A RE-EVALUATION OF THE ROLE OF KILLER WHALE (*ORCINUS ORCA*)
PREDATION IN THE DECLINE OF SEA OTTERS (*ENHYDRA LUTRIS*) IN THE
ALEUTIAN ISLANDS

by

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ABSTRACT

Sea otters in the Western Aleutian Islands have experienced a drastic population decline since the 1990s and Estes et al. (1998) hypothesized that killer whale predation is responsible. This hypothesis has not been challenged nor tested empirically. The aim of this study was twofold: 1) to conduct a literature review of the evidence that killer whales caused the sea otter populations to decline, re-examining alternative explanations, and 2) to empirically test the "killer whale predation hypothesis" by comparing sea otter behavioural responses to artificial killer whale cues (playbacks of killer whale vocalizations and blows) in the Aleutian Islands to the response of sea otters to the same cues in British Columbia, where they do not suffer intensive killer whale predation. The literature review revealed that the existing data are inconclusive and further research into other possible causes is needed. For example, high contaminant levels observed in sea otters coupled with intensive military occupation in the Aleutian Islands warrants further investigation into the role that toxins have played in the health of otters. Increases in shark populations in the Aleutian Islands concomitant with the sea otter population declines also calls for further research into alternative marine predators. The empirical test revealed that sea otters in the Aleutian Islands responded to both treatment and control playbacks of killer whale vocalizations while the sea otters in British Columbia did not. This suggests that there is some form of environmental difference between the two sites, but, because sea otters did not respond more strongly to the sounds of killer whales than to controls, it does not support the notion that killer whale predation caused the discrepancy. This is the first experimental evidence that killer whales may not have preyed on sea otters to the extent suggested by Estes and colleagues, if at all. Together, the results from the review and the playback experiments indicate that the situation is more complex than previously acknowledged and further research into alternative mechanisms driving the sea otter population down is required to ensure proper conservation and management of the species.
TABLE OF CONTENTS

Abstract .............................................................................................................................. ii

Table of Contents ......................................................................................................... iii

List of Tables ................................................................................................................ v

List of Figures ............................................................................................................... vi

Acknowledgements .................................................................................................... vii

CHAPTER I - INTRODUCTION ...................................................................................... 1

INTRODUCTION ........................................................................................................... 1

STUDY SYSTEM ............................................................................................................ 6

LITERATURE CITED ...................................................................................................... 9

CHAPTER II - Declines of sea otter populations in the Aleutian Islands: A review of the
killer whale predation hypothesis .................................................................................. 14

INTRODUCTION ........................................................................................................... 14

Sea otter population decline: current hypotheses ......................................................... 15

DISCUSSION ................................................................................................................ 16

Starvation and Disease ................................................................................................. 18

Contaminant Exposure ................................................................................................. 18

Killer Whale Predation ................................................................................................. 24

1. Increase in Observed Attacks .................................................................................. 25

2. Sea Otter Refuge Use .............................................................................................. 28

3. Observed vs. Estimated Attacks ............................................................................. 30

The Sequential Megafaunal Collapse Hypothesis ....................................................... 30

Other Marine Predators ............................................................................................... 32

CONCLUSION .............................................................................................................. 33

LITERATURE CITED ..................................................................................................... 35
CHAPTER III – In the footprints of collapse: Inferring the cause of a sea otter population decline using regional variation in behaviour

INTRODUCTION ............................................................................................................. 43

METHODS ..................................................................................................................... 45

Field Research ............................................................................................................. 45

Recordings and Playback Sequences ......................................................................... 47

Dorsal Fin Decoy ......................................................................................................... 49

Behavioural Observations ......................................................................................... 50

Statistical Analysis ..................................................................................................... 52

RESULTS ....................................................................................................................... 54

Vocalization Playbacks .............................................................................................. 54

Blow Playbacks .......................................................................................................... 59

DISCUSSION .................................................................................................................. 60

Sensory Modalities ..................................................................................................... 60

Interpretation of Results ............................................................................................ 63

Response to Blow Playbacks ..................................................................................... 63

Response to Vocalization Playbacks .......................................................................... 64

LITERATURE CITED .................................................................................................... 70

CHAPTER IV – GENERAL CONCLUSIONS ................................................................ 77

GENERAL CONCLUSIONS ......................................................................................... 77

FUTURE RESEARCH ................................................................................................ 78

LITERATURE CITED .................................................................................................... 80
LIST OF TABLES

Table 3.1. Summary of experimental trials conducted in Adak and Nuchatlitz ............... 54

Table 3.2. Eigenvalues, variance explained, and factor loadings of the two principal components produced in the PC analysis of sea otter behaviour in response to killer whale vocalization playbacks. .................................................................................................................. 55
LIST OF FIGURES

Figure 2.1. Map of the Aleutian Islands .......................................................... 16

Figure 2.2. Map of Adak Island, showing Kuluk Bay and Clam Lagoon ............. 21

Figure 2.3 Average number of sea otters lost per year between 1992 and 2000 at islands in the Aleutian archipelago with a history of military occupation and military free islands ....... 22

Figure 3.1 Map of the Aleutian archipelago and Adak Island, illustrating the three locations around Adak where studies were conducted ................................................. 46

Figure 3.2 Map of the Nuchatlitz area on the northwest coast of Vancouver Island ...... 47

Figure 3.3 Sample spectrogram of a west coast transient killer whale vocalization playback sequence ................................................................. 48

Figure 3.4 Principal component scores of sea otter behavioural response to underwater vocalization playbacks and controls in Adak and Nuchatlitz ........................................ 55

Figure 3.5 Change in sea otter disturbance behaviour in Alaska and BC after exposure to killer whale vocalization and control playbacks underwater ........................................... 56

Figure 3.6 Change in time sea otters spent traveling in Adak and BC after exposure to killer whale vocalization and control playbacks underwater ........................................ 57

Figure 3.7 Sea otters’ change in periscoping/looking behaviour compared to baseline behaviour in Adak and the Nuchatlitz ................................................................. 58

Figure 3.8 Change in maintenance behaviour in Adak and Nuchatlitz after exposure to killer whale vocalization and control playbacks underwater ........................................ 59
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CHAPTER I – INTRODUCTION

Identifying factors responsible for population declines is crucial for designing effective conservation strategies. To identify these factors, Caughley (1994) proposed the “declining population paradigm”, which attempts to understand the processes by which populations decline and the means by which agents of decline may be identified. Caughley (1994) also emphasized that some of the most common errors when diagnosing causes of population declines are correlated with flawed scientific method, such as equating association with causality, failing to identify and see through confounding factors, and failing to replicate or control experiments. Identifying causes of decline can be accomplished through experimental manipulation, but often this method is not possible as threatened populations and the factors that threaten them are not amenable to manipulation (Green 2002). In view of this difficulty, I propose that current behaviours of animals can in some cases be used to infer the causes of recent demographic collapses. This is the first study to apply this approach to conservation biology using playback experiments and focuses on a dramatic decline of sea otters (*Enhydra lutris*) in the Aleutian Islands, Alaska, during the 1990s.

Learned and innate components of behaviour are critical to individual survival, and are major players in the fates of populations. It is therefore essential that conservation strategies be built on a foundation of behavioural understanding. For example, knowledge of behaviours associated with habitat use, dispersal, and migration are necessary to predict the impact of habitat loss (Woodroffe and Ginsberg 2000) and to design effective reserves. An understanding of mating behaviour illuminates the profound effects of exploitation and disturbance on population growth rates (Greene et al. 1998). With advances in technology, we are capable of collecting long-term demographic data on tagged individuals. These long-term focal follows
have contributed a better understanding of individuals’ behaviours, such as feeding, breeding, migration, etc. This better understanding of behaviours has led to improved monitoring of populations (Caro 1999) and improved conditions of individuals reintroduced or translocated for conservation reasons.

It is crucial to consider a variety of behavioural traits when selecting individuals for reintroduction, because expression of these traits can affect survival. For example, foraging behaviour, antipredator behaviour, communication, locomotion, and habitat choice will affect the success of a reintroduction. Fischer and Lyndmayer (2000) conducted a review of reintroduction projects and discovered a failure rate of 69% among Australian reintroductions of animals into areas containing predators. Wildlife conservationists must understand the mechanisms underlying antipredator behaviour before releasing predator-naive animals back into predator rich areas (Blumstein 2002), because predation is often implicated as a key factor responsible for failure (Beck et al. 1991; Short et al. 1992; Miller et al. 1994).

Antipredator strategies involve a combination of innate components and some greater or lesser degree of refinement through experience (Kullberg and Lind 2002). Animals can be genetically predisposed to avoid danger (Sterelny 2004), or individuals can learn to avoid it through experience or observing conspecifics (‘social learning’). Conventional wisdom holds that antipredator behaviour is relatively ‘hard-wired’ or innate, because this behaviour must be functional the first time an individual encounters a predator (Blumstein 2002). However, individuals of many taxa exhibit more effective evasive behaviours after direct experience with predators, proximity to conspecifics exhibiting antipredator behaviour, or awareness of conspecifics being eaten by predators (Griffin 2004; Curio 1993).

Antipredator behaviours are expected to be primarily innate when predator and prey have shared a long evolutionary history (Chivers et al. 2001; Riechert and Hedrick 1990). Predator recognition that requires little or no experience has been demonstrated in a wide variety
of taxa, including the Seychelles warbler, *Acrocephalus sechellensis* (Veen et al. 2000) and Arctic charr, *Salvelinus alpinus* (Vilhunen and Hirvonen 2003). Although animals can learn, the propensity to learn is inherited genetically, as are instincts (Tinbergen 1968). Evidence from lab studies (Curio et al. 1978; Magurran 1989; Mathis et al. 1996; McLean et al. 1996) and several field studies (Deecke et al. 2002; Maloney and McLean 1995) suggests that learning plays an important role in the recognition of predators (Shriner 1999).

Individuals can also learn to recognize harmless heterospecifics over time, thus distinguishing between threatening and non-threatening cues. This is termed ‘habituation’. Habituation, the gradual decrease in response over repeated exposure to a stimulus, is generally considered the simplest form of learning (Shettleworth 1994). Disturbance studies reveal that some animals exposed to high levels of human activity may habituate (e.g., Fowler 1999) while others may not (e.g., Rees et al. 2005). This may be a result of interspecific differences in both learning ability and environmental conditions that would allow learning to occur. Conditions favouring learning in an animal’s lifetime include predictability and consistency in stimulus exposure (Johnston 1982; Recarte et al. 1998).

Predators apply strong selective pressure on the behaviour, morphology, life history, and physiology of their prey. For example, most species have evolved a combination of morphological defences and behaviours, such as vigilance or group living, to mitigate the potential impacts of predation. Detecting and avoiding predators is critical to an individual’s survival and fitness, but avoidance is also costly, as it tends to reduce time and energy available for other essential activities such as foraging or mating (Brown et al. 2006).

On an ecological time scale, the risk of predation can vary yearly, seasonally, daily, or even minute-by-minute. An animal’s fitness is enhanced if it is able to accurately match its behaviour to current levels of predation risk; thus, anti-predator traits may be plastic and only expressed, for example, at particular ontological stages or during times and in places where
predation risk is known to be high. Here, I present a brief summary of vigilance behaviour and predator sensitive foraging theory.

The term ‘vigilance’ is used to describe an animal’s behaviour when it is alert and scans its surroundings to detect a predator before it is too late to take effective action (e.g. fight or flight). Vigilance almost always involves multiple senses, although the relative importance of sensory systems in detecting predators varies between species. It is generally assumed that terrestrial herbivores compromise their ability to detect predators when feeding with their heads down and compromise food intake when scanning for predators with their heads up (Lima 1990).

There is good evidence that many mammals and birds forage in groups to increase the effectiveness of vigilance while reducing individual costs (Elgar 1989; Lima and Dill 1990; Lima 1995). Each individual in a group of conspecifics can potentially benefit from increased predator detection, coordinated group defense, increased probability of escape if a predator is encountered, and a broadly dispersed probability of death (Bertram 1978; Turner & Pitcher 1986). Sometimes in these group situations, individuals take turns serving as sentries (e.g. dwarf mongoose, Rasa 1987; Florida scrub jay, McGowan and Woolfenden 1989; meerkats, Clutton-Brock et al. 1999), which watch for predators from a prominent position while other members of the group continue to forage, and give alarm calls when a predator is detected (Bednekoff 2001).

Ecological theory has traditionally examined predator-prey interactions in terms of direct consumption – predators consume their prey and thereby reduce prey density. Such density reductions can have major impacts on prey population dynamics and on the entire ecosystem (Sih et al. 1985). Predators, however, can also have indirect, behaviourally-mediated impacts on their prey, by inducing them to restrict or alter their foraging activity to reduce risk (e.g. Lima and Dill 1990). These changes in behaviour come with associated costs to other fitness -
enhancing activities, such as foraging. Recently, emphasis has been placed on assessing these non-lethal effects of predators on their prey (e.g. Lima 1998).

There is a trade-off between eating and avoiding to be eaten, as in the previously discussed case of terrestrial herbivores. Individuals of most species must consider predation risk in all decisions about when to feed, where to feed, what to eat, or even how to handle food (Sih 1980; Lima and Dill 1990). Foraging theory predicts that changes in foraging behaviour in response to a perceived risk may result in substantially reduced energy intake, or even starvation (Stephens and Krebs 1986; McNamara and Houston 1987; Abrams 1991; Sinclair and Arcese 1995). Individuals must divide their time between foraging and hiding from predators, as these two behaviours are not mutually exclusive. The foraging arena theory describes prey in two states; 1) where they are available to predators while foraging (the “foraging arena”), and 2) where they are unavailable to predators in a refuge (Walters and Martell 2004). In the refuge, prey species are safe from predators, but access to resources is limited.

Risk-sensitive foraging leading to reduced energy intake has been described in many species, including desert baboons (Cowlishaw 1997), deer mice (Holtcamp et al. 1997), various bird species (Martindale 1982; Lima 1985; Valone and Lima 1987) squirrels (Lima et al. 1985; Newman et al. 1988), antelope (Underwood 1982), and moose (Edwards 1983).

Current evidence suggests that predators may have more pronounced impacts on community dynamics by inducing risk-averse behaviours than by direct consumption (Werner and Peacor 2003; Abrams 1984 for theoretical review) because of shifts in the behaviour of large numbers of animals simultaneously (Preisser et al. 2005). Moreover, top-down control appears to be stronger in water than on land (Polis and Strong 1996), suggesting that predator impacts on community dynamics may be stronger in aquatic than in terrestrial ecosystems (Shurin et al. 2002). The reason for this difference is unknown. However, Shurin et al. (2002)
suggested that this variation could be explained by the fact that predator effects on primary producers in aquatic systems are greater than those observed in terrestrial ecosystems.

Study System

Sea otters (*Enhydra lutris*) are the smallest marine mammal in North America, and the largest member of the family Mustelidae, which consists of 70 species, including river otters, skunks, weasels and badgers. The modern sea otter arose in the North Pacific at the beginning of the Pleistocene, 1-3 million years ago and has not dispersed to other oceans since that time. There are 3 subspecies of *Enhydra lutris*: *lutris*, ranging in the Western Pacific, *nereis*, the Southern sea otter, and *kenyoni*, the northern sea otter ranging from the Aleutian Islands in Alaska along the coast to British Columbia and Washington. *Enhydra lutris kenyoni* was the subject of this study.

The sea otter is red-listed by the World Conservation Union (IUCN 2006) as “endangered”, as its populations have undergone extensive population declines. In Alaska, the sea otter is listed as “threatened” (USFWS 2000) due to the dramatic declines observed over the last 15 years throughout the southwest stock. In Canada, the sea otter was recommended for down-listing from "threatened" to "special concern" in April 2007 by COSEWIC (Committee on the Status of Endangered Wildlife in Canada) but at the time of writing is still listed as “threatened” under the Species At Risk Act (SARA).

Sea otters in the Western Aleutian Islands have experienced a drastic population decline since the 1990s (Estes et al. 1998; Estes et al. 2005). The observed magnitude across the range was approximately 78% over 6 years, resulting in a loss of almost 40,000 otters in the Aleutians (Estes et al. 1998). Predation by killer whales has been hypothesized as the cause of the drastic decline (Estes et al. 1998). Springer et al. (2003) proposed a mechanism referred to as the “sequential megafaunal collapse” (SMCH), which hypothesises that top-down forces, in
particular predation by killer whales, has resulted in sequential population declines of various marine mammals. The hypothesis proposes that the depletion of the great whales by industrial-scale whaling from the 1940s - 1960s caused killer whales to shift their diet to more abundant marine mammal prey, first by focusing on harbour seals (*Phoca vitulina*), fur seals (*Callorhinus ursinus*), sea lions, and finally, the species with the lowest caloric value, sea otters. This hypothesis remains controversial with detractors focusing on whether or not the declines were in fact sequential throughout the range of sea otters (e.g. Mizroch and Rice 2006). However, no authors commenting on the hypothesis (e.g. DeMaster et al. 2006; Trites et al. 2006) have challenged the possibility that killer whales were responsible for the drastic sea otter population declines, despite the sparse and speculative evidence supporting it.

Chapter two of this thesis is a literature review of the evidence in support of the killer whale predation theory, as well as alternative explanations of the sea otter population decline in the Aleutian Islands. The objective of this chapter was to take a fresh look at the possible causes of the population decline suggested by the original authors and to examine alternative causes.

To supplement the evidence reviewed in chapter 2, I empirically tested the killer whale predation hypothesis in chapter 3. To test the hypothesis, I measured sea otter behavioural responses to artificial killer whale cues in the Aleutian Islands and compared their behaviour to the response of sea otters to the same cues in British Columbia, where sea otter populations are not threatened by intensive killer whale predation. In chapter 3 I present the results of two experimental tests: the response of sea otters to 1) killer whale blow sounds, and 2) killer whale vocalization sounds. A third experimental test involved the presentation of an artificial killer whale dorsal fin to the sea otters at both locations; these tests were carried out in Adak and BC, but proved to be challenging; therefore, no analyses were performed on the dorsal fin data. Behavioural responses are often the best available estimators of the fitness consequences of
disturbance, and prey behaviours, such as foraging time and shifts in habitat, have been used to indicate non-lethal effects of predation (Lima and Dill 1990). This study is the first to experimentally test Estes et al.'s (1998) hypothesis, and to use current animal behaviours to infer the causes of a population decline.
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CHAPTER II:
Declines of sea otter populations in the Aleutian Islands: A review of the killer whale predation hypothesis

Introduction

Populations of sea otters (Enhydra lutris kenyoni) in the Western Aleutian Islands have experienced widespread declines of similar timing over the past 15-20 years (Estes et al. 1998; Doroff et al. 2003; Estes et al. 2005). The observed magnitude across the range was approximately 78% over 6 years (Estes et al. 1998), culminating in a loss of almost 40,000 otters. This is one of the largest population declines observed in recent history and thus a major conservation issue. The North Pacific 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), changes in salinity (Royer 2005), and marked declines of Steller sea lions (Eumetopias jubatus), whiskered auklets (Aethia pygmaea), Pacific ocean perch (Sebastes alutus), and red king crabs (Paralithodes camtschaticus) (Schumacher and Kruse 2005). Such concurrent declines imply one or more common underlying mechanisms.

Several authors have proposed that over-fishing in the Aleutian Islands resulted in the loss or decline of species in various trophic levels, thus driving ecosystem-wide changes (e.g. Trites and Larkin 1992). As an alternative, Springer et al. (2003) proposed the “sequential megafaunal collapse” hypothesis, which hypothesises that predation by killer whales (Orcinus orca) has resulted in consecutive declines of populations of several species of marine mammals. Springer et al. posit that overexploitation of great whales by industrial-scale whaling from the 1940s - 1960s (although see Springer et al. 2008 for amendment of this theory) caused killer

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whales to switch to more abundant marine mammal prey, first by targeting harbour seals \((Phoca vitulina)\), then fur seals \((Callorhinus ursinus)\), then sea lions, and finally, the species with the lowest caloric value, sea otters. This hypothesis remains controversial, with sceptics focusing on the degree to which declines truly were sequential (e.g. Mizroch and Rice 2006). However, most authors (e.g. DeMaster et al. 2006; Trites et al. 2006) have not challenged the theoretical possibility that killer whales were responsible for the drastic sea otter population declines.

In Alaska, the southwest distinct population segment (DPS) of the northern sea otter is listed as “threatened” (USFWS 2000). A recovery outline was published by US Fish and Wildlife Service (USFWS 2005), listing predation by killer whales and increased vulnerability to catastrophic events such as disease epidemics and oil spills as primary threats to the viability of this population. However, there remains considerable uncertainty regarding the cause of the declines (USFWS 2005). Here, I re-examine existing hypotheses on the population declines of sea otters, and suggest directions for future research to elucidate mechanisms underlying the observed trends.

**Sea Otter Population Decline: Current Hypotheses**

Population declines result from decreased reproduction, emigration, increased mortality, or a combination of these causes. It has been suggested that the sea otter declines are the result of increased mortality, for which North Pacific transient killer whales are responsible (Estes et al. 1998; Angliss and Lodge 2004).

Decreased reproduction and emigration have been rejected as explanations for two reasons. First, birth rates and pup survival rates of radio-tagged individuals at Amchitka (in the Rat Islands) and Adak (in the Andreaoif Islands) were similar to those of stable populations between 1992 and 1996 (Fig. 2.1, Estes et al. 1998). Thus, reduced reproduction was unlikely. Second, declines were synchronous across the Aleutian archipelago and there did not appear to be population build-ups on some islands to account for losses on others, making emigration
unlikely. Moreover, 52 radio-tagged animals at Adak and 98 at Amchitka did not emigrate, moving a maximum distance of only 4.31 and 6.95 km respectively. By the process of elimination, Estes et al. (1998) concluded that increased mortality caused by increased predation remains the only plausible explanation for such a widespread and dramatic population decline.

Despite the compelling case put forth by the authors, the killer whale predation hypothesis is inferential and with limited empirical support. In light of this uncertainty, I re-examined the evidence for killer whale predation and discuss alternative explanations for the sea otter decline.

**Discussion**

Primary causes of adult mortality in wildlife populations include disease, toxins, starvation, or predation. The first three have been rejected by Estes et al. (1998) as potential causes of the sea otter declines, as any of these sources of mortality should result in substantial numbers of beach-cast carcasses, few of which were found during surveys. Fishermen have
reported that when sea otters die in fishing nets or are shot, the carcasses often float at the surface and eventually wash up on coastlines (pers. comm. Estes, J.). Aleut hunters contrarily suggest that the carcasses may sink, especially if malnourished (Laughlin 1980). Moreover, wind in conjunction with current largely determines how many carcasses are deposited on beaches (Hyrenbach et al. 2000), making deposition rates highly variable.

Weather conditions and poor logistical support hinder regular monitoring in the Aleutian Islands and make accurate surveys of the coastline challenging. Beached sea otter carcasses could be scavenged and lost prior to surveys. Carcass drift experiments with sea birds have revealed that relatively few (0–59%) birds that die at sea ever reach the shore (Bibby & Lloyd 1977, Bibby 1981), and carcasses that are beached are vulnerable to terrestrial scavengers. The arctic fox for example, introduced on many of the Aleutian Islands, is a known marine mammal scavenger, with remains of carrion from sea lion carcasses washed ashore making up a substantial portion of stomach contents (West 1987).

Changes in atmospheric and oceanic circulation patterns can determine where and when carcasses may 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, changes in sea surface temperatures and changes in depth of ocean current patterns (Hirons et al. 2001). The Pacific decadal oscillation (PDO) – a climate shift in the north Pacific lasting 10-30 years – has two phases: warm and cool (Mantua and Hare 2002). There was a cool regime from 1947-1976, and a switch to the warm phase in 1977, lasting until at least the mid 1990s (Mantua et al. 1997). Warm phases are associated with low pressures over the North Pacific, which cause enhanced counter-clockwise winds, while cool phases are associated with clockwise winds (Mantura and Hare 2002). Changes in these wind patterns would change the location of beach-cast carcasses and/or the probability of them washing ashore at all. Because
environmental conditions vary, comparisons of mortality events through time based solely on
beach-cast carcasses are not entirely reliable (Piatt and Van Pelt 1997).

**Starvation and Disease**

Sea urchins, a preferred sea otter prey, increased in number over the course of the sea
otter declines, providing some evidence against nutritional limitation as the cause for mortality
(Estes et al. 1998). However, information on the quality of this prey is not available, and no
surveys of any other prey species were reported (Estes et al. 1998). Although it is unlikely that
starvation is the cause of the population decline, surveys of other sea otter prey and of the
quality of prey would supplement the evidence.

Estes et al. (1998) discount the hypothesis that disease was the primary factor driving
debacles because there were no signs of disease in 66 sea otters captured throughout the range of
the decline (Estes et al. 1998). These 66 otters were captured in 1997, while the decline was
assumed to have started in the mid 1980s. The decline was well underway when these samples
were taken, and because the animals captured were alive, they could have in fact represented a
sample of healthy individuals that did not succumb to previous disease outbreaks.

**Contaminant Exposure**

When contaminants such as polychlorinated biphenyls (PCBs), dichloro-diphenyl-
trichloroethane (DDT) or mercury enter the food web, they pose a high risk to organisms at
higher trophic levels through biomagnification - the progressive build up of persistent
substances by successive trophic levels (Connell 1990). There is evidence for bio-uptake and
biomagnification in sea lions (Lee et al. 1996), sea otters (Estes et al. 1997), birds (Estes et al.
1997; Bustnes et al. 2000) and sea urchins (Sokolova et al. 1995).

Sea otters inhabit coastal areas and therefore are considered vulnerable to contaminants
such as organochlorine compounds (OCs). Chronic effects of elevated concentrations of
contaminants include impairment of reproduction and neurological function, behavioural
alterations that could affect survival, and suppression of immune system function (Macdonald et al. 2003a). Estes et al. (1998) reported that increased contaminant concentrations were identified in sea otters, but were restricted to small areas and thus inconsistent with the widespread declines of the otters. However, the previous year, Estes et al. (1997) reported high levels of PCB and DDT in sea otters at Adak in the Aleutian Islands, and in bald eagle eggs at Adak, Amchitka, Kiska and Tanaga. Susceptibility of sea otters to PCB toxicity is unknown; however, the concentration levels found in the otters at Adak are similar to levels that have been associated with population declines and extinctions of Eurasian otters (Mason 1989; Mason and Ratford 1994; Lopez-Martin and Ruiz-Olmo 1996). The PCB concentration levels observed in the Estes et al. (1997) study were also similar to those causing reproductive failure in mink (Mustela vision), a close relative of the sea otter (Aulerich and Ringer 1977). Mink are considered to be a useful surrogate for sea otters because of their close relatedness (Wren 1991). Mink are susceptible to a variety of environmental contaminants (Wren 1991); therefore, the results of the contaminant studies in Adak (Estes et al. 1997) illustrating high levels of contaminants in sea otter livers at Adak should not be overlooked.

The presence of contaminants in sea otters from the Aleutian Islands demands explanation. There are two main sources of contaminants: 1) point source pollution, and 2) long-distance transport, both of which are likely occurring in the Aleutian Islands.

Often described as remote wilderness refuges, the Aleutian Islands have a long history of extensive military occupation and disturbance from World War II through the Cold War, ending in 1989. Approximately 50% of the Islands surveyed for sea otters by Doroff et al. (2003) had some form of military occupation or what are referred to as “Formerly Used Defence Sites” (FUDS), while the remaining islands surveyed were within approximately 30 km (range: 2 km-30 km) of one of these sites. In an attempt to clean up the waste left by the military, 34 military cleanup sites were identified in these purportedly pristine islands (Stout 2001). Many of these
sites have significant PCB contamination, fuel spills, harmful wastes including solvents, pesticides, heavy metals, chemical warfare materials and radioactive waste, unexploded ordnance, military ship wrecks, nuclear testing sites, petroleum products, toxic metals and abandoned and leaking barrels of various chemicals and fuels (Stout 2001). Hazardous material spills have been common; thousands of 55-gallon drums were left to rust and release their contents into the environment (Stout 2001). Gasoline and ammunition were dumped into the ocean, spawning grounds were filled in or exploded and oil spills occurred often (NPFEP 2007). Chemical warfare materials have been disposed of by burning, detonation, burial, and open ocean dumping (ATSDR 2002). Hazardous substances were disposed of on and around Adak Island over a 40-year period; known materials include transformer oils containing PCBs, petroleum, chlorinated solvents and batteries (NPFEP 2007). Several hundred one-ton containers of chemical warfare material were also disposed 15 kilometers north of Adak Island, approximately 1000 meters below the surface, likely releasing their contents sometime after the 1950s (US AAF 1945, from ATSDR 2002).

The official “cleanup” began in the early 1990s (EPA 2000) - approximately the same timing as the expected onset of sea otter population declines. During cleanup efforts, contaminants were disturbed and thus released into the terrestrial and marine ecosystems, and there is the concern that wastes were improperly disposed. For example, an individual was convicted of knowingly dumping 500,000 gallons of jet fuel (JP-5) into Sweeper Cove, which opens into Kuluk Bay (Fig 2.2) in 1989 (United States Court of Appeals 1993). Although this is the only incident that has been documented to this extent, it is likely that additional similar incidents occurred but were not reported. The military activities in this region represent a long-term, geographically widespread source of contaminants and the ecological impact that this occupation has had on terrestrial and marine ecosystems may be extensive.
Sea otters have only been sampled for contaminant exposure at Adak Island. However, using the population survey data used by Doroff et al. (2003) a comparison of the change in numbers of animals on military occupied sites vs. military-free sites suggests that more individual animals disappeared from islands that had a history of military occupation between 1992 and 2000 (median of 30 animals lost per year compared to an average of 4 animals lost per year respectively, Mann-Whitney Rank Sum Test, $T = 127$, $N = 14, 15$, $p < 0.001$; Fig 2.3).

To ensure that the numbers of otters that occupied military sites were not larger to begin with because the islands selected for defence sites were inherently larger, I compared the number of otters at each type of site in 1965. At military sites, there were generally more individuals ($\text{mean} \pm \text{SE} = 449 \pm 140$) than at military-free sites ($219 \pm 78$), but they were not statistically different (Mann-Whitney Rank Sum Test, $t = 219$, $N = 14$, $p = 0.48$). The 1992 sea otter survey counts were not used for this comparison because the authors (Doroff et al. 2003)
stated that the decline likely began in the mid 1980’s; therefore the populations would already have been experiencing a decline and might not be representative of baseline numbers.

![Box plot showing the average number of sea otters lost per year between 1992 and 2000 at Islands in the Aleutian archipelago with a history of US military occupation (14 sites, median = 30 animals lost per year) and military free islands (15 sites, median = 4 animals lost per year). Mid line is the median, the box represents the interquartile range (25%-75%), open circles are outliers and whiskers represent range of the data. Significantly more sea otters disappeared from past military sites than military free sites (Mann-Whitney Rank Sum Test, T = 127, N = 14, 15, p = < 0.001).](image)

Long-distance transport is a second means by which contaminants could enter the Aleutian’s ocean environment. Concentrations of contaminants are transported from warm regions to colder climates, where they condense and precipitate into the oceans. During the winter months there is a low pressure system called the Aleutian Low that draws storms and airborne contaminants from Southeast Asia along the Aleutian Archipelago (Simonich and Hites 1995; Stabeno et al. 1999). Atmospheric transport from Asia provides the initial long-distance transport, with air-sea exchange or fog water providing means for transporting the contaminants into the Bering Sea (Jantunen and Bidleman 1995; Bailey et al. 2000; Li et al. 2002; Macdonald et al. 2003b). This method of contaminant transport would result in a west-to-east decrease in
contaminant concentrations along the Aleutian archipelago. DDT is still commonly used in Japan and in the former Soviet Union; it is possible that these chemicals are being transported via atmospheric or oceanic currents to the North Pacific.

Sea otter primary prey at Adak Island include sea urchins, followed by various bivalves, crabs, fish, worms, and finally, sea cucumbers (Reisewitz et al. 2006), but fish are an important part of otter diets in the Aleutian Islands (Riedman and Estes 1990). In 1996, blue mussel and rock sole samples were collected for contaminant analysis from areas around Adak. Blue mussel data indicated that arsenic, cadmium, chromium, copper, lead, nickel, selenium, zinc, chlorinated pesticides, PCBs, Polycyclic aromatic hydrocarbons (PAHs), and petroleum products all had the potential to pose ecological risks (EPA 2000). Moreover, cancer risks and non-cancer hazards were above a level of concern for the subsistence seafood harvester consuming fish and shellfish from Kuluk Bay at Adak (EPA 2000). Overall, organisms that feed on benthic or epibenthic biota, such as sea otters, are at a high risk from chemical contamination via ingestion of food and by direct dermal contact.

Sea otters are not the only species to contain high concentrations of contaminants in the Aleutian Islands. In a study of green-winged teal in the Aleutian Islands/Bering Sea, more than 25% of the teal had PCBs and mercury levels high enough to cause reduced hatchability or deformities in chicks, and all of the teal eggs contained some level of PCBs and DDT/DDE (Scharf 1995).

Cormorants (Phalacrocorax spp.), which are similar in habitat and trophic level to sea otters, were tested for contaminant levels at Attu, Kiska, Adak, Amlia and Amak (Rocque and Winker 2004). The authors found high levels of PCBs, but levels that were not believed to be harmful to the birds. A pattern of west-to-east declines in OCs and PCBs was also documented, consistent with the global transport hypothesis, but the west-to-east declines were not a smooth pattern. Two former military sites, Attu and Adak, had higher levels of contaminants, which is
consistent with the suspicion that past military sites are major point sources of pollution in the Aleutians. Anthony and colleagues (1999) also found west-to-east decrease in contaminant concentrations along the Aleutian archipelago in bald eagles, suggesting an Asiatic source of the pollutants.

High levels of mercury were found in glaucous-winged gulls (Burger and Gochfeld 2007), eiders, tufted puffins and pigeon guillemots (Burger et al. 2007) around the Aleutian Islands. Selenium was also detected in Aleutian guillemots, especially near Kiska (Burger et al. 2007). High PCB levels have also been detected in North Pacific albatrosses at concentrations that are toxic in other fish-eating seabirds (Guruge et al. 2001).

Contaminant exposure should not be disregarded as a potential contributor to the sea otter population decline. High levels of contaminants have been identified in several species throughout the Aleutian archipelago, including the sea otter. In particular, much higher concentrations of PCBs have been identified in otters at Adak compared to otters in California and Southeast Alaska (Estes et al. 1997). The various modes of contaminant transport in the Aleutians, such as long-distance transport from Asia and Russia, and point source contaminant from past military sites suggest that wildlife around the Aleutian Islands are vulnerable and at risk of health adverse affects. The possibility of a causal link between environmental toxins and the sea otter decline has been recognized and should be investigated thoroughly before it is too late, as was potentially the case with the California condor (Gymnogyps californianus) during the 1970s and 1980s (Kiff 1989; although see Snyder and Meretsky 2003 for continued debate). More data is needed to fully evaluate the potential role of environmental contaminants in the sea otter decline, as the current data are incomplete (Evans et al. 1997).

**Killer Whale Predation**

The current generally favoured hypothesis, that predation by killer whales caused the sea otter population decline, is based on three lines of evidence: 1) there was an increase in the
number of observed attacks during the 1990s, coincident with the decline, 2) populations did not
decline in areas considered inaccessible to killer whales while populations declined in adjacent
habitats, considered accessible to killer whales, and 3) the estimated number attacks necessary
to account for the rate of decline is similar to the observed number of attacks (Estes et al. 1998).
Here, I evaluate each line of evidence independently, then synthesize evidence for the killer
whale predation hypothesis.

1. Increase in Observed Attacks

Killer whale and sea otter interactions have been observed in the past with very few
reports of predation by the whales (e.g. Kenyon 1969). If sea otters responded to whales during
these encounters, the otters returned to “normal” behaviours within a few minutes (e.g. Beckel
1980). However, in 1991, the first “attack” by a killer whale on a sea otter was purportedly
observed in the Aleutian Islands, with nine more to follow between 1991 and 1997 (Hatfield et
al. 1998). Of the nine attacks described by Hatfield et al. (1998), six occurred in the Aleutian
Islands, while the other three were in Prince William Sound, where sea otter populations were in
fact increasing between 1993 and 2000 (Bodkin et al. 2002). The estimated timing of the onset
of the decline does not match the timing of the increase in observations of killer whale-sea otter
encounters. Doroff et al. 2003 estimated that the decline likely began in the mid 1980s. This is
inconsistent with the observations of killer whale-sea otter interactions beginning in the 1990s.

Active pursuit in an apparently predatory manner but where no kill can be confirmed is
generally referred to as “harassment” as opposed to “attack” because it cannot be assumed that
the event involved the intent of the whale to kill and consume the prey species (Ford et al.
1998). Of the six killer whale-sea otter interactions described by Hatfield et al. (1998), only one
of the described accounts can be considered an attack, while the other five should be considered
harassment, as discussed below.
The first two accounts reported by Hatfield et al. (1998) occurred at Amchitka Island in 1993 involving one adult male killer whale and three smaller whales. The first observation involved a sea otter moving away from a splash made by the male killer whale and into a kelp bed. The interaction ended there and no attack was observed. The second observation occurred a half hour later, but this time one of the smaller whales followed a sea otter for a short time until the otter swam over a shallow rocky area and was no longer pursued by the killer whale. Both of these “attacks” ended with the sea otters swimming away and the killer whales abandoning their chase.

The third and fourth accounts occurred in 1994 at Amchitka 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 believed to have been made and the otter was not seen again. 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. It is important to mention here that killer whale biologists argue that when a potential prey disappears underwater, it is not confirmed as a predatory event, but rather a harassment event (Ford et al. 1998). The researcher that documented these “attacks” did not observe the sea otters after the interaction with the killer whales, nor did they observe or confirm that the otter was consumed. These “attacks” should perhaps be considered “harassment” to remain consistent with killer whale behavioural terminology.

The only consumptive predation event observed was the fifth account, which describes a lone male killer whale engulfing a sea otter at the surface of the water at Adak Island in 1995. After consuming the otter, the whale was not seen again. The sixth and last account occurred the following year, also at Adak and again involved 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 10-20 seconds, 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 five minutes.

Of the six killer whale-sea otter encounters described, three accounts did not result in sea otter deaths, as the otters were seen after the encounter and the killer whales were observed swimming away. Therefore, these three should be considered “pursuits”, not attacks. Of the remaining three accounts, a sea otter was observed in a killer whale’s mouth on only one occasion. Prey, such as a seal, is generally seen in the mouths of killer whale predators during 68% of observed attacks (Baird and Dill 1995); therefore, we would expect more reports of sea otters actually being seen in the mouths of killer whales. Moreover, handling of prey often occurs below the surface so to confirm a kill, the observation of blood and/or pieces of blubber are often used in the field (Baird and Dill 1995; Saulitis et al. 2000). Of the two accounts described by Hatfield and colleagues (1998) that involved possible contact between a killer whale and a sea otter, there was no evidence of sea otter remains, blood or fur at the surface. According to many killer whale biologists, these events would not confirm a kill and should be described as encounters or harassment.

Like many other predators, 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 will ‘play’ with an animal, such as sea birds (Stacey et al. 1990) and harbour seal pups (Gaydos et al. 2005). The whales breach on the victim or toss and ram it until it dies, but is not consumed. This behaviour could be part of the hunting learning process, 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, it may be responsible for substantial mortality in some marine mammal and seabird populations. Killer whales also harass animals without killing them. Mammal-eating killer whales have also been
observed harassing river otters in British Columbia, but no kills or consumption have been documented (Ford et al. 1998). In Glacier Bay, 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).

It is unknown whether the killer whales observed during the attacks described above were transient (mammal-eating) or resident (fish-eating) whales. Although fish-eating killer whales have never been observed consuming mammal prey, juvenile and calf fish-eating killer whales are also known to harass marine mammals (Ford et al. 1998). Most of these observed harassment events have involved the chasing and ramming of porpoises or seals, with the victims either escaping or disappearing without confirmation that they were consumed. These observations are similar to the non-consumptive sea otter-killer whale interactions described by Hatfield et al. (1998) and evidence also suggests that fish-eating whales are more common in the Aleutian Islands and Bering Sea region compared to the mammal-eating ecotype (1000 residents, CI = 379–2,585 compared to 250 transients, CI = 97–644) (Zerbini et al. 2007). Further research focused on killer whale abundance estimates and foraging behaviour in the Aleutian Islands is essential to understand what role they played in the sea otter population declines.

2. Sea Otter Refuge Use

Anecdotal evidence suggests that sea otter population numbers are stable in areas in the Aleutian Islands considered to be inaccessible to killer whales such as small lagoons, compared to adjacent areas that are open along the coast. For example, 65% of tagged animals in Kuluk Bay, an open, coastal environment at Adak Island, disappeared from the site, compared to only 12% that disappeared from Clam Lagoon (Figure 2.2), an area assumed to be inaccessible to killer whales at Adak (Estes et al. 1998). However, observations indicate that killer whales do in fact enter Clam Lagoon (Craig Matkin, pers. comm. via Lance Barrett-Lennard). Moreover,
otter declines have now been identified in Clam Lagoon, where the population was reduced from 100 animals in 2000 to 51 in 2003 (Doroff et al. 2004), a 49% decrease over three years (16.3%/year).

The comparison conducted by Estes et al. (1998) between predator refugia and open environments was conducted at one location around Adak Island and was not replicated elsewhere. Other differences between Kuluk Bay and Clam Lagoon could account for the disappearance of the otters. Kuluk Bay experienced the most intense military activity around Adak. During the early 1990's, “clean-up” of the military base began (see “contaminants” section for further information). The highest concentrations of PCBs that have been recorded were from Kuluk Bay (Anthony et al. 1999). The levels of PCB, various metals and petroleum products reported in blue mussels, a prey source for sea otters, all had the potential to pose ecological risks in Kuluk Bay, while the levels measured in adjacent Clam Lagoon were below the hazardous level (EPA 2000).

In 1989, 500,000 gallons of jet fuel (JP-5) was knowingly dumped into Sweeper Cove, which opens into Kuluk Bay; the breakdown products of JP-5 are unknown so it isn’t known whether they are toxic or not, but some chemicals that attach to matter can remain in the environment for more than a decade (U.S. Department of Health and Human Services 1998). There is little known about the health effects of JP-5, however, neurological effects such as coordination and concentration difficulties, fatigue, headache, apparent intoxication, anorexia, and significant increases in neurasthenia (fatigue, depressed, lack of initiative, dizziness, sleep disturbances), as well as possible links to cancer have all been documented in humans (U.S. Department of Health and Human Services 1998). This confounding factor complicates the interpretation of the changes in sea otter abundances across the different areas. This example suggests that we cannot conclude that Kuluk Bay’s open environment and thus exposure to predators was the reason for the disappearance of the otters.
3. Observed vs. Estimated Attacks

Using life-table statistics, 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 (78% between 1991 and 1997) and calculated the expected number of observed attacks based on that estimate. They found that the expected number, 5.05, compared favourably with the 6 actual observed attacks between 1991 and 1997. However, as discussed in the previous section, only one of these “attacks” should be considered a consumptive predation event while the remaining five were unconfirmed attacks or “harassment”. The number of observations that should be considered attacks – minimum of one and maximum of three - are in fact lower than the expected number calculated by the authors and do not compare favourably with the expected number of five.

The Sequential Megafaunal Collapse Hypothesis

It is irrelevant whether populations of otters declined through surplus killing or “consumptive” predation under the hypothesis of Estes et al. (1998), as both would have an equivalent effect on the population. However, from a killer whale perspective, it does matter. The sequential megafaunal collapse hypothesis (SMCH) (Springer et al. 2003) and the killer whale predation hypothesis (Estes et al. 1998) predict that killer whales shifted their diet from harbour seals and sea lions to the less nutritious sea otter after their initial primary prey species declined. If the SMCH is correct, a subsequent significant change should occur for killer whales in the North Pacific. Now that sea otter populations have declined we would expect that killer whales would either switch to another less nutritious prey source, move into more profitable areas following depletion of sea otters, or killer whales should suffer reduced survival and reproductive rates, and subsequently decline as a result (Holling 1959). This has not yet been observed.
Theory also predicts that once a predator declines as a response to lower primary prey numbers, the primary prey would be released from predation pressure and allow it to persist (Jones 2003). In 2003, sea otters were continuing to decline by 29% per year between 2000 and 2003 (Estes et al. 2005), while there has not been any evidence for a decline in killer whale abundances, nor have there been observations of another diet shift for killer whales. Stabilization of declining species is an expected result of prey switching by predators (Mills et al. 1995), but continued declines suggest that predator numbers are not tracking prey numbers (Georgiadis et al. 2007), or Allee effects (Courchamp et al. 1999) could explain the elevated rates of decline (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 “by-catch” (“apparent competition”) (Holt 1977, 1984). Secondary prey populations may be at greater risks than primary prey populations. If a predator reduced populations of secondary prey, there would not be a corresponding reduction in predator abundance because the predators are maintained by an abundant primary prey population (Jones 2003). Therefore, we would only expect sea otters to continue to decline if the predator’s primary prey (e.g. harbour seals) are abundant. This is not what is observed with killer whales and sea otters in the Aleutian Islands, nor is it what the SMCH suggests. However, the continued population declines of sea otters and the simultaneous even rate of decline (Geogiadis et al. 2007) across the Aleutian archipelago perhaps do suggest incidental predation and other marine predators should be considered. The unusual rate of decline in sea otters suggests that something dramatic should have occurred with a potential predator population if predators were the cause of the decline.
Other Marine Predators

Recent evidence indicates that populations of some species of sharks have increased in the North Pacific. Like killer whales, sharks are apex predators and fluctuations in their populations may have significant effects on community structure. During the 1990s, surveys by the International Pacific Halibut Commission and bycatch data from the halibut fishery indicate that Pacific sleeper shark abundance increased in the northern Gulf of Alaska (Kruse et al. 2001), the central Gulf of Alaska (Mueter and Norcross 2002) and in the Bering Sea/Aleutian Island region (Gaichas 2002). Salmon sharks have 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 sharks along the Aleutian Archipelago (Okey et al. 2007).

The reasons for these increases are not known. The main hypotheses suggested, include: 1) a 1992 moratorium on high seas drift gillnets, eliminating an important source of incidental shark mortality, and 2) increases in sea temperature with the Pacific Decadal Oscillation since the 1970’s increasing the abundance of their prey and shifting their distribution (University of Washington 2002; Okey et al. 2007).

Sleeper sharks were once thought to be lethargic, bottom-dwelling predators, but are now known to move continuously in the water column and be stealth predators of fast moving prey (Cherel and Duhamel 2004; Taggart et al. 2005; Sigler et al. 2006; Van den Hoff and Morrice 2008). Sleeper sharks and sea otter habitats overlap during the night, when sharks ascend above 100m, occasionally to depths of 2m (Hulbert et al. 2006). Marine mammals, such as harbour seals and cetaceans, appear to be important prey for pacific sleeper sharks in Alaska (Taggart et al. 2005; Sigler et al. 2006). Stomach contents of 165 pacific sleeper sharks were analysed from Alaskan waters; 14% contained marine mammal tissue, comprising one-third of the mass of diet items (Sigler et al. 2006). Van den Hoff and Morrice (2008) documented one
bite on an elephant seal carcass around Macquarie Island (to the south of Australia) from a sleeper shark (*Somniosus antarcticus*). The observation of only one bite mark suggests that either shark encounters are rare, or survival from sleeper shark attacks is low. They conclude that it's clear that sleeper sharks will attack an elephant seal if their distribution overlaps.

Although salmon sharks feed primarily on fish, there have been anecdotal observations of salmon shark predation on sea otters in Alaska (Conservation Science Institute 2007). Great white sharks have shown some signs of increasing in Alaskan waters (Wright 2007). White sharks are known to prey on sea otters in California (Ames and Morejohn 1980).

Despite the lack of direct evidence for shark predation on sea otters, the simultaneous increase in shark populations and decline of sea otter populations is reason to further investigate the role that sharks may have played in the decline. Sharks often attack their prey below the surface, making it difficult to observe predation events (Frid et al. 2006). Likewise, direct evidence for killer whale predation on sea otters is scant, and based on the weight of evidence rather than observation.

**Conclusion**

The sea otter population decline has been described as potentially the biggest sea otter conservation issue of recent times. In view of this catastrophic event, it is crucial that research continues to investigate the causes of the sea otter population decline in the Aleutian Islands to ensure that proper management and conservation strategies are implemented. This review has revealed that the existing data are inconclusive and further research needs to be conducted into possible causes of the population decline of sea otters. The killer whale predation hypothesis is compelling and has focused attention on the role of predators in the structuring of north Pacific ecosystems and stimulated many interesting and productive discussions and debates. Nevertheless, at this point I feel that disproportionate attention given to the killer whale
hypothesis has diverted attention away from equally or more important issues, such as contaminants, disease exposure, or other predators. Additional research is necessary to further examine the killer whale hypothesis and to determine the role of contaminants, starvation, disease and alternative predators.
Literature Cited:


In the footprints of collapse: Inferring the cause of a sea otter population decline using regional variation in behaviour

INTRODUCTION

Population declines of wildlife are a widespread and global phenomenon, but identifying the processes that underlie them 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. I propose that in some cases, current behaviours of animals can be used to infer the causes of recent demographic collapses. This is the first study to apply this approach to conservation biology and focuses on a dramatic decline of sea otters (*Enhydra lutris*) in the Aleutians, Alaska, during the 1990s.

Estes et al. (1998) hypothesized that killer whales (*Orcinus orca*) in the North Pacific responded to declines in the abundance of harbour seals (*Phoca vitulina*) and Steller sea lions (*Eumetopias jubatus*) in the Aleutian Islands by switching to sea otters, subsequently causing catastrophic declines in otter populations. The most straightforward test of this hypothesis would be to measure predation directly; however, the current scarcity of sea otters prohibits direct observation of mortalities. In addition, killer whales may have moved into more profitable areas following depletion of sea otters, as predicted by predator-prey theory. In view of these difficulties, I conducted a novel alternative test allowing us to “look back in time” by assessing the behavioural responses of sea otters to predators that may have been substantial threats earlier in their lives, but which may not be a threat at present. Based on Estes et al.’s hypothesis, I predicted that otters would exhibit stronger antipredator responses to killer whales in areas of

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2 A version of this chapter will be submitted for publication. Kuker, K. In the footprints of collapse: Inferring the cause of a sea otter population decline using regional variation in behaviour.
recent declines than in areas where sea otter numbers have steadily increased. I used artificial cues (playbacks and decoys) to test this prediction.

Individual animals use various sensory cues to assess predation risk and make subsequent behavioural decisions (Lima and Dill 1990). To respond with antipredator behaviour, prey must first identify the potential danger using some or all sensory modalities (e.g. visual, olfactory or acoustic). Playbacks of acoustic stimuli have been used as an experimental tool to investigate predator-prey interactions. A recent literature review conducted by Blumstein et al. (2008) demonstrated the ability of species belonging to several taxonomic groups to identify their predators using acoustic cues and found that 25 of 30 (83%) species of birds and mammals responded to playback vocalizations of their predators. Moreover, this acoustic recognition of predators may depend on specific cues, and thus would typically involve learning as the recognition mechanism (Berger et al. 2001; Blumstein et al. 2000a; Gil-da-Costa et al. 2003) rather than innate recognition.

For example, Deecke et al. (2002) showed that harbour seals respond with anti-predator behaviour to the calls of the mammal-eating transient killer whale, but habituate to the calls of harmless fish-eating resident killer whale in the same area. Howler monkeys were also able to learn and retain antipredator behaviours in response to harpy eagles’ calls (Gil-da-Costa 2003). Red colobus monkeys assess the risk of predation and respond appropriately with antipredator behaviours when exposed to the ‘hoot’ and ‘drumming’ of hunting chimpanzees (Noe & Bshary 1997). Many small mammals have been shown to respond appropriately to the calls and/or sounds of potential predators, such as various small rodents (voles, dormice and jerboa) to the calls of tawny owls (Hendrie et al. 1998) and the California ground squirrel to the rattling sound of different snake predators (Swaisgood et al. 1999). Fish also recognize predators using acoustic cues. For example, shad detect dolphin echolocation clicks and respond by immediately grouping together on the side of the tank opposite the transducer emitting the sound (Mann and
Lu 1998). Among birds, American crows, petrels and hornbills (Hauser and Caffrey 1994; Mougeot and Bretagnolle 2000; Rainey et al. 2004 respectively) also identify their predators by acoustically detecting the territorial calls of their avian predators. No studies, however, have used playback experiments and current animal behaviours to infer the causes of demographic catastrophes in the recent past.

Here, I report on the first experimental test of the hypothesis that killer whale predation caused the decline of sea otter populations in western Alaska (Estes et al.’s 1998). Specifically, I tested the prediction that sea otters would respond more to the perceived presence of killer whales in the Aleutian Islands, an area where the decline had occurred, than in an area where killer whale predation is thought to be rare and the population is not declining, in British Columbia, Canada.

METHODS

Field Research

Behavioural responses of sea otters to artificial killer whale cues were studied at two main sites with purportedly different levels of killer whale predation pressure: Adak, Alaska in the Aleutian Islands (Fig 3.1) in 2007 (impact site), and the Nuchatlitz Islands, on the northwest coast of Vancouver Island (Fig 3.2) in 2006 (control site). Two lines of evidence suggest that killer whale predation is rare in BC: 1) sea otter populations are growing in BC at close to their theoretical maximum rate (Watson et al. 1997; Nichol et al. 2005), and 2) there are no observations of killer whales attacking sea otters during intensive studies in the region, including numerous observations of transient killer whales in proximity to swimming or resting otters.

Adak Island, located in the central Aleutians (51°53’ N, 176°39’ W) was populated by approximately 390 sea otters in 2003 (Estes et al. 2003). I observed animals at three locations around the Island: Bay of Islands, Shagak Bay, and Clam Lagoon (Fig 3.1). Bay of Islands
consists primarily of small bays and inlets with rocky complex substrate and depth ranging from approximately 4m to 125m in the channels. Shagak Bay is an open Bay with depths reaching 40m in the centre and few small kelp beds. Outside the Bay’s entrance is a large kelp bed consisting of *Laminaria spp.* and *Alaria fistulosa* (Estes and Duggins 1995) spanning several metres offshore and all along the coast. Clam Lagoon is somewhat different in that it is mainly soft bottom/mud substrate and 22m deep near the centre. There is a small channel approximately 30m wide into the Lagoon, covered by a bridge. Clam Lagoon was assumed to be inaccessible to killer whales at Adak; however, recent observations indicate that killer whales may enter Clam Lagoon (Craig Matkin, pers. comm. via Lance Barrett-Lennard).

Figure 3.1: Map of Aleutian archipelago and Adak Island, Alaska, illustrating the three locations where playback studies were conducted. 1) Bay of Islands, 2) Shagak Bay, 3) Clam Lagoon (Aleutian Island map created in R 2005 using PBSmapping package, Adak map created in ArcView 3.2).
For the part of the study focused on a non-declining population of sea otters and where killer whale predation is known to be rare, I chose the Nuchatlitiz area, located on the northwest coast of Vancouver Island (49°48'30.04" N, 126°57'10.01" W; Fig 3.2) and has approximately 300-500 sea otters (Gregr et al. 2008). The habitat resembles Bay of Islands in the depth, substrates, complexity and shelter.

The response of sea otters to the presence of killer whales was estimated experimentally by broadcasting recordings of killer whale calls underwater and recordings of blows in air and by displaying an artificial dorsal fin at ranges of 100 to 200 metres from individual sea otters. Only solitary animals were tested to avoid any group effect on vigilance, which would be difficult to control given the likely variability in group size between the different regions.

**Recordings and Playback Sequences**

Killer whale calls were played underwater using a Marantz PMD660 solid state recorder and an LL916 underwater speaker (Lubell Labs) deployed at a depth of approximately 5m from a small boat (5m and a 4m long inflatable) anchored 200-300m offshore. Killer whale blows
were played above the water using a Marantz PMD660 solid state recorder and a Mineroff Field Speaker (frequency range 100Hz – 12 kHz) from the same boats.

Ten vocalization playback sequences were based on sections of background noise from ten separate recordings of west coast BC or False Pass Alaska transient killer whales, digitally spliced into a 1-min sequence. For treatment playbacks, five killer whale calls from the same ten recordings were spliced into the sequence at 30s, 35s, 40s and 45s (Fig 3.3). For control sequences, additional sections of background noise were spliced in instead of the calls. Playback protocol involved slow ramping up of the stimulus level to avoid startle responses caused by the sudden onset of background noise. The volume was slowly faded in over the first 30s of the sequence and faded out during the last 10s. Sound intensities of sequences were adjusted so that their peak amplitudes matched.

Figure 3.3: Sample spectrogram of a west coast transient killer whale vocalization playback sequence (software: Raven). The first 2 calls start at 30 seconds, followed by 3 more calls every 5 seconds, and then slow vamping down of the sound. (Recording made on July 3rd, 2006 by Volker Deecke).

Killer whale blows were recorded on a Sony DAT using a Sennheiser MKH 70 condenser microphone from a small (7m) vessel at a distance of 5-50m from the whales. Playback sequences were prepared in the same way as vocalizations, however, only five
separate recordings of blows were obtained and only four blows were spliced into the 1-min sequence, again at 30s, 35s, 40s, and 45s.

Each otter was tested with a single playback to avoid habituation. The type of playback (treatment or control) conducted on each otter was chosen at random. To ensure several animals did not hear or see the cues frequently, all experiments were performed a minimum of 500 metres from groups of animals (rafts). To avoid pseudoreplication, each of the ten playback sequences was played only once, and, to the best of my knowledge, individual otters were only exposed to one playback. A waiting period of at least 15 minutes between trials was established to ensure animals that may have been within hearing range of a previous trial had moved out of the study site.

Samples were omitted from analyses if, 1) the observer lost sight of the otter before the minimum time period of 2-4 minutes ended, 2) the observer was not certain that the original focal otter was being observed, 3) weather conditions were marginal allowing for some missed behaviours, or 4) another otter entered the site resulting in confusion over which otter was the focal animal.

**Dorsal Fin Decoy**

How sea otters use visual cues to assess predation risk is unknown. If vision is important, the visual cues used by otters to identify potential killer whale predators are unknown. A visually realistic dorsal fin decoy was constructed using measurements taken from a BC female transient killer whale. The decoy was towed 200m behind a 4m inflatable boat. This proved to be difficult in rough weather conditions and the presence of the moving boat made it difficult to assess the response to the fin; therefore, no analyses were conducted on the dorsal fin experiments.
Behavioural Observations

A shore-based observer, blind to the type of trial presented, employed an all-occurrences sampling technique (Altmann 1974) using the focal otters for 2-4 minutes prior to, and 2-4 minutes after playbacks. All behaviours performed by the focal sea otter were recorded, including all events, such as dives or surfacing, and all states such as resting, foraging, or travelling. These activities were then classified into three behavioural categories for analysis: "Maintenance behaviours", "disturbance behaviours", and "underwater".

Observations were recorded using a voice recorder and transcribed immediately following the trial during the 15 minute wait period. A summary of the trial was also recorded after each session. Observations ended when the otter was lost, another otter was in the region, or, if the otter was underwater at the end of the 2 minute period, the observer would wait until the animal surfaced and continued to document the behaviour following surfacing.

Because the duration of pre- and post-playback periods varied, the percentage of time allocated to each of the behaviour categories (while at the surface) was calculated for each period. The 'after' period commenced as soon as the first vocalization or blow sound was played, 30 seconds into the playback recording (Fig. 3.3). The strength of the response was expressed as the percentage change in behaviour while at the surface; the 2-4 minutes preceding stimulus presentation were used as a baseline from which the difference in time allocation following stimulus presentation was calculated. The activities recorded were classified into three behavioural categories for analysis. These categories were exclusive, independent, and contained a set of behaviours with the same properties, as recommended by Martin and Bateson (2004). The following behaviour categories were used in this study:
1) Disturbance Behaviour:

The following three activities were classified together as “disturbance behaviour” because they are associated with avoiding danger and vigilance (Williams 1989, Curland 1997; Hatfield et al. 1998).

i) Periscoping: Periscoping occurred when the head and upper torso of the sea otter extended out of the water vertically (Hatfield et al. 1998), a behaviour typically used by otters to scan their surroundings (Kenyon 1975), or when “on guard” (Fisher 1939). This behaviour indicates the otter is assessing its environment because it is associated with scanning the surrounding water and it affords the animal a better vantage to search for, identify and assess the predator if it is above the water.

ii) Looking: Looking occurred when the animal intently oriented its head in the direction of the boat (the source of the killer whale sounds), or when the animal remained motionless at the surface with its head intently oriented in a particular direction. Unlike periscoping, the animal’s body was not extended out of the water. This behaviour was also defined by Packard and Ribic (1982) as a discrete action pattern that resembles a form of vigilance. To avoid detection by predators, other marine mammals have also been known to remain motionless at the surface (Jefferson et al. 1991). The term “looking” is not meant to imply that the otter is using vision as a primary sensory modality, as it could also be orienting its nose to better receive olfactory cues.

iii) Traveling: Sea otters have been shown to increase their amount of time travelling in areas with high disturbance (Curland 1997). During travel, animals at the surface swim ventral-up or ventral-down in a consistent direction, propelling themselves mainly with their hind paws (Kenyon 1969; Tarasoff et al. 1972; Williams 1989). In otters, swimming is energetically expensive because of the small body mass, proportionally high buoyancy, and transitional style of propulsion (Tarasoff and Kooyman 1973, Williams 1989; Williams 1999).
2) Maintenance Behaviour:

The following three activities were not disturbance behaviours and were categorized together. Disturbed or vigilant animals tradeoff these three activities (foraging, resting and grooming) with the disturbance activities listed above (Lima and Bednekoff 1999).

i) Foraging: An animal was identified as foraging if it was handling or eating a prey item on the water surface.

ii) Resting: An animal lying stationary at the surface with front paws extended out of the water.

iii) Grooming: This behaviour included rolling at the water surface and vigorously rubbing the fur.

3) Underwater:

Because it was not possible to identify the animal’s behaviour while below the surface, I measured the time the animal spent underwater. Heithaus and Frid (2003) suggested that, at risk from subsurface predators, air breathing aquatic species’ are most vulnerable while at the surface, as scanning underwater for predators is mutually exclusive with breathing, and there are fewer dimensions to escape. Harbour seals, for example, in the presence of transient killer whale predators may increase their time spent underwater (Deecke et al. 2002, Womble et al. 2007). However, since sea otters are positively buoyant and need to swim continuously to remain stationary underwater, it is unlikely that sea otters use the same escape strategies as other aquatic air breathing animals (e.g. whales, seals or sea turtles).

Statistical Analysis

To determine what behavioural categories might represent a disturbance response for sea otters, a principal components analysis (PCA) was conducted using mean changes from baseline behaviour. Analysis included the 3 behavioural categories described above. A two-factor ANOVA, using location (Adak or Nuchatlitz) and treatment type (control or treatment) was
performed on the first and second principal components to determine which of the components varied, if any.

After conducting the multivariate analysis, two-factor ANOVAs using location and treatment type as the two factors were used to test if there was any variation in the mean change in percentage of time allocated to the three behavioural categories (disturbance, maintenance, or underwater). The two-factor ANOVA tested the following three null hypotheses: 1) the behavioural changes in Alaska and BC have the same mean, 2) the behavioural changes in response to treatments and controls have the same mean, and 3) location and treatment type do not interact. Multiple comparison procedures were performed by the Holm-Sidak post hoc test.

When the data were not normal (Shapiro-Wilk Test for normality) the two-factor ANOVA was performed on the rank transformed data, following the recommendation of Conover (1999). The only non-parametric two-way ANOVA is the Schreier-Ray-Hare extension of the Kruskal-Wallis test (Schreier et al. 1976). This test was avoided if possible because it is very conservative, has less power than an ANOVA, and there is debate over whether a Kruskal-Wallis test can be extended to a two-way analysis (Toothaker and Chang 1980; Dytham 2003). Furthermore, Zar (2003) suggests if sample sizes are equal, as they were in this case, the assumptions of normality and equal variance are not critical. Therefore, a two-way ANOVA was used and when the data were not normal, the test was also conducted on rank transformed data. If both analyses gave similar p-values, the parametric analysis was considered valid. If the results of the two-way ANOVA on the data and the rank transformed data were not similar, the Schreirer-Ray-Hare test was used. Data were not transformed to attempt to meet the assumptions of normality because the direction of change was important to maintain and no transformation allowed for this. Levene’s test of equal variance was used to test for heteroscedasticity. All analyses were conducted in JMP (JMP ver. 4.0), SigmaStat (ver. 3.11, 2004) and SPSS (ver. 11.5, 2002).
RESULTS

A total of 42 vocalization/control, 50 blow/control, and 33 visual dorsal fin/control trials were conducted in Adak and Nuchatlitz (Table 3.1). Sixty animals at Adak were exposed to playbacks between May and July of 2007 during 124.5 hours of observations, and 66 sea otters were sampled for response to playbacks in the Nuchatlitz during May and June of 2006 during 150.5 hours of observation. Due to the very small population size of sea otters at Adak, both singletons and mother/pup pairs were subjected to the playbacks. Responses by mother/pup pairs were not significantly different from singletons for both blow and vocalization playbacks (Wilcoxon Signed-rank test p>0.1 for all behaviours) and were pooled for all subsequent analyses.

### Table 3.1: Summary of playback and dorsal fin trials conducted in Adak and Nuchatlitz BC.

<table>
<thead>
<tr>
<th>Trial Type</th>
<th># animals in Adak</th>
<th># animals in BC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Killer whale vocalization playback</td>
<td>11 (10)</td>
<td>10</td>
</tr>
<tr>
<td>Vocalization control</td>
<td>10</td>
<td>11 (10)</td>
</tr>
<tr>
<td>Blow playback</td>
<td>10 (9)</td>
<td>15 (12)</td>
</tr>
<tr>
<td>Blow control</td>
<td>12 (11)</td>
<td>14 (12)</td>
</tr>
<tr>
<td>Dorsal fin decoy</td>
<td>9</td>
<td>8</td>
</tr>
<tr>
<td>Dorsal fin control – boat approach</td>
<td>8</td>
<td>8</td>
</tr>
<tr>
<td>Total</td>
<td>60</td>
<td>66</td>
</tr>
</tbody>
</table>

**Vocalization Playbacks**

A multivariate analysis illustrates a difference between Alaska and British Columbia behavioural responses to playback experiments. The principal components analysis (Fig. 3.4, Table 3.2) shows that PC 1, which is highly correlated with “disturbance behaviour”, accounts for 63% of the variation in behavioural responses between sites. A two-way ANOVA on the first principal component showed that location strongly influences responses ($F_{1,36} = 10.2$, $P=0.003$), but treatment type does not ($F_{1,36} = 0.48$, $P = 0.495$). There was no interaction
between location and treatment ($F_{1,36} = 1.03, P = 0.317$). A similar test on PC 2, which is highly correlated with time spent underwater, showed no differences in location, treatment type, or in the interaction ($P > 0.7$ for all three).

Table 3.2: Eigenvalues, variance explained, and factor loadings of the two principal components produced in the PC analysis of sea otter behaviour in response to killer whale vocalization playbacks.

<table>
<thead>
<tr>
<th></th>
<th>PC 1</th>
<th>PC 2</th>
</tr>
</thead>
<tbody>
<tr>
<td>Eigenvalues</td>
<td>1.89</td>
<td>0.95</td>
</tr>
<tr>
<td>Variance Explained</td>
<td>63%</td>
<td>32%</td>
</tr>
<tr>
<td><strong>Factor Loadings:</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Underwater change</td>
<td>-0.23472</td>
<td>-0.97003</td>
</tr>
<tr>
<td>Maintenance change</td>
<td>-0.68241</td>
<td>0.21050</td>
</tr>
<tr>
<td>Disturbance change</td>
<td>0.69226</td>
<td>-0.12140</td>
</tr>
</tbody>
</table>

Figure 3.4: Principal component scores of sea otter behavioural response to underwater vocalization playbacks (solid) and controls (open) in Adak, Alaska (squares) and Nuchatlitiz, BC (circles). The first principal component accounts for 63% of the variance, and PC2 accounts for 32%.
When examining change in the proportion of time allocated to disturbance behaviours, sea otters at Adak increased their time engaged in travelling, periscoping and looking more than sea otters in BC ($F_{1,36} = 8.6, P = 0.006$), but there was no significant effect for the treatment factor ($F_{1,36} = 0.159, P = 0.693$) or for the interaction between location and treatment type ($F_{1,36} = 1.778, P = 0.191$). Overall, when exposed to underwater sound (killer whale vocalizations or control background noise), sea otters at Adak significantly increased their time spent conducting disturbance behaviours (traveling, periscoping and looking) compared to BC otters (Fig 3.5). While the ANOVA only indicates an effect of location, there is a trend in the direction of the prediction that sea otters respond to the killer whale vocalizations; the Holm-Sidak post hoc test explains a significant difference in the change in disturbance behaviours between Adak treatments and BC treatments ($t = 3, P = 0.005$).

![Figure 3.5: Change in sea otter disturbance behaviour in Alaska and BC after exposure to killer whale vocalization and control playbacks underwater. Mid line is the median, the box represents the interquartile range (25%-75%), * are extreme values, open circles are outliers and whiskers represent full range of the data. The increase in time spent traveling, periscoping and looking in Alaska after tests is significantly higher than the change observed in BC ($p=0.006$).](image)
The disturbance behaviour category was broken down into two components to further investigate sea otter behavioural differences: 1) traveling, and 2) periscoping/looking. Again, there was an effect of location on sea otter travelling behaviour with otters at Adak increasing the time spent travelling after exposure to underwater playbacks ($F_{1,36} = 10.3$, $P = 0.003$, Fig 3.6). There was no effect of treatment type ($F_{1,36} = 0.006$, $P = 0.936$) or interaction between location and treatment ($F_{1,36} = 0.134$, $P = 0.72$). While location had an effect on travelling behaviour, there was no effect of location on periscoping/looking behaviour ($F_{1,36} = 0.91$, $P = 0.35$, Fig 3.7) or of treatment type ($F_{1,36} = 0.298$, $P = 0.59$), but there was weak statistical support for an interaction between location and treatment ($F_{1,36} = 3.82$, $P = 0.059$).

Figure 3.6: Change in time sea otters spent traveling in Adak and BC after exposure to killer whale vocalization and control playbacks underwater. Mid line is the median, the box represents the interquartile range (25%-75%), open circles are outliers and whiskers represent full range of the data. The increase in time spent travelling at Adak after all playbacks is significantly higher than the change observed in BC ($P = 0.003$).
To ensure that the observed increase in time spent travelling for the Adak animals was in response to the playbacks of both vocalizations and control background noise, rather than a location effect of otters simply travelling more in Adak overall, I compared the average time animals were travelling during all baseline periods in Adak and Nuchatlitz, before any stimuli was presented. There was no difference between Alaska and BC (Mann-Whitney Rank Sum $T=1676, N=40, N=44, P=0.833$). Therefore, it appears that the increase in time otters spent travelling in Adak is a response to the tests of both controls and treatments.

When examining the change in proportion of time engaging maintenance behaviours, there was no effect of location (Scheirer-Ray-Hare test, $df = 1, SS = 577.6, H = 1.06, P = 0.3$) or treatment (Scheirer-Ray-Hare test, $df = 1, SS = 90, H = 0.16, P = 0.69$), nor was there an interaction between location and treatment type (Scheirer-Ray-Hare test, $df = 1, SS = 6.4, H = 0.01, P = 0.92$; Fig 3.8). However, the behavioural response of sea otters in Adak varied significantly more compared to BC ($Levene F_3 = 10.6, P<0.0001$). There was also no change in
the time sea otters spent underwater after vocalization and control playbacks ($F_{1,36} = 0.3, P = 0.6$), or at different locations ($F_{1,36} = 1.2, P = 0.3$), nor was there an interaction ($F_{1,36} = 0.03, P = 0.9$).

![Figure 3.8](image)

Figure 3.8: Change in maintenance behaviour in Adak and Nuchatlitz after exposure to killer whale vocalization and control playbacks underwater. Mid line is the median, the box represents the interquartile range (25%-75%), * are extreme values, open circles are outliers and whiskers represent full range of the data. There was no statistical support for an effect of location, treatment or interaction ($P > 0.05$ in all cases), but the percentage of time sea otters in Adak allocated to maintenance behaviours varied significantly more than animals in BC ($Levene F_3 = 10.6, P < 0.0001$).

**Blow Playbacks**

A multivariate analysis illustrates that there was no difference in the behavioural responses of otters in Alaska or BC to killer whale blow playback treatments. The principal components analysis also revealed that there was no difference in the sea otters’ behavioural responses to control or treatment playbacks. A two-way ANOVA on the first principal component using ‘location’ and ‘treatment type’ as grouping variables indicates that there was no difference in response to blow playbacks or controls at either location ($P > 0.2$). A similar test on PC 2 also showed no significant differences at all ($P > 0.5$).
DISCUSSION

The killer whale predation hypothesis predicts two significant results in the data: A) Adak treatments should have a bigger effect than BC treatments, and B) Adak treatments should have bigger effect than Adak controls. The results of this study statistically support prediction A but not prediction B. Therefore, overall, there is mixed statistical support for the hypothesis that otters in Alaska are more fearful of killer whales than otters in BC are. However, because my results did not support prediction B, it is difficult to confirm that killer whale sounds were viewed as threatening to the sea otters.

Experimental playbacks of killer whale vocalizations and controls both elicited changes in the behaviour of sea otters in Adak, but not in Nuchatlitz. In particular, disturbance behaviours (travelling, periscoping and looking) at Adak increased significantly following underwater playbacks of killer whale vocalizations and controls compared to sea otter response to the playbacks in BC. Sea otters at Adak also reduced the time spent conducting maintenance behaviours (foraging, resting or grooming) following vocalization and control playbacks, but there was no statistical support for this change. However, the change in maintenance behaviours varied significantly more in Adak compared to BC. Playbacks of killer whale blows had no effect on behaviour at either Adak or the Nuchatlitz. Before discussing the various possible explanations that could account for the results, it is essential to consider sea otter sensory modalities.

Sensory Modalities

Many marine mammals rely primarily on sound to detect the approach of predators. The sea otter, however, is one of the most recent mammals to adapt to an aquatic lifestyle and is one of the ‘youngest’ of all the marine mammals (apart from the polar bear), first appearing in the fossil record only 1-3 million years ago (Berta and Sumich 1999). In many ways, sea otters are
intermediate between terrestrial carnivores such as the river otter, and marine carnivores such as
the seal.

Sea otters are likely acoustically “amphibious”, similar to pinnipeds, and must detect and
use sound in both air and water. There are no conventional audiometric data available for sea
otters, but underwater audiometric data collected for pinnipeds indicate they have a hearing
range with peak sensitivity from 1 – 20 kHz (Ketten 1998). Behavioural audiograms of the
North American river otter, Lontra canadensis, which have similar ear anatomy to the sea otter
(Ketten 1998), indicate an in-air hearing range of approximately 450 Hz to 35 kHz (Gunn,
1988). Sea otters make vocalizations in air that range from ~800 Hz to 30 kHz (McShane et al.
1995), which suggests that these frequencies are within their hearing range. The underwater
killer whale calls used in this study were in the range of ~2-20 kHz and blows were between
approximately 200 Hz – 17 kHz, both falling within the expected underwater and in-air hearing
ranges of the sea otter.

Anecdotal evidence from dorsal fin trials in this study and from discussions with other
biologists (pers. com. Jane Watson) suggests that sea otters do not use vision as a primary
sensory modality when detecting predators or other disturbances. Sea otters forage at night,
providing further evidence that vision is not a primary sensory modality used by otters and
Wilkin (2003) found that sea otters had a higher success rate foraging at night than in the day.

Anatomical studies suggest that sea otters have large accommodative range – the ability
to bring items into focus at various distances – and well developed visual acuity both above and
under water (Murphy 1990). Visual acuity, the capacity of the visual system to extract detailed
information, is not simply a factor of accommodative range; not only do the eye’s optics extract
the information, but is also determined by the brain and retinal neural processing of the
environment (Katzir and Howland 2003). For example, despite the fact that clawless otters are
emmetropic in both air and water, their acuity is not high in either media (Schusterman and
Barrett 1973). Animals likely cope with these blurred images by making use of other sensory modalities and other signals (e.g. detecting movement).

Gentry and Peterson (1967) conducted the only behavioural study of sea otter visual acuity, revealing that otters were capable of discriminating small and large objects underwater; however, brightness differences caused by the differently sized objects may have affected their results (Forbes and Smock 1981). Gentry and Peterson (1967) were unable to test the aerial vision of the sea otter, as the animal did not respond when the targets were presented above the surface of the water. This lack of response may suggest that otters are unable to discriminate objects in air.

Olfaction is a difficult sensory modality to test in the wild. In both British Columbia and Alaska, sea otters were observed periscoping under various scenarios. While periscoping, the otters often had their head tilted, eyes directed upwards and nostrils visibly flaring (personal observations). We did not conduct experiments using the killer whale odours, but we suspect, based on our behavioural observations, that olfaction provides a key source of information to sea otters to detect predators, conspecifics and mates.

Further evidence that olfaction might play a key role in sea otter behavioural ecology is found in their anatomy, phylogeny and foraging behaviour. Ecological constraints on cetaceans call for the nasal passages to be open infrequently, perhaps reducing the importance of nasal chemoreception (Berta et al. 2006). The sea otter spends most of its life at the surface of the water, where olfaction could remain an important sensory modality despite adaptations to the marine environment. Most mustelids possess acute olfactory sensitivity (Negus 1958), and the sea otter possesses a highly-derived nasal cavity structure (Berta et al. 2006). Moreover, sea otters both in captivity and in the wild have been shown to use taste and smell to preferentially reject butter clams (*Saxidomus giganteus*) with high levels of saxiton, a neurotoxin sequestered by butter clams (Kvitek et al. 1991; Kivtek and Bretz 2004). Hammock (2005) tested olfactory
sensitivity in sea otters and found that they have sensitivity consistent with other terrestrial mammals, thus, it is plausible that sea otters could use chemosensory cues to detect the presence of a predator. Killer whale blows carry an odour, which, to a sensitive nasal passage could likely be detected at great distances.

**Interpretation of Results**

**Response to Blow Playbacks**

Conducting playback studies to marine mammals in the field presents many challenges (for complete review see Deecke 2006). Realistic playbacks of the stimuli are essential to elicit an accurate response by the focal animal. Obtaining recordings of killer whale blow sounds involves close encounters with the animals in calm weather with little or no background noise. The blow recordings obtained for this study were collected by experienced killer whale biologists using optimum equipment under ideal conditions; the recordings were as realistic as was practical, provided the inherent noise unavoidable in doing this type of study. However, it is possible that the background noise contained other background sounds, such as faint boat engine noise, and that this may account for the similar behavioural response of otters to both control and treatment stimuli.

Individual animals can learn to recognize harmless heterospecifics over time by learning what cues are not potential threats. Habituation is the gradual decrease in response over repeated exposure to a stimulus, as individuals learn that there are neither adverse nor beneficial consequences to a stimulus (Thorpe 1963). During observations in Adak, minke whales (*Balaenoptera acutorostrata*) were frequently seen approximately 200-300m from shore outside Shagak Bay and Bay of Islands. Repeated exposure to the sound of minke whale blows could result in sea otters learning that the sounds are not a threat and therefore, unable to discriminate among different whale blow sounds, ignore them all. During a calm day at Adak, a minke whale was observed foraging ~200m from a sea otter – the same focal otter we were following. We
opportunistically documented the otter's response to the minke whale blows and found no change in behaviour. Whales were also seen in proximity to sea otters in the Nuchatlitz. On several occasions, gray whales (*Eschrichtius robustus*) were seen foraging within 300m of sea otter rafts, but the otters showed no response.

**Response to Vocalization Playbacks**

The recordings of killer whale vocalizations were obtained from transient animals in British Columbia and False Pass, Alaska, in the Eastern Aleutian Islands. The sea otters may not have associated the sounds with killer whale predators from the central Aleutians, however, it is not inconceivable that killer whales would travel between False Pass and Adak, a distance of approximately 1000km, allowing sea otters the opportunity to hear, and learn the sounds of the whales. Even without exposure to the exact calls used in this study, they could have responded to an unfamiliar killer whale call. Deecke et al. (2002) found that harbour seals in British Columbia responded to both local mammal-eating killer whale vocalizations and to unfamiliar killer whale calls recorded in Alaska. It is also possible that the whale calls I used in this study may not be perceived by the otters as 'realistic'. However, Deecke et al. (2002) played some of the same sequences from the same recordings of killer whale vocalizations that I used to harbour seals and the playbacks frightened the harbour seals, suggesting the calls were realistic to seals, and by inference are likely realistic to sea otters.

The most significant difference in behaviours observed in this study was the change in disturbance behaviour of otters in Adak compared to BC. The fact that sea otters at Adak responded almost equally to control sounds and killer whale calls makes it difficult to confirm that killer whale sounds were viewed as particularly threatening. Sea otters in Adak are likely exposed to boats and humans less frequently than in BC, which might explain the response of sea otters to both control and treatment sounds in Adak. Bottlenose dolphins also respond more strongly to boats at sites with little boat disturbance compared to sites where boat traffic is
common (Bejder et al. 2006). However, negative interactions with humans in Nuchatlitz BC and the lack of exposure to humans in Adak could balance out this effect. Moreover, if sea otters were responding to human disturbance we would expect this to be evident in response to all the treatments in Adak, but this was not observed. Sea otters at Adak did not respond to killer whale blows which were broadcast identically to the killer whale calls, except that the speaker was in-air rather than underwater. Thus, if human presence caused increased vigilance at Adak, the behavioural response to the killer whale blows and controls should have been the same as to the killer whale calls and control noise, but this was not the case.

Population numbers, and thus group sizes at the two field sites (Adak and the Nuchatlitz) are also very different. Larger group sizes are thought to increase the probability of detecting predators (Pulliam 1973) and to dilute predation risk (Bednekoff and Lima 1998). Sea otters do not forage in groups; however, they do aggregate in sexually-segregated rafts while resting. Garshelis et al. (1984) suggest that the gregariousness observed in sea otters has evolved in response to predation pressure, to promote social interactions, or to assist in finding food. Group formation is not observed in European otter species where there is little predation risk, but species in habitats with predators, such as sea otters and the smooth-coated otter (*Lutra perspicillata*) form groups (Kruuk 2006).

Although playbacks were presented to solitary otters at a minimum distance of 500m from rafts, the presence of rafts could be considered a “refuge” for the otters. Theory predicts that individuals in a group are safer from a predator that targets one prey item at a time (Bednekoff and Lima 1998). Because sea otter population numbers at Adak are so low and groups of animals are not present, this refuge is not available which may increase their individual vigilance effort, taking time away from resting. If sea otters in Adak are generally more wary as a result of decreased group sizes, then increased vigilance behaviour could simply be an artefact of the decline. In other words, any agent could have caused the decline itself, and
as a result, sea otters were left in smaller group sizes with heightened vigilance in response to any novel stimulus.

Killer whales have been suggested as the cause of the sea otter decline (Estes et al. 1998). The results of this present study are moderately consistent with the view that top-down processes drove the sea otter population down in Alaska, and, to some extent, point to marine predators as the likely culprit. However, we cannot conclude confidently that killer whales are responsible for declining populations of sea otters. Because sea otters also responded to the control playbacks of background noise in Adak, it is plausible that another marine predator could have contributed to the population decline and the otters are responding to any underwater acoustic disturbance. Other marine predators include Pacific sleeper sharks (*Somniosus pacificus*) and salmon sharks (*Lamna ditropis*).

Like killer whales, sharks are apex predators and fluctuations in their populations may have significant effects on community structure. During the 1990’s, surveys by the International Pacific Halibut Commission and bycatch data from the halibut fishery indicate that Pacific sleeper shark abundance increased in the northern Gulf of Alaska (Kruse et al. 2001), the central Gulf of Alaska (Mueter and Norcross 2002) and in the Bering Sea/Aleutian Island region (Gaichas 2002). Salmon sharks have also increased during this time period, forming aggregations of hundreds of animals in Bays and Inlets (Gaichas 2002; Okey et al. 2007). Sleeper sharks were once thought to be lethargic, bottom-dwelling predators, but are now known to move continuously in the water column and be stealth predators of fast moving prey (Cherel and Duhamel 2004; Taggart et al. 2005; Sigler *et al.* 2006; Van den Hoff and Morrice 2008). Sleeper sharks and sea otter habitats overlap during the night, when sharks ascend above 100m, occasionally to depths of 2m (Hulbert et al. 2006). Marine mammals, such as harbour seals and cetaceans, appear to be important prey for pacific sleeper sharks in Alaska (Taggart *et al.* 2005; Sigler *et al.* 2006). Although salmon sharks feed primarily on fish, there have been
anecdotal observations of salmon shark predation on sea otters in Alaska (Conservation Science Institute 2007).

Despite the lack of direct evidence for shark predation on sea otters, the simultaneous increase in shark populations and decline of sea otter populations is reason to further investigate the role that sharks may have played in the decline (see review chapter for more detail). Sharks often attack their prey below the surface, making it difficult to observe predation events (Frid et al. 2006). Likewise, direct evidence for killer whale predation on sea otters is scant, and based on the weight of evidence rather than observation.

The behaviour of sea otters at Adak was extremely variable. At Adak, there was significant variation in the change in percentage of time engaging maintenance behaviours compared to BC. Subject to subject variation and individual “personalities” of animals is becoming increasingly acknowledged in the literature (e.g. Boissey 1995; Dall et al. 2004; Dingemans and Reale 2005; Bell 2007; Smith and Blumstein 2008). Studies have shown that the degree of “boldness” or “shyness” displayed by an individual is consistently expressed across a wide range of behavioural scenarios, referred to as “personalities” (Frost et al. 2007). For example, individual rainbow trout (*Oncorhynchus mykiss*) can be categorised into bold and shy personalities, with bold individuals spending more time in risky habitats and foraging more aggressively, while shy individuals spend less time in risky habitats and forage more cautiously (Sneddon 2003). Birds (Verbeek et al. 1996) and rodents (Koolhaas et al. 2001) also demonstrate consistent personalities across similar scenarios.

In BC, there was no significant change in sea otter behaviour after the playbacks and there was little variation in the response. A possible explanation in line with the hypothesis tested here, is that otters may be more wary in general in Alaska than in BC and change behaviours more often, which might be because of killer whale predation. Animals in BC do not perceive killer whales to be a threat; therefore they were not threatened by the playbacks; as a
result, they did not alter their behaviours. In Adak, there was significant variation in the change in maintenance behaviours after exposure to killer whale calls and controls. One could postulate that otters in Adak switch between behaviours more often than those in BC, or, if predators are a threat, that the variation in behaviour might be explained by individual differences, discrete antipredator strategies, or different levels of experience with marine predators.

Some sea otters in Adak could in general be more fearful (Boissey 1995) to stressful situations, such as competition or predation, whereas others may be more bold, paying little or no attention to the same threat. Such variation could explain why some individual otters decreased their maintenance behaviours by 100% and increased their disturbance behaviours by 100% after exposure to predator stimuli, whereas other otters showed little or no response.

Even if individual personalities are not consistent across different scenarios, individual sea otters in Adak could have adopted different antipredator strategies (Cresswell, 1993, 1994; Caro 2005), explaining the high variance in behaviours observed. When a predator is detected, one individual might boldly approach the predator, whereas another might be more timid and seek refuge (Magurran 1993; Coleman and Wilson 1998; Bell 2005). For example, individual Jefferson’s salamanders (*Ambystoma jeffersonianum*) from the same population respond differently to a single predator stimulus by varying the intensity of their antipredator displays and behaviours (Brodie 1989).

Prey wariness can change as a function of intrinsic factors, such as previous experience with predators (Smith 1996). These differences can have a profound effect upon the decisions made by animals. Although predation rates may once have been extremely high, they are likely lower now because there are few otters, and with low conspecific encounter rate it is unlikely that an otter would observe a predation event. This could result in the high variation in behavioural responses observed in Adak. In contrast, BC otters likely have little or no
experience with predators, which could explain both the lack of response and the lack of variation in response.

It is likely that we will never be able to identify the cause of the current sea otter decline with certainty. The current theory of killer whale predation is based on a "weight of evidence" approach. The results of this study are consistent with top-down processes reducing the sea otter populations in the Aleutians Islands. However, because I failed to detect a difference between the response of otters to control and treatment playbacks of killer whale sounds in Adak, my results do not provide evidence that the increased vigilance of otters in Adak results from predation by killer whales. The trend, although non-significant, was in a direction supporting the hypothesis and more research might show significant effects. The results of this study in fact suggest that other marine predators, such as sharks, should also be considered. Moreover, species extinctions and endangerments are often caused by two or more agents of decline (Caughley and Gunn 1996); a combination of factors, such as predation, climate change, and pollutants (see review chapter for more detail) could be at play in the Aleutian Islands, and this possibility should not be ignored. Further investigation into the levels of various contaminants in sea otters and the possible effects on the population should be prioritized. Finally, this was the first study to use current animal behaviours to address the cause of a population decline several years after the decline occurred, and proved to be a useful approach to conservation biology.


PBSmapping. 2006. Developed by: Jon Schnute, Nicholas Boers, Rowan Haigh. PBS Mapping 2. R package version 2.05.


CHAPTER IV – GENERAL CONCLUSIONS

This thesis challenges a widely-known conjecture that killer whale predation caused sea otter populations in the Aleutian Islands to decline at a precipitous rate, first proposed ten years ago by Estes et al. (1998). Since that time, there have been no papers published to further investigate, test, or refute this hypothesis. Chapter 2 of this thesis set out to re-examine the potential causes of the sea otter population decline in the Aleutian Islands and chapter 3 set out to empirically test the hypothesis that the decline was caused by killer whale predation. This was the first study to re-examine the existing evidence in support of the killer whale hypothesis, to empirically test the hypothesis, and to re-assess alternative hypotheses.

The main findings from both chapter 2 (review) and chapter 3 (playback experiments) suggest that killer whale predation may not have been the cause of the sea otter population decline. As discussed in these chapters, support of the killer whale predation hypothesis is inconclusive and examination of other causes of the decline needs further research. The killer whale predation hypothesis is presented as established fact in ecology text books and other sources (e.g. Krebs 2001; Ray et al. 2005), while, as presented in this thesis, the evidence is far from conclusive. Conservation planning should nevertheless proceed even with uncertainties in understanding the causes, but research into alternative explanations for population declines should meanwhile continue when planning is based on the weight of available evidence. Disproportionate attention given to one hypothesis could divert attention away from equally or more important issues. As discussed in Chapter 2, toxins, disease, other marine predators such as sharks, or a combination of factors, are alternative explanations for the declines in sea otter populations in the Aleutians and warrant further investigation.

Understanding the processes by which populations are driven to extinction by agents external to them (the declining-population paradigm of conservation biology, Caughley 1994) is
essential to effectively manage and conserve species at risk. There are various ways to detect, diagnose and halt population declines. This thesis contributed to two theoretical areas of the declining-population paradigm: the review of potential causes of the sea otter decline and the novel use of the analysis of behavioural responses to predator cues to assess past exposure to specific predators.

Previous authors have used acoustic playbacks experiments to demonstrate the ability of various taxa to recognize and respond evasively to the sounds of predators (e.g. Noe and Bshary 1997; Hendrie et al. 1998; Mann and Lu 1998; Swaisgood et al. 1999; Blumstein et al. 2008) and to learn antipredator strategies in response to predator stimuli (e.g. Berger et al. 2001; Gil-da-Costa 2003). Most of these studies have investigated prey response to stimuli of a known predator. In this study, the extent to which killer whales prey on sea otters is unknown and direct observations of predation events are rare. This is the first study to use playback experiments and geographic variation in current behaviours to determine whether a novel predator has exerted selective pressure on a prey species. This method proved to be a useful tool in conservation biology, contributing to the declining-population paradigm by providing a novel means by which agents of decline can be identified.

**Future Research**

This study has produced new information on the potential causes of the population decline of sea otters in the Aleutian Islands. However, it has also raised many questions that need to be answered in future research, including:

1) Are the trends of geographic variation in behaviour between the Aleutian Islands and British Columbia present in other species, such as harbour seals or Steller sea lions?

2) What is the role of shark predation on sea otters in the Aleutian Islands?
3) What are the effects of high contaminant levels in sea otters, and what levels are found in otters at other Islands?

4) What is the quality of sea otter prey at various locations around the Aleutian Islands, and what is the biomass of prey species other than sea urchins?

5) What are the environmental causes of the differences in disturbance behaviour observed in this study?

6) Are there fitness costs to the high disturbance behaviours observed at Adak?

7) Are the stress levels of individuals in depleted areas higher than those in areas where the population is stable or growing, and if so, could biochemical responses to that stress be further comprising the population in depleted areas?

8) Would a larger sample size of sea otter behaviour from other Aleutian Islands reveal similar or different patterns than those observed in this study?
Literature Cited


The University of British Columbia

Animal Care Certificate

Application Number: A05-1848

Investigator or Course Director: Lance Barrett-Lennard

Department: Zoology

Animals Approved: sea otter

Start Date: March 1, 2006
Approval Date: December 13, 2005

Funding Sources:

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<td>BC Wild Killer Whale Adoption Program</td>
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</tbody>
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The Animal Care Committee has examined and approved the use of animals for the above experimental project.

This certificate is valid for one year from the above start or approval date (whichever is later) provided there is no change in the experimental procedures. Annual review is required by the CCAC and some granting agencies.

A copy of this certificate must be displayed in your animal facility

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ANIMAL CARE CERTIFICATE

Application Number: A05-1848

Investigator or Course Director: Lance Barrett-Lennard

Department: Zoology

Animals: Otter sea otter

Start Date: March 1, 2006 Approval Date: February 28, 2007

Funding Sources:

Funding Agency: Vancouver Aquarium Marine Science Centre
Funding Title: BC Wild Killer Whale Adoption Program

Unfunded title: N/A

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has successfully completed the online training requirements of the Canadian Council on Animal Care (CCAC) / National Institutional Animal User Training (NIAUT) Program

Certificate #: 2126 - 07

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