 50 percent of levels observed in the 1950s (1.8 million animals), northern fur seals were listed as depleted under the MMPA in 1988 (Muto and Angliss 2016). The current minimum population estimate for the Eastern Pacific Stock of fur seals (those that breed in Alaska) is 548,919 (Muto and Angliss 2016). While known human-caused mortality and serious injury does not exceed the stock's Potential Biological Removal (PBR) level, the population is declining for unknown reasons; therefore, the stock remains depleted (below the Optimal Sustainable Population, OSP, level) (Muto and Angliss 2016).

Steller Sea Lions

NMFS recognizes two stocks of Steller sea lions in the northeastern Pacific Ocean, a western and an eastern stock with the stock boundary at Cape Suckling (144°W). The western stock of Steller sea lions has declined by 85 percent. The decline may have begun as early as the late 1960s or early 1970s and was first observed in the eastern Aleutian Islands (Braham et al. 1980). The decline spread west through the Aleutian Islands and east throughout the western and central Gulf of Alaska, reaching its maximum rate of approximately 15 percent per year between 1985 and 1989 (Loughlin et al. 1992; York 1994). Through the 1990s, the decline slowed across the range of the western stock to approximately 5 percent per year (Sease and Gudmundson 2002). Since 2000, the decline appears to have stopped and counts of animals at rookeries and haul-out sites have increased by approximately 5 percent per year (Angliss and Outlaw 2006), but there has been considerable regional variation in trend (Sease and Gudmundson 2002, Burkanov and Loughlin 2005, Fritz et al. 2013). In contrast to the western stock, the eastern stock of Steller sea lions has increased since the 1960s and 1970s, when regular surveys were initiated, with an overall trend of 4.2 percent increase per year between 1979-2010 (NMFS 2013, Allen and Angliss 2015).

Both stocks of Steller sea lions were listed as threatened under the Endangered Species Act (ESA) in 1990. In 1997, the status of the western population of Steller sea lions was changed to endangered. A recovery plan for Steller sea lions was completed in 1992 and revised in 2008 (NMFS 1992, NMFS 2008). The revised plan includes updated information on status, completed recovery actions, remaining threats, and recovery criteria. The revised plan further recommended reviewing the status of the eastern population to consider delisting. In 2013, NMFS delisted the eastern stock of Steller sea lions under the ESA, as the population had met the delisting criteria.

Harbor Seals

NMFS recognized 12 stocks of harbor seals in Alaska, 9 of which seem to be stable or increasing and 3 of which appear to be decreasing (Muto and Angliss 2016). Harbor seals declined from the late 1970s to the 1980s throughout much of their range from the central Gulf of Alaska (Prince William Sound and Kodiak Island) west through the Aleutian Islands (Pitcher 1990, Small et al. 2003). In Prince William Sound, harbor seals declined sharply from the 1980s (Small et al. 2003, Ver Hoef and Frost 2003) but they may now be increasing there (Muto and Angliss 2016). Harbor seals in the North Kodiak stock are increasing, but the South Kodiak stock remains reduced to only about 20 percent of 1970s levels (Jemison et al. 2006). Overall estimates in the Aleutian Islands suggest a decline of 67 percent from 1977 to 1999 (Small et al. 2003); however, a slightly increasing trend was observed from 2007 to 2011 (Muto and Angliss 2016). Harbor seals are not currently listed as depleted under the MMPA or as threatened or endangered under the ESA.

Sea Otters

Sea otter populations in the Aleutian Islands have undergone several cycles of depletion and recovery. While the causes of some cycles are known, the causes of others are not. Commercial hunting in the 18th and 19th centuries led to fragmentation and near extirpation of the species (Kenyon 1969). The remaining populations began to recover after they were protected in 1911, beginning in the central Aleutians and gradually spreading throughout the archipelago (Doroff et al. 2003). By the 1950s, sea otters had recovered to pre-commercial hunting levels around some of the islands (Estes 1990). Population growth continued until the 1980s, when an estimated 55,000-74,000 animals inhabited the archipelago (Estes 1990, Doroff et al. 2003). Sea otter abundance in the Aleutian Islands declined by about 17-18 percent per year from 1990 to the early 2000s (Doroff et al. 2003), with an even more rapid decline in the early 2000s (Estes et al. 2005). In 2005, the FWS listed the southwestern Alaska sea otter stock as threatened under the ESA. A recovery plan for the southwest Alaska distinct population segment of northern sea otters included information on the latest status and trends, information on threats, recovery criteria, and actions necessary for recovery (USFWS 2013).

Ecological Role of Transient Killer Whales in the North Pacific Ocean: Data Gaps and Hypotheses

The temperate North Pacific Ocean experienced a regime shift in 1976/1977, and perhaps again in 1989 and 1999 (Hare and Mantua 2000, Minobe 2002, Bond et al. 2003). These regime shifts were defined by changes in the physical environment, but they have had pervasive effects throughout the trophic structure of the ecosystems, including changes in the distribution and abundance of important species, such as key forage fishes (Benson and Trites 2002, Anderson and Piatt 1999). In addition, over the past century humans have manipulated North Pacific ecosystems through large-scale removals of whales, fish, pinnipeds, and sea otters. Historical and modern industrial whaling in the North Pacific targeted blue, fin, humpback, sei, gray, bowhead, right, and sperm whales (Rocha et al. 2014). Commercial harvests of northern fur seals by Russian explorers began in 1786 and continued without regulation for more than 80 years (NMFS 1993). Female fur seals were hunted by the U.S. between 1956-1698. Steller sea lions were killed for bounties between 1913 and 1959, and they were commercially harvested from 1959 to 1972. Over 20,000 Steller sea lions were also taken incidentally or killed intentionally during groundfish fishery operations between the 1960s and 1980s. Sea otters were hunted commercially from 1741 until 1911, when such hunting was prohibited.

Humans have also modified the North Pacific Ocean by introducing pollution and contaminants. In spite of their remoteness from human population centers, the North Pacific Ocean has been and continues to be exposed to a wide range of contaminants from point sources (e.g., coastal development, oil and gas operations, military installations) and indirect sources (e.g., atmospheric and ocean currents that distribute the byproducts of human activities occurring thousands of miles away). Tissues of a number of species of marine mammals contain contaminants such as polychlorinated biphenyls (PCBs). At the top of the food chain, transient killer whales carry some of the highest contaminant concentrations (Ross et al. 2000, Rayne et al. 2004, Krahn et al. 2007, Buckman et al. 2011). Such high concentrations raise serious concerns about the health impacts on these animals, which are hard to investigate in these relatively inaccessible pelagic animals.

Trophic interactions have also been implicated as possible drivers of population dynamics of transient killer whale prey. Specifically, Springer et al. (2003) hypothesized that killer whale predation sequentially depleted populations of harbor seals, northern fur seals, Steller sea lions, and sea otters after commercial whaling from the 1950s to 1970s had drastically reduced the large whale prey biomass available to killer whales. This has become known as the sequential megafauna collapse hypothesis. This hypothesis was contested immediately by other scientists, and alternate hypotheses were proposed regarding the ecological interactions among killer whales, whales and whaling, and how these could have driven the declines of pinnipeds and sea otters.

The quality and quantity of data available to evaluate hypotheses about what has caused declines in North Pacific marine mammals varies with species. To date, because of a large infusion of federal funding to assist in evaluation of the role of fisheries in their population decline, the most detailed information and analyses have been conducted on Steller sea lions. The National Research Council completed a comprehensive review of available data and concluded that no hypothesis could be ruled out, but top-down sources of mortality were identified as a threat that should be further investigated (NRC 2003). Less is known about harbor seals and northern fur seals. Many scientists agree that there is sufficient data to indicate that the decline in sea otters has been caused by top-down sources, primarily predation, and the recovery plan (USFWS 2013) identified predation as the top threat. Some scientists still raised questions about whether killer whales are the only predators responsible, or if sharks may also play a role. They have also suggested that contaminants and disease should be investigated further (Kuker and Barrett-Lennard 2010).

The next sections of the report review available information on competing hypotheses regarding the cause of the pinniped and sea otter declines in the North Pacific Ocean surrounding Alaska.

Sequential Megafaunal Collapse Hypothesis

In 2004 when Congress posed its question, there were two related hypotheses that implicated killer whale predation as a primary cause of the pinniped and/or sea otter declines in waters around Alaska. Estes et al. (1998) hypothesized that pinnipeds in the Aleutian Islands region declined due to diminished prey resources and, as a result, killer whales that had preyed upon pinnipeds switched to sea otters and caused the sea otter decline. Springer et al. (2003, 2008) expanded upon the prey-switching idea to include the supposition that large-scale commercial whaling in the North Pacific Ocean and Bering Sea in the 1950s to 1970s substantially reduced the availability of prey for killer whales, causing them to shift their foraging first from calves of large whales to pinnipeds (harbor seals, fur seals, and Steller sea lions, in that order) and then to sea otters.

The explanations suggested for killer whales to shift to killing more pinnipeds and sea otters than whales include: a decrease in the biomass of whales available as prey for killer whales caused by industrial whaling (Springer et al. 2003, 2008); a decrease in available whale carcasses caused by the cessation of industrial whaling (Whitehead and Reeves 2005); a decrease in the biomass of pinnipeds (to explain a predatory shift to otters; Estes et al. 1998); and an increase in the biomass of gray whales post-industrial whaling that attracts and/or leads to an increase in abundance of transient killer whales, which then prey on other marine mammals as the gray whales continue their seasonal migration past the geographical area concerned (Whitehead and Reeves 2005, DeMaster et al. 2006).

Large whales as prey source for transient killer whales

A key element of the sequential megafaunal collapse hypothesis is the assumption of a historical reliance of transient killer whales on great whales as a major component of their diet. In support of the supposition that transient killer whales consumed great whales, Springer et al. (2008) provided a review of both historic and recent killer whale attacks on great whales including bowhead, blue, fin, sperm, and humpback whales (Andrews 1916, Tarpy 1979, Jefferson et al. 1991, Pitman et al. 2001, Reeves et al. 2006). Reeves et al. (2006) also reviewed accounts of attacks on gray, bowhead, and sperm whales. Although such accounts in the literature are rare, Springer et al. (2008) inferred that the number of expected observations would be rare even if attacks were common. Doak et al. (2006) estimated probabilities of witnessing attacks based on estimated predation rate and concluded that there was a low probability of researchers in the field observing attacks. This conclusion was based on the low level of research effort on the water and vast geographic areas covered by the whales. More recently researchers have made more reliable observations of killer whale predation on gray whales, including cow-calf pairs and juveniles, specifically at Unimak Pass in the Aleutian Islands where migrating gray whales go through a confined geographic area and represent a high density of prey (Barrett-Lennard et al. 2011).

Springer et al. (2008) also provided information on the high proportion of great whales with evidence of scars or rake marks from killer whales (Jefferson et al. 1991, George et al. 1994, Ternullo and Black 2002, Naessig and Lanyon 2004, Branch and Williams 2006). The presence of many surviving whales with scars and rake marks led the authors to conclude that attacks must be common.

Springer et al. (2008) also cited behavioral observations of large whales avoiding killer whales or cooperatively thwarting predation attempts as evidence of regular killer whale predation on large whales (Corkeron and Connor 1999, Pitman et al. 2001, Weller 2002). Reeves et al. (2006) noted some specialization in roles among large whales defending against attacks. Ford and Reeves (2008) reviewed both fight and flight responses by large whales in response to transient killer whales. Others noted that killer whales work cooperatively to attack large whales (Jonsgard 1968, Tarpy 1979, Jefferson et al. 1991, Pitman et al. 2001). Springer et al. (2008) and Reeves et al. (2006) contended that it would be unlikely that both predator and prey would develop such behaviors if attacks were not regular events.

Attacks on live animals may not have been the only source of large whale prey for killer whales in the whaling era. Whitehead and Reeves (2005) reviewed information on scavenging records and described ample anecdotal evidence of killer whales scavenging on the carcasses of whales killed by whalers. They hypothesized that with modern industrial whaling, scavenging became widespread and commonplace.

Reductions in great whale populations from whaling

Springer et al. (2003) summarized International Whaling Commission (IWC) data and reported that altogether half a million whales were removed from the North Pacific Ocean and southern Bering Sea by the mid-1970s, leaving all great whale stocks in the region depleted. Springer et al. (2003) reviewed IWC information and reported that, specifically between 1949 and 1969, a minimum of 62,858 whales were removed within 200 nm of the Aleutians and north coast of the Gulf of Alaska. Rocha et al. (2014) estimate nearly 2.9 million large whales were killed worldwide from 1900-1999, with 563,696 killed in the North Pacific. Based on the numbers and estimated biomass from individual species of large whales, Springer et al. (2003) reported that combined biomass in the 1990s and early 2000s was approximately 14 percent of pre-exploitation levels. The estimates were later adjusted in Pfister and DeMaster (2006) to 18 or 46 percent of pre-exploitation levels with and without inclusion of sperm whales, respectively. Rocha et al. (2014) estimated 314,942 sperm whales were killed in the North Pacific alone from 1900-1999. These catches likely left sperm whales severely depleted in the North Pacific (Ivashchenko et al. 2014). Ivashchenko et al. (2011) noted that the Soviet Union conducted illegal whaling worldwide from the 1940s-1970s, illegally killing an estimated 180,000 whales of multiple species and causing a number of population crashes, and falsifying the catch data submitted to the IWC. Intense illegal catches of North Pacific right whales were conducted in the 1960s (Ivashchenko et al. 2012).

Transient killer whale prey switching to include pinnipeds and sea otters

The next element of the sequential megafaunal collapse hypothesis relies on transient killer whales switching from their preferred prey of large whales to pinnipeds. Springer et al. (2003) contended that killer whales altered their diet in response to changing prey availability. As an example of the possibility of prey switching in killer whales, Springer et al. (2003) cited shifts in diet observed in the Southern Ocean where one particular killer whale morphotype fed on whales at high latitudes during austral summer and switched and fed on pinnipeds, fish and squid at lower latitude during austral winter (Mikhalev et al. 1981), although it is not clear that the whales in these different areas were actually of the same population or ecotype. Currently available information does not indicate whether similar shifts may have occurred in the North Pacific Ocean. Barrett-Lennard and Heise (2006) described two phases for potential changes in dietary preferences and hunting behaviors in killer whales, (1) innovation, in which a new behavior is developed, and (2) cultural transmission, in which acquired behaviors of few individuals are passed on to a larger group. Barrett-Lennard and Heise (2006) also noted that whales tended to maintain preferences, possibly to the point of depleting prey populations. With currently available information it is not clear whether killer whales in the Gulf of Alaska were in fact already feeding on pinnipeds (regularly or at least occasionally) even before large whale populations had been substantially depleted in the North Pacific.

Effects of killer whale predation on pinnipeds and sea otters

The purported switch in transient killer whales from preying on large whales to pinnipeds could have increased predation rates on several species in sequence and driven their sequential population declines. Springer et al. (2003) described a sequence of declines starting with harbor seals, then fur seals, followed by Steller sea lions, and lastly sea otters. Their 2003 analysis included harbor seal counts from Tugidak Island (Pitcher 1990), measures of average pup production of fur seals on St. Paul and St. George Islands (York 1987), estimated abundance of the western stock of Steller sea lions (Sease et al. 2001), and sea otter counts from the Aleutian Islands (Doroff et al. 2003). After updating their analysis of the sequential nature of declines in 2008 they came to the same conclusion, that declines were sequential and not synchronous (Springer et al. 2008). They described this as transient killer whales “fishing down” the food chain, depleting one prey resource and then switching to the next available, but perhaps less preferred, prey resource.

Multiple sources, including the USFWS’s sea otter recovery plan (USFWS 2013), Springer (2003, 2008), and Wade et al. (2007), found that the most compelling evidence for predation driving declines may be for sea otters. Although killer whales are rarely observed preying upon sea otters (Vos et al. 2006, Matkin et al. 2007, Wade et al. 2007), researchers in the Aleutian Islands and Prince William Sound have noticed killer whale interactions with otters in recent years, including at least one confirmed kill. A dead transient killer whale in Prince William Sound was found with the remains of five sea otters (and nine harbor seals) in its stomach (Hatfield et al. 1998, Vos et al. 2006). Such interactions with sea otters, which had not been observed previously, are still rare compared to observations of predation on harbor seals or Steller sea lions (Hatfield et al. 1998). This suggests that killer whales, at least in those regions, may have changed their behavior; however, it must be noted that the observations collected to date on killer whale-sea otter interactions are anecdotal in nature.

Other evidence comes from sea otter populations in areas inaccessible to killer whales. Estes et al. (1998) observed that a population of sea otters living inside Clam Lagoon (Adak, Alaska) was protected from killer whale predation and their population numbers remained stable, whereas sea otter populations outside the lagoon declined dramatically. At the same time, a large portion of radio-tagged sea otters outside Clam Lagoon “disappeared” (their radio-tags were not heard by radio-tracking equipment on shore), while radio-tagged animals within Clam Lagoon were reliably detected. Estes et al. (1998) inferred from these observations that the tagged animals outside Clam Lagoon fell prey to killer whales or died of other causes, although it is also possible that the tagged animals may have moved out of range of radio-tracking instruments on shore (which was not possible for animals in the enclosed Clam Lagoon population) or their tags may have failed for some other reason. Other studies of radio-tagged animals at Amchitka and Adak Islands, however, provided no evidence for long-distance (> 7 km) movements of sea otters (Estes et al. 1998). Those studies also showed that birth and pup survival (to weaning) rates were comparable to those of stable populations, suggesting that increased mortality rather than decreased reproduction was the cause of the decline. In the absence of contradictory evidence, the limited evidence for a predatory cause of the sea otter decline provides a plausible, but not conclusive, argument.

Even as critics of Springer et al.’s (2003) sequential megafaunal collapse hypothesis acknowledging sea otter decline may be the strongest case supporting the hypothesis (Wade et al. 2007), scientists still point to other alternatives worthy of further investigation. Kuker and Barrett-Lennard (2010) raised issues for additional study, such as other potential predators such as sharks that are known to feed on pinnipeds and sea otters. The extent to which other natural predators may be contributing to sea otter or pinniped declines is not known. Kuker and Barrett-Lennard (2010) also raised issues regarding the need for additional investigation into disease and contaminants.

Metabolic models support plausibility of sequential megafaunal collapse hypothesis

Springer et al. (2003) described metabolic models to evaluate the plausibility of the transient killer whales’ ability to consume enough prey to explain large population declines. Williams et al. (2004) estimated the number of pinnipeds transient killer whales could consume based on estimates of killer whale metabolic needs and caloric value of prey. For diet scenarios of killer whales consuming 100 percent Steller sea lions to meet their metabolic needs, Williams et al. (2004) estimated that fewer than 40 transient killer whales could have caused the Steller sea lion decline. For otters in the Aleutian Islands, Williams et al. (2004) estimated that fewer than 5 transient killer whales, consuming 100 percent sea otters, could account for the sea otter population decline.

Sparse evidence for alternative causes of declines (bottom-up)

One line of reasoning cited by Estes et al. (1998) and Springer et al. (2003, 2008) to support their sequential megafaunal collapse hypothesis is a lack of evidence for other causes of declines, other than predation. Estes et al. (1998) dismissed disease, toxins, and starvation as causes of elevated sea otter mortality since these causes would produce substantial numbers of carcasses on the beach, yet very few were found. Analyses of disease exposure in Steller sea lions during the period of population decline found no evidence of significant exposure to diseases known to cause marine mammal die-offs, specifically influenza A, morbilliviruses, brucellosis, and leptospirosis (Danner et al. 1998, Burek et al. 2005). Less extensive analyses of harbor seal disease exposure indicated that harbor seals had not been exposed to influenza A (Danner et al. 1998).

Estes et al. (1998) also reported evidence that argued against decreased reproduction (e.g., caused by food limitation) as the driving force in the pinniped and sea otter population declines. Springer et al. (2008) cited studies indicating that nutritional limitations did not drive the sea otter decline (Estes et al. 2004, Laidre et al. 2006). While Springer et al. (2008) discussed the oceanic regime shifts that occurred in the mid-1970s, as well as human removal of large quantities of fish by fisheries, they question whether these events led to prey depletion for pinnipeds. In fact there were increases in abundance of some prey species in some areas during the same time period (Fritz and Hinckley 2005, Brown 2007). In addition, Springer et al. (2008) noted that several indices of physical condition of adult and pup sea lions demonstrated better individual condition in declining stocks than in increasing stocks (Merrick et al. 1997, Rea et al. 1998, Adams 2000, Rea et al. 2003). This again points to a lack of support for population declines driven by prey limitation. Iverson et al. (2004) noted harbor seal pups in Prince William Sound, where the population was in decline, were in similar condition to pups in healthy populations. Finally, if prey were the limiting factor for marine mammals, Springer et al. (2008) argued that they would also expect to see declines in the seabird populations that feed on the same prey; however, there was a lack of declines reported for other species (Springer 2007, Dragoo et al. 2007).

Alternative Hypotheses and Challenges to the Sequential Megafaunal Collapse Hypothesis

In the absence of clear evidence to confirm or refute the sequential megafaunal collapse hypothesis, since 2004 (when Congress posed its question), several new killer whale predation hypotheses have been proposed. Some of these hypotheses suggest that a shift in killer whale predation could have caused the declines, but they differ mainly in terms of the proposed ecological conditions that could have led to a shift in killer whale behavior of the magnitude necessary to cause the declines. These proposed conditions and the likelihood that they would result in killer whale behavioral changes large enough to drive population declines have been the focus of much of the debate regarding the predation hypotheses. Other hypotheses focus on offering alternative explanations for the declines, rather than attempting to disprove that killer whales could have caused the declines.

Hypotheses that Killer Whales Could Have Caused Declines, But in a Different Manner than the Sequential Megafaunal Collapse Hypothesis

<u>Large whales were not a major component of killer whale diet</u>

Wade et al. (2007) summarized observations of transient killer whale predation and reported that the majority of attacks observed involved pinnipeds and small odontocetes, with few observations of lethal attacks on large whales. Others also noted relatively few reports of predation on living large whales, particularly in the North Pacific (Mizroch and Rice 2006). Mizroch and Rice (2006) reviewed stomach content analyses of killer whales and reported that less than 3 percent of mammal eating killer whales had large whale remains in their stomachs. Wade et al. (2007) also reviewed historical reports of killer whales preying on marine mammals in the North Pacific prior to 1950 and found that most involved predation on harbor seals, northern fur seals, Steller sea lions, and Pacific walrus. In contrast to the sequential megafaunal collapse hypothesis, Wade et al. (2007) concluded that pinnipeds have always been the primary prey for transient killer whales, even before the depletion of large whale populations. They also disagree with the assertion that large whale predation is common, but rarely witnessed, and instead asserted that the lack of direct observations of dramatic and obvious kills by researchers studying large whales and transient killer whales indicates that large whale predation is rare. They noted that killer whale predation on other species, such as pinnipeds and small cetaceans, is witnessed regularly by observers studying these species. Wade et al. (2007) recognized an exception to the rare nature of large whale attacks -- researchers have more recently observed killer whales attacking gray whales more regularly, specifically at Unimak Pass in the Aleutian Islands where there is a high density of gray whales during certain times of year when whales are migrating through the confined area of the Pass (Barrett-Lennard et al. 2011).

Wade et al. (2007) reviewed the data on tooth rakes and scars on large whales and did not find support for the assertion that transient killer whales in the North Pacific commonly attack large whales. They cited studies that indicate scars from attacks are likely obtained in the whales' first year of life and in low latitudes (Mehta et al. 2007, Steiger et al. 2008). Based on this information, Wade et al. (2007) suggested that the timing and locations of attacks are in conflict with the sequential megafaunal collapse hypothesis.

While Springer et al. (2003) cited the behavioral reactions of large whales to killer whales as evidence of predation, and other researchers have hypothesized that risk of predation may be a factor driving the long migrations of large whales (Corkeron and Connor 1999), scientists have also made arguments against these hypotheses. Jefferson et al. (1991) described considerable evidence of non-responsiveness, or lack of avoidance responses by large whales to killer whales and Clapham et al. (2001) argued that there are few observations of attacks and predation is not common enough to become an evolutionary force resulting in long migrations. Wade et al. (2007) asserted that the available data indicate transient killer whales focus on smaller prey that can be captured with minimum risk and energy expenditure and may pursue large whales only when densities are high enough that killer whales can find weak or debilitated individuals.

<u>Industrial whaling reduced great whale populations, but did not remove prey source for transient killer whales</u>

The largest number of large whales removed by commercial whaling occurred in the 1800s and first half of 1900s, well before pinniped declines. Mizroch and Rice (2006) reviewed whaling trends and concluded that by 1968 killer whales would have been exerting pressure on pinniped populations, which is not consistent with the Springer et al. (2003) timeline that noted declines began in mid-1970s.

Wade et al. (2007) made the case that, even considering the removal of large whale biomass by industrial whaling, consistent large whale biomass was available as a food source for killer whales and that biomass from large whales always exceeded the biomass of pinnipeds and other potential prey. Springer et al. (2003) reported approximately 14 percent of original biomass from large whales remaining, though the published estimate was 18 percent (Pfister 2004). Pfister and DeMaster (2006) estimated current biomass of large whales would be 46 percent of pre-exploitation biomass. Wade et al. (2007) estimated available large whale biomass as 45-54 percent of historical depending on whether sperm whales were included.

Wade et al. (2007) noted there was a large population of gray whales in the North Pacific by 1970 and increasing through the 1980s, as well as increased populations of other large whale species. Mizroch and Rice (2006) reported minke and gray whales were not depleted by post WW II industrial whaling. DeMaster et al. (2006) suggested that rather than switching to pinnipeds, transient killer whales would have been expected to switch from large whale species in decline due to whaling (e.g., fin and sperm whales), to other species of large whales that were not hunted (e.g., minke whales) or that were increasing (e.g., humpback and gray whales).

Although they did not agree with the assertion that transient killer whales regularly attacked large whales, Wade et al. (2007) noted that even if they did, there had been no dramatic or sudden drop in available biomass and, therefore, no need for transient killer whales to switch prey species. In addition, Wade et al. (2007) suggested that small cetaceans like Dall's porpoise and harbor porpoise, known prey items for transient killer whales, were consistently available as prey. Fur seals also continued to represent a large biomass even after population declines (Pfister and DeMaster et al. 2006). Regardless of any changes from historical abundances, pinnipeds and small cetaceans still only contribute a small percentage to overall marine mammal biomass. Large whale biomass is always an order of magnitude larger.

In reviewing this topic, researchers have acknowledged the need to consider seasonal changes in the types of marine mammal biomass that are available to transient killer whales (Trites et al. 2007a). Pfister and DeMaster (2006) estimated changes in seasonal availability of large whales, small cetaceans and pinnipeds to transient killer whales, from historical levels of marine mammal abundance. They noted that additional research is needed to better estimate pre-commercial whaling abundances. In a fairly typical case of seasonal variability in killer whale prey availability, northern fur seals spend the summer months at rookeries where breeding and pupping occur. During that time, adult females alternate time caring for their pups on shore with weeklong foraging trips within 200-300 km from the rookery (Robson et al. 2004). In the winter, however, northern fur seals disperse across the Pacific Ocean, with some traveling to the U.S. west coast, some to the Western Pacific and others traveling to the central Pacific Ocean, where they forage in the productive transition zone between sub-arctic and sub-tropical waters (Ream et al. 2005). Fur seals are more accessible as potential prey for transient killer whales near rookeries and as they travel to and from the rookeries on foraging trips than they are during the winter when they are dispersed across the North Pacific Ocean.

Several large whale species also undergo large migrations and their availability as prey for killer whales changes seasonally. Migratory gray whales, in particular, are targeted by transient killer whales as they migrate through passes in the Aleutian Islands chain (Matkin et al. 2007, Barrett-Lennard et al. 2011). At this time, dense large whale biomass is concentrated in Unimak pass. There is also variability in the presence and vulnerability of certain age classes. With the exception of minke whales, baleen whale calves and juveniles are killed most frequently (Reeves et al. 2006).

Prey with smaller annual home ranges (e.g., sea otters and Steller sea lions) or predictable seasonal presence on rookeries may be easier to exploit than those that disperse broadly for much of the year (e.g., northern fur seals). Steller sea lions and harbor seals do not travel nearly as far as fur seals or large whales, and both species tend to remain near rookeries or haul-out sites during the summer breeding, pupping, and molting seasons. (e.g., Lowry et al. 2001, Raum-Suryan et al. 2004, Small et al. 2005). Sea otters have fairly small home ranges year-round (<10 km^2), although adult males may move 50-100 km seasonally as they migrate between male aggregations and breeding areas (Garshelis and Garshelis 1984, Gorbics and Bodkin 2001).

The movements of other transient killer whale prey, such as Dall's porpoise and harbor porpoises, are not well known. It is reasonable to expect that their distribution changes seasonally, although not to the same extent as the large whales. Even though accurate abundance estimates are available for several prey species based on summer surveys (Angliss and Outlaw 2007), those estimates do not reflect density and distribution of the species in other seasons.

Declines of whales, pinnipeds and sea otters were/are not sequential

One aspect of the sequential megafaunal collapse hypotheses that has been an ongoing source of controversy is the claimed sequential nature of the pinniped declines, followed by the sea otter decline. DeMaster et al. (2006) statistically analyzed data on timing of the declines of pinnipeds and sea otters and did not find support for a conclusion that the declines were sequential. Wade et al. (2007) plotted trends and argued that the declines appeared to be concurrent rather than sequential, with northern fur seals and Steller sea lions declining simultaneously in the Bering Sea and Aleutian Islands, Steller sea lions and harbor seals declining simultaneously in the Gulf of Alaska, and sea otter declines following. In the updated analyses of the sequence of population declines, both researchers included additional data sets. Springer et al. (2008) continued to maintain that the declines were sequential; in contrast, Wade et al. (2009) maintained they were not.

Geographic areas inconsistent with the Sequential Megafaunal Collapse Hypothesis

As evidence against the sequential megafaunal collapse hypothesis, Wade et al. (2007) looked at additional geographic areas that have increasing pinniped populations. Wade et al. (2007) noted specific geographic areas from southeast Alaska to California where transient killer whales occur and where industrial whaling depleted populations of large whales; however, populations of pinnipeds and/or sea otters were stable or increasing following the cessation of industrial whaling. Some populations of harbor seals, Steller sea lions, and sea otters increased in the 1980s and 1990s, showing they were not limited by transient killer whale predation (Trites et al. 2007a). These increases are largely attributed to protection from harvest and culling by humans.

Scientists have questioned why the mechanisms and assumptions associated with the sequential megafaunal collapse hypothesis would apply to the North Pacific Ocean around Alaska, but not further south along the west coast of North America. Some scientists suggested that environmental changes (i.e., regime shifts) are the most likely explanation for differential trends between the west coast pinnipeds and sea otters (Trites et al. 1999, Trites et al. 2007a, Trites et al. 2007b). Others argued that the different trends reflect differences in the magnitude and type of commercial fisheries and the resulting impact of fish removals on pinnipeds (Alverson 1992, Hansen 1996, Hennen 2006).

Hypotheses That Something Other Than Killer Whale Predation Caused Declines

Environmental change

Some data indicate that Steller sea lion numbers declined and recovered repeatedly over the past 4,500 years and were last at critically low numbers during the 1870s–1930s (Maschner et al. 2014). Steller sea lions appear to have been more abundant during cool periods and less abundant during the warmer periods (Maschner et al. 2014). It is clear that the climate and oceanography of the North Pacific Ocean changed substantially following the 1976-1977 regime shift and that substantial changes occurred in North Pacific ecosystems at the same time (e.g., Mantua et al. 1997, Francis et al. 1998, Hare and Mantua 2000). Although the causal mechanisms by which environmental changes translate into ecological shifts are not clear, the sheer number of ecological shifts that coincided with the 1976-1977 regime shift, including changes in abundance of various fishes and severe declines in numbers of fish-eating seabirds and marine mammals, strongly suggests that the changes are linked (e.g., NRC 1996, Benson and Trites 2002, Hunt et al. 2002). It would not be surprising that populations of pinnipeds would respond to such changes in their prey base.

Steller sea lions, northern fur seals, and harbor seals all have diverse diets (e.g., Pitcher 1981, Sinclair and Zeppelin 2002, Zeppelin and Ream 2006). Although some researchers concluded that the overall biomass of prey available to them may not have declined dramatically (Fritz and Hinkley 2005), others noted that the types of prey they are able to exploit may have changed (Trites and Donnely 2003). Some researchers suggested that changes in prey communities resulted in lower quality (Alverson 1992, Rosen and Trites 2000) or less diverse (Merrick et al. 1997) prey for Steller sea lions.

Commercial fishing

The potential for interactions between commercial fishing and pinnipeds is clear, including direct effects (e.g., bycatch, shooting) and indirect effects (e.g., removal of prey biomass, changes in prey composition and availability). Large numbers of Steller sea lions (approximately 20,000) were caught and injured or killed incidentally in the Alaska groundfish fishery from the 1960s through the 1980s (Loughlin and Nelson 1986, Perez and Loughlin 1991). In addition, an unknown, but presumably large, number of Steller sea lions were shot illegally during this period by fishermen who believed the sea lions were competing for target fish species. NMFS considered the evidence regarding the interactions and their impact on Steller sea lions to be sufficient to require modifications to the manner in which the fishery was executed. Therefore, in 1990, NMFS reduced the number of allowed incidental takes of Steller sea lions by fisheries, increased enforcement of the take limits, and instituted 3 nautical mile no-trawl zones around important Steller sea lion rookeries.

In addition to the direct fisheries mortality associated with fishery bycatch and shootings, fisheries can also affect the prey base of marine mammals and cause nutritional stress. Many fisheries are in competition with marine mammals for the same prey species. Many studies have supported the conclusion that western Steller sea lions were nutritionally stressed in the 1980s relative to the 1970s (e.g., Calkins et al. 1998, Pitcher et al. 1998, Benson and Trites 2003, and Trites and Donnelly 2003). In particular, a number of studies reported changes in diets, body size, survival rates, and reproductive rates that are consistent with Steller sea lions having experienced a nutritional insult in the western portion of their range between the 1970s and 1980s (Trites and Donnelly 2003). Most notably, Steller sea lions were smaller in length, girth, and weight in the 1980s compared to animals prior to the population decline (Calkins et al. 1998). There was also an increase in juvenile mortality (York 1994) and a decrease in productivity as measured by pup counts, an increase in the incidence of failed pregnancies, and a reduction in pregnancy rates of lactating females (Pitcher et al. 1998). In 1991, NMFS modified the pollock fishery management plan to disperse the fishing effort for pollock over space and time, with the goal of reducing the likelihood of local depletion of fish stocks. In 1992, NMFS expanded the no-trawl zones around 37 rookeries to 10 nautical miles. Hennen (2006) found that Steller sea lion abundance trends were negatively correlated with local fishing effort prior to 1991, but not afterward. This suggested that the changes in fishing practices after 1991 had mitigated the inferred impact of fishing on sea lions. An NRC review (2003) concluded there was no indication of nutritional stress in the 1990s, but Holmes et al. (2007) suggested, based on demographic models, that decreased fecundity continued through 2004, suggesting nutritional stress.

Because of the political and scientific focus on the Steller sea lion decline and investigations of potential fishery interactions, more is known about the likely effects of such interactions on Steller sea lions than on other pinnipeds or sea otters around Alaska. Northern fur seal foraging areas overlap considerably with the Alaska pollock fishery and pollock is an important prey item for them. The possible effects of commercial fishing activity on harbor seals are unknown, though some scientists suggest that if fishing affected Steller sea lions, then it may have affected harbor seals in a similar manner. No evidence or analytical results are available to support or counter that contention. Neither is it clear how commercial fishing activity could have impacted sea otters other than through bycatch or indirect effects of ecosystem changes caused by fishing. Such indirect ecosystem effects, though possible, seem unlikely, and fishing is not considered to have contributed to the sea otter decline (USFWS 2013).

Contaminants or disease epidemics

Contaminants and disease have been considered as causes of the pinniped and sea otter declines. Estes et al. (1997) suggested that high contaminant levels in the Aleutian Islands could have contributed to declines of pinnipeds, sea otters, and sea birds in the region. In particular, organochlorine levels measured in sea otter livers were similar to those causing reproductive failure in mink and population declines in Eurasian otters (Estes et al. 1997). Subsequent analyses, however, suggested that the high contaminant levels were restricted to specific islands (particularly those that had hosted military facilities in the past), while the declines were geographically broad (Estes et al. 1998).

Analyses of disease exposure in Steller sea lions during the period of population decline found no evidence of significant exposure to diseases known to cause marine mammal die-offs, specifically influenza A, morbillivirus, brucellosis, and leptospirosis (Danner et al. 1998, Burek et al. 2005). As mentioned above, some evidence suggests that Steller sea lions exhibited lower growth and reproductive rates during the 1980s, which has been attributed to nutritional stress but also could have resulted from reduced fitness caused by disease or contaminants. Less extensive analyses of harbor seal disease exposure indicated that harbor seals had not been exposed to influenza A (Danner et al. 1998).

In contrast, an unusual mortality event (UME), was declared for sea otters in 2006 in response to large numbers of stranded sea otters encountered, beginning in 2002, from the eastern Aleutian Islands to the central Gulf of Alaska. This disease outbreak appears to have started after the larger decline in sea otters was well underway and, thus, is unlikely to have contributed substantially to the initial decline. Any disease outbreak or similar event that leads to increased mortality would be expected to result in increased strandings, as is the case for the most recent UME. While Estes et al. (1998) ruled out disease as the cause of the decline based on lack of unusually high strandings, much of Alaska's coastline is remote and unobserved, other than by researchers during surveys or by local inhabitants of the few communities along the coast. There is the possibility that some insidious, but unknown, effects of disease or contaminants on health and foraging ability could be tied to an increased susceptibility to predation. Based on the opportunistic nature of stranding response, and the fact that some effects of contaminants or disease would only be detected through targeted studies, researchers have concluded that these factors cannot be ruled out as contributors to the declines in pinnipeds and sea otters.

Entanglement in marine debris

A wide variety of marine species have been observed entangled in marine debris, including northern fur seals, Steller sea lions, harbor seals, and sea otters. Among the four species, the problem seems most severe for northern fur seals, presumably because of the long distances that fur seals travel each year across the Bering Sea and Eastern North Pacific Ocean through regions with intensive fisheries and relatively high concentrations of marine debris (Fowler 1987). The proportion of juvenile male northern fur seals that were observed entangled in marine debris on Pribilof Island rookeries increased from the mid-1960s to the mid-1970s. However, that proportion was always small (less than one percent) and declined to between 0.2 and 0.4 percent by the early 2000s (Zavadil et al. 2003). Animals observed on land, however, are those that have survived to travel to the rookery from the site of entanglement. Fur seals have been observed entangled in large fragments of derelict fishing nets at sea, with most dead and others in poor condition. Without an accurate estimate of the proportion of northern fur seals, Steller sea lions, harbor seals, and sea otters entangled in debris at sea, it is not possible to evaluate the contribution of entanglement in marine debris to the population declines at this time.

Combination of causes

As described above, there are numerous potential factors that may have contributed, or are contributing, to pinniped and sea otter population declines, many of which cannot be ruled out with existing studies and data. An important consideration is how multiple factors, which individually may not be drivers on their own, may work in concert and result in cumulative impacts that affect survival or reproduction. DeMaster et al. (2006) concluded, based on available information, that a combination of bottom-up and top-down forces drove the dynamics of harbor seal, sea lion and fur seal populations into decline around the Aleutian Islands.

Conclusions

This report has endeavored to "*review available evidence regarding the theory that rogue packs of killer whales are wiping out discrete populations of the most endangered marine mammals*." In the report we have presented an overall review of hypotheses and evidence to address three questions: (1) Did killer whale predation contribute to the decline of pinnipeds and sea otters in the North Pacific Ocean surrounding Alaska? (2) Is killer whale predation currently contributing to the decline or impeding the recovery of pinnipeds and sea otters in the North Pacific Ocean surrounding Alaska? and (3) Has the decline in pinniped and sea otter prey impacted the population(s) of killer whales in the North Pacific Ocean surrounding Alaska?

As discussed in this report, there are many competing hypotheses on the causes of pinniped and sea otter declines around Alaska, including predation by killer whales, impacts of fishery interactions, and/or stress from contaminants and disease. Significant attention, research and resources have been focused on determining the cause of pinniped and sea otter declines around Alaska. The information and research discussed in this report indicate that there is no definitive evidence or agreement in the scientific community about the cause(s) of the pinniped and sea otter declines in this area.

Our inability to definitively or by weight of evidence answer the question of what drove, or is driving, declines in pinniped and sea otter populations is not because of a lack of examination of the issues and existing data. Scientists and managers have made strides to gather new information about transient killer whales and their prey to inform the debate. This scientific debate regarding the hypotheses continues but there is some common ground that creates opportunities for collaboration and identification of future research and monitoring questions. It seems unlikely that we will ever have all of the essential pieces of information to definitively answer the question of whether transient killer whales caused the decline of pinniped and sea otter populations in the North Pacific Ocean.

While we accept that such ecological questions may go unanswered, it is important to acknowledge the progress that has been made toward understanding the components and processes that make up the North Pacific ecosystem. Researchers continue to refine new techniques for analyzing historical data and to develop new technologies and methods for studies that may provide new insights into past events. Even if historical diets could be described accurately from the available samples, we would still need to develop techniques to estimate the historical abundance of transient killer whales. Only then would it be possible to extrapolate population-wide predation rates from diet data for individuals.

The research community is actively gathering new relevant information. For example, recent studies include new estimates of transient killer whale abundance (Durban et al. 2010, Allen and Angliss 2015), diet composition (Dahlheim and White 2010), and killer whale predation on gray whales at Unimak Pass (Barrett-Lennard et al. 2011). The various hypotheses for the causes of pinniped and sea otter declines in the North Pacific are based on fundamentally agreed-upon scientific information and perhaps the best way to move forward is to develop a collaborative vision of research goals to help understand the ecosystem processes and predator-prey dynamics at work in the North Pacific Ocean.

The controversy over the cause of decline of marine mammal populations in the North Pacific Ocean is illustrative of the need for integrated, long-term, ecosystem-scale research to address some of the most pressing issues in natural resource management. Integrated research efforts focusing on both killer whales and their prey must collect the information that will assist in determining whether killer whales are impacting the population dynamics of their prey (e.g., causing declines or impeding recovery). Such efforts require collaboration among researchers and research groups that currently focus on different aspects of the issue. The principal research questions that remain to be answered regarding the ecological role of transient killer whales in the North Pacific Ocean are:

- How many transient killer whales are in the North Pacific Ocean surrounding Alaska and how has this changed over the last 50 years?
- What are their distribution and movement patterns?
- How does transient killer whale predation affect prey populations?

Although some information exists to address each of these questions, further research is required to account for regional and seasonal variation in transient killer whale abundance, distribution, diet, etc. In order to answer these questions in detail, a long-term, ecosystem-scale research program needs to be initiated. The general components of any research program designed to address ecosystem-scale issues would include:

- Long-term research at selected sites to study relevant components of the ecosystem and the processes that control the dynamics of interest (in this case, the productivity and survival of transient killer whales and their prey);
- Periodic, broad-scale research efforts (e.g., surveys) to provide context and information for extrapolating the findings from specific study sites; and
- Further development of technology and analytical techniques to collect data remotely (to reduce the need to physically follow specific animals or capture and handle them to gather the necessary observations and data).

To implement ecosystem-based research and management, we need to monitor individual species and their connections to other species, through the food web and through other interactions, such as competition. Continued and expanded efforts guided by recovery and conservation plans are needed to improve our capabilities to manage marine mammals as functioning elements of their ecosystems.

For marine mammals in the North Pacific and other ecosystems, we need comprehensive research and monitoring programs to evaluate the status of marine mammal stocks in the context of their ecosystem and consider both natural and anthropogenic impacts on the stocks. We already have many of the tools needed to assess health parameters, survival, and reproduction, although in many cases we need to expand the geographic scope of current efforts and collect data in all seasons. Continued monitoring of pinniped populations, using new tools and technology to help us determine causes of mortality, particularly in declining populations, will inform management and recovery. Programs must also track human-caused direct mortality and incorporate cumulative impact analyses. Current levels of research and resources are not sufficient to answer the myriad of questions about the ecological role of marine mammals, or of even just transient killer whales, in their ecosystems.

Acknowledgments

The Commission would like to acknowledge the efforts of the numerous scientists who conducted the research that formed the basis of the evaluation and findings presented in this report. The Commission particularly appreciates the time and effort of those experts who participated in our 2005 workshops and contributed to this report. The Commission would further like to acknowledge the efforts of the three authors of this report and of the members of its Committee of Scientific Advisors and staff who reviewed it.

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Appendix 1 – Relevant Research Sponsored by the Marine Mammal Commission

Development of predator-prey models for transient killer whales and their marine mammal prey

Previously, simple models of killer whale consumption were constructed to test the plausibility of killer whale impact on other species (e.g., number of whales times predation rate on Steller sea lions equals estimated impact). More detailed data on predation rates relative to availability of alternative prey are becoming available and can better reveal dynamic relationships. Such data require more sophisticated models to understand how the impact of killer whale predation is distributed among available prey populations. The Marine Mammal Commission provided funds to develop more complex predator-prey models. The project was completed successfully; "agent-based" models were created and simulations were run to validate the model and test the effects of a variety of prey and predator conditions. Of particular interest, the model suggested that changes in prey availability on the order of those observed in recent decades would be expected to have profound effects on transient killer whales. The model also highlighted the importance of the sex and age structure of killer whale populations and the long life span of individuals, which can result in time lags between changes in prey populations and a corresponding change in the killer whale population. In some simulations, the prey population began its recovery over 30 years before the killer whale population, and numbers of killer whales sometimes remained stable for decades into a prey decline before dropping. These types of likely complexities in the relationship between killer whales and their prey highlight the need for long-term research programs to document the relevant dynamics. A report of this project is available from the Commission (Mock and Testa 2007).

Investigations of killer whale predation in southeastern Alaska

One central assumption of many hypotheses regarding the impact of transient killer whale predation on marine mammals is that killer whales shift their predatory focus from one species to another when their preferred prey becomes depleted. The Marine Mammal Commission provided funds for a case study of killer whale predation in Glacier Bay in southeastern Alaska where the relative availability of prey species has changed dramatically in recent years. Harbor seals in Glacier Bay have declined over 70% during the past decade, while sea otters in the bay have increased from zero in 1992 to 2,400 in 2004. The study was designed to investigate if killer whales switched from harbor seals to sea otters as the species changed in abundance. No substantial shifts in prey selection were observed. Killer whales seen in previous years were seen in Glacier Bay again, preying upon the same species previously reported. Although few predation events were observed in the one-year study, no sea otter predation was detected. Interestingly, the proportion of harbor seal predation events was lower than in previous years, and the proportion of harbor porpoise predation events was higher. This highlights the fact that killer whales have many prey species to choose from—not just the pinnipeds and sea otters that declined and are the focus of so much debate. A report of this study is available from the Commission (Straley 2007).

Investigation of killer whale impacts on a population of harbor seals in Hood Canal, Washington

The presence of transient killer whales in Hood Canal, Washington, in 2005 provided a unique opportunity to examine the effects of killer whale predation on a population of harbor seals. In January 2003 and January 2005, harbor seals in Hood Canal were subjected to unprecedented, extended foraging by transient killer whales. Distinct groups of transient killer whales entered Hood Canal and remained there for 59 days in 2003 and more than 130 days in 2005. Prior to 2003 transient killer whales had not been observed in Hood Canal, and harbor seals were believed to have been naïve to killer whale predation. During both the 2003 and 2005 events, staff of the Washington Department of Fish and Wildlife and others regularly observed killer whale predation on harbor seals throughout Hood Canal. That predation was expected to have significantly reduced seal abundance based on predictions using various energetic models and observed predation rates. Following the 2003 event, however, the expected loss of about 900 seals from an estimated initial population of 1,200 should have caused a significant population decline but was barely detectable during surveys of the Hood Canal seal population. Although a number of potential reasons for this discrepancy have been suggested, including a rebound in seal numbers due to immigration and/or population growth, one of the most plausible explanations is that the Hood Canal harbor seal population responded to killer whale foraging pressure by changing their behavior and spending an increased amount of time hauled out on shore, thereby artificially inflating the abundance of seals observed onshore during the surveys. When killer whales entered Hood Canal in 2005, an effort was mounted to study the haul-out patterns of the harbor seals to determine if those patterns changed in response to killer whale presence. The study found that seals in fact did alter their haul-out behavior while killer whales were present. The study also discovered that harbor seals in Hood Canal haul out primarily at night during the summer, which indicated that estimates of seal abundance based on daytime aerial surveys greatly underestimated the abundance of seals in the canal. The results of this study were published in PLOS ONE (London et al. 2012).

Investigation of the importance of baleen whales as prey for killer whales

One leading hypothesis regarding the impact of killer whale predation on marine mammals suggests that large-scale removal of baleen whales by whaling in the high-latitude North Pacific forced transient killer whales to prey upon pinnipeds and sea otters, causing sequential declines in populations of those species (Springer et al. 2003). This hypothesis assumes that large whales were important prey for transient killer whales in the North Pacific. To evaluate this assumption, the Commission provided funds for the completion and publication of an ongoing investigation examining indirect evidence of killer whale attacks (scars) using long-term photographic databases of several mysticete species.

The study first analyzed the "rake" scars visible on mysticete whales to determine if they were, in fact, caused by killer whales. The comparison of scars to dentition patterns of killer whales and other likely culprits indicated that the scars observed on humpback whales were caused by killer whales, though rake scars on at least one North Atlantic right whale appeared to be caused by an animal smaller than a killer whale. Based on the findings from the scar identification study, the prevalence of rake scars from killer whales was evaluated for a sample of baleen whales in 24 regions worldwide. The study found considerable geographic variation in the proportion of whales with rake marks, ranging from 0% to >40% in different regions. In every region, the great majority of the scars seen were present on the whales' bodies when the animals were first sighted. This suggested that most killer whale attacks on baleen whales target young animals, probably calves on their first migration from low-latitude breeding and calving areas to high-latitude feeding grounds. The results from this study were published in Marine Ecology Progress Series (Mehta et al. 2007).