Exxon Valdez Oil Spill
Restoration Project Final Report

Pigeon Guillemot Restoration Research in Prince William Sound, Alaska

Restoration Project 070853
Final Report

Kirsten S. Bixler[1]
Daniel D. Roby[1]
David B. Irons[2]
Melissa A. Fleming[3]
Joseph A. Cook[3]

[1] Oregon State University
U.S. Geological Survey - Oregon Cooperative Fish & Wildlife Research Unit
Department of Fisheries and Wildlife
104 Nash Hall
Corvallis, OR 97331

[2] U.S. Fish and Wildlife Service
Migratory Bird Management
1011 East Tudor Road
Anchorage, AK 99503

[3] Museum of Southwestern Biology
Department of Biology
University of New Mexico
Albuquerque, NM 87131

November 2010

Exxon Valdez Oil Spill
Restoration Project Final Report

Pigeon Guillemot Restoration Research in Prince William Sound, Alaska

Restoration Project 070853
Final Report

Kirsten S. Bixler[1]
Daniel D. Roby[1]
David B. Irons[2]
Melissa A. Fleming[3]
Joseph A. Cook[3]

[1] Oregon State University
U.S. Geological Survey - Oregon Cooperative Fish & Wildlife Research Unit
Department of Fisheries and Wildlife
104 Nash Hall
Corvallis, OR 97331

[2] U.S. Fish and Wildlife Service
Migratory Bird Management
1011 East Tudor Road
Anchorage, AK 99503

[3] Museum of Southwestern Biology
Department of Biology
University of New Mexico
Albuquerque, NM 87131

November 2010

Pigeon Guillemot Restoration Research in Prince William Sound, Alaska

Restoration Project 070853
Draft Final Report

Study History: Restoration Project 070853 was initiated to address the lack of population recovery of Pigeon Guillemots (*Cepphus columba*) in Prince William Sound (PWS), a species injured by the 1989 *Exxon Valdez* oil spill (EVOS). The objectives of this project were to (1) ascertain the merit of mink (*Neovison vison*) control for the recovery of the Pigeon Guillemot population nesting on the Naked Island group (i.e., level of mink predation on guillemot nests, source of the mink population, uniqueness of the mink); (2) determine if availability of preferred prey species limits the recovery of the guillemot population on the Naked Island group; and (3) devise a feasible restoration plan for guillemots at the Naked Island group, the most important historical nesting location for the species in PWS.

This study follows several years of research on the potential factors that prevent population recovery of Pigeon Guillemots within PWS. Previous studies demonstrated that direct exposure to residual oil from EVOS may have reduced survival of adult guillemots for at least a decade after the spill. In addition, a reduction in the availability of preferred prey species (i.e., schooling forage fishes) and an increase in the failure rate of guillemot nests due to predation lowered the reproductive success of Pigeon Guillemots during the 1990s compared to before EVOS. The lack of evidence of direct oil exposure in guillemots by 2004, however, suggested that the mechanisms limiting the recovery of the population in PWS had changed since the last intensive study on guillemots was conducted a decade ago.

This project provides current information on the two remaining potential mechanisms constraining the recovery of the population of Pigeon Guillemots at the Naked Island group (i.e., availability of schooling forage fishes and nest predation; the first two objectives of this study). During 2007 and 2008, data were collected on guillemot population trends, the presence or absence of mink, the effect of predation on mortality of guillemot eggs and chicks, changes in nesting habitat use by guillemots, and availability of schooling forage fish at the Naked Island group and in surrounding areas to assess the relative importance of these potential limiting factors using a weight of evidence approach. Data on population size, population trajectory, and nesting distribution of Pigeon Guillemots at the Naked Island group were then compared to similar data collected across the remainder of PWS to test whether the trends were consistent with one of the two limiting factors currently thought to prevent population recovery. These research results are presented as an appendix to this report, and constitute the M.Sc. thesis of Kirsten S. Bixler, submitted to Oregon State University in partial fulfillment of the requirements for a M.Sc. degree in Wildlife Science.

The source of the mink population at the Naked Island group and the degree of similarity with populations from other regions of PWS and with fur farm mink stock were investigated as part of this project using mitochondrial DNA sequencing and nuclear microsatellite genotyping (Objective 1). The results of the mink genetics study are presented as an appendix to this report, which was prepared by Drs. Melissa A. Fleming and Joseph A. Cook of the Museum of Southwestern Biology at the University of New Mexico.

A restoration plan for the recovery of Pigeon Guillemots at the Naked Island group in PWS (Objective 3) was then developed, which includes all feasible alternatives for restoration action. The selection of the preferred alternative was based upon the conclusions drawn from the investigations described in the two appendices, as they relate to the efficacy of mink control for guillemot population restoration (Objective 1) and the availability of high-lipid schooling forage fishes to nesting guillemots (Objective 2). This restoration plan comprises the core of this report, and was written by Kirsten S. Bixler, Dr. Daniel D. Roby (Co-PI), and Dr. David B. Irons (Co-PI).

Abstract: A restoration plan for Pigeon Guillemots (*Cepphus columba*) in PWS was prepared to address the species' lack of population recovery following injury by the 1989 *Exxon Valdez* oil spill. Predation on nests and adults by mink is now the primary limiting factor for guillemot reproductive success and population recovery at the most important historical nesting site for guillemots in PWS (i.e., the Naked Island group). Mink on the Naked Island group are descended in part from fur farm stock and apparently arrived on the island group about 15-30 years ago. Eradication of mink at these islands was selected as the preferred restoration alternative because it is feasible and most likely to result in the recovery of guillemots in PWS. Other alternatives are either currently unavailable or unlikely to be effective. An eradication effort is likely to be successful due to both well-developed methods and the low likelihood of re-colonization. Potential negative effects of the preferred alternative are either negligible or largely avoidable. The Naked Island group guillemot population would likely double within the first 10 years following mink eradication, and the Sound-wide population of guillemots would likely increase within 15 years of mink eradication at the Naked Island group, once the Naked Island group had become a source population for other parts of PWS.

Key Words: Alaska, *Cepphus columba*, forage fish, limiting factors, American mink, *Neovison vison*, Pigeon Guillemot, population recovery, predation, Prince William Sound, reproductive success, restoration

Project Data: Description of data – mink tissue samples for genetic analyses were collected from lethally sampled animals trapped in Prince William Sound. Tissues were processed and archived at the Museum of Southwestern Biology, University of New Mexico. Observational data on population size, nesting success, and diet of guillemots were archived at the Office of Migratory Bird Management, U.S. Fish and Wildlife Service in Anchorage, Alaska.
Format – Numerical data were archived as Excel spreadsheets. Custodian – contact David B. Irons, U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road, Anchorage, Alaska 99503, David_Irons@fws.gov

Citation: Bixler, K.S., D.D. Roby, and D.B. Irons, M.A. Fleming, and J.A. Cook. 2010. Pigeon Guillemot restoration research in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project Draft Final Report (Restoration Project 070853), Oregon State University, Corvallis, Oregon.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF APPENDICES

A Restoration Plan for Pigeon Guillemots (*Cepphus columba*) at the Naked Island Group for Population Recovery in Prince William Sound

EXECUTIVE SUMMARY

The Pigeon Guillemot (*Cepphus columba*) is now the only marine bird species in Prince William Sound (PWS), Alaska that is listed as "not recovering" on the Exxon Valdez Oil Spill Trustee Council's Injured Resources List and has shown no sign of population recovery. Since 1989, the population of Pigeon Guillemots in Prince William Sound (PWS) has undergone a continuous and marked decline, with no sign of stabilization. Given this alarming trend, restoration is warranted for the recovery of Pigeon Guillemots in PWS. The logical location to focus restoration effort for guillemots is the most important historical breeding location in the Sound, the Naked Island group in central PWS. These islands provide an opportunity for recovery of a significant proportion of the PWS guillemot population, although the Naked Island group constitutes only about 2% of the total shoreline in PWS. One fourth of all guillemots nesting in PWS in 1989 (just after the spill) were located at the Naked Island group. Restoration of guillemots at the Naked Island group to the number counted at that time would result in a substantial increase in the Sound-wide population. Most of the available information on the factors limiting the Pigeon Guillemot population in PWS originates from research on guillemot population size, nesting success, and diet conducted at the Naked Island group during 15 breeding seasons between 1978 and 2008. These data, placed in a historical and socioeconomic context, permit the development of a restoration plan designed to facilitate the population recovery of Pigeon Guillemots in PWS.

A few historical events have had a considerable impact on Pigeon Guillemots nesting at the Naked Island group in PWS. First, fox farming occurred at the Naked Island group for more than 50 years beginning in 1895. The foxes (*Alopex lagopus*) almost certainly caused severe declines in the populations of native fauna, including Pigeon Guillemots, as they did across many formerly fox-free islands in Alaska. Nearly a century later, the EVOS caused acute mortality from oiling estimated at between 500 and 1,500 Pigeon Guillemots in PWS in the immediate aftermath of the spill. There was evidence that guillemots were exposed to and negatively affected by residual oil for at least a decade after the spill. However, there was no longer an indication of guillemot exposure to residual oil from EVOS by 2004. Studies have demonstrated that EVOS and/or a climatic regime shift associated with the Pacific Decadal Oscillation affected guillemots in the Sound through reduced availability of preferred forage fish species. The prevalence of high-lipid schooling forage fish in the diet of guillemot chicks at the Naked Island group was significantly lower in the decade after EVOS, and this change was associated with lower nestling survival and growth rates, and lower overall nesting success. The level of predation on guillemot nests at the Naked Island group also increased significantly during the 1990s when compared to pre-spill, potentially limiting the recovery of Pigeon Guillemots at this location.

The primary limiting factor for guillemot reproductive success and population recovery at the Naked Island group is now apparently predation of nests and adults by American mink (*Neovison vison*). Guillemot population trends at the Naked Island group compared to the rest of PWS are

consistent with this hypothesis. At sites outside of PWS, guillemot population declines and even local extirpation of breeding guillemots due to predation by mink have been successfully and rapidly reversed through mink eradication as a restoration action. Although a precise estimate of the guillemot population response to proposed mink eradication at the Naked Island group is not possible, all available evidence suggests that eliminating mink predation on guillemot nests and adults would result in a measureable increase in the breeding population and productivity of Pigeon Guillemots at the Naked Island group. Nest predation by mink may also have caused declines in populations of other seabirds nesting at the Naked Island group, including Arctic Terns (*Sterna paradisaea*), Parakeet Auklets (*Aethia psittacula*), Tufted Puffins (*Fratercula cirrhata*), and Horned Puffins (*Fratercula corniculata*). The presence of foraging marine mammals and large flocks of piscivorous birds provide supporting evidence that predation by mink and not limitations in food supply have caused the declines in seabirds breeding at the Naked Island group. The introduction or range expansion of mink in areas outside of PWS have caused rapid population declines in a wide variety of taxa, including several species of ground-nesting birds, small mammals, amphibians, and crustaceans.

Mink are native to the mainland and nearshore islands of PWS. The natural distribution of mink on the more isolated, offshore islands in PWS is, however, less well known. Observational data suggest that mink were absent on the Naked Island group until about 15-30 years ago. Data from both mtDNA sequencing and nuclear microsatellite genotyping suggest that the mink on the Naked Island group are descended in part from fur farm mink stock, and evidence suggests that mink were introduced to the Naked Island group by humans.

The Naked Island group is part of Chugach National Forest with the exception of one small privately-owned parcel on Peak Island. The islands are used periodically for camping, hiking, deer hunting, and fishing. Although frequently exploited for their fur in other parts of PWS, trapping of mink at the Naked Island group occurs rarely. Pigeon Guillemots contribute to the success of ecotourism in PWS through their conspicuous, vocal, and charismatic displays along the shoreline.

The restoration objective for Pigeon Guillemots in PWS is population recovery, which in this case is defined as a stable or increasing population. All reasonable potential restoration alternatives have been considered and assessed for their likelihood of facilitating guillemot population recovery. The preferred alternative (Alternative A) is the eradication of mink (i.e., the removal of all individuals of the species) at the Naked Island group. The suggested method is trapping with lethal body grip traps set along the coastline during fall, winter, and especially early spring (when snow cover is present and mink are largely restricted to the shoreline), supplemented with hunting using dogs, as necessary. Successful eradication will likely require multiple years of effort, likely 3-5 years. Long-term monitoring of the islands should be conducted periodically when mink are most easily detected (i.e., when snow cover is present) and any mink discovered should be immediately trapped and the carcass saved for genetics analysis. The culling of mink (Alternative B) would result in suppression of the mink population at the Naked Island group, rather than complete elimination. This alternative was rejected for three primary reasons: (1) the level of culling effort necessary to cause a significant reduction in predation rates on guillemots is unknown, (2) culling would have to occur on an annual basis to be effective, (3) the ultimate economic cost and the total number of animals killed under a culling program would far exceed that of eradication, and (4) because even a single mink can devastate a guillemot colony, culling is unlikely to effectively enhance the recovery of the Pigeon Guillemot population. Alternative C, enhancement of the guillemot food supply during the nesting season, included the release of high-lipid hatchery-reared juvenile fish (i.e., Pacific herring, *Clupea pallasi*, and/or Pacific sand lance, *Ammodytes hexapterus*) near foraging areas of Pigeon Guillemots at the Naked Island group. Although this alternative may be an effective restoration technique for guillemots and other species in the future, it was eliminated because there is currently no stock enhancement program for herring or sand lance in PWS, plus it fails to address the primary cause of guillemot egg and chick mortality at the Naked Island group. The construction and installation of guillemot nest boxes (Alternative D) to enhance the availability of sites inaccessible to mink was considered and rejected as well. A few nest boxes were installed at the Naked Island group during the 1990s, but there was a low incidence of use by guillemots, most likely because there was an abundance of available, unoccupied natural cavities. The population of Pigeon Guillemots at the Naked Island group is now significantly lower than it was during the 1990s, and thus nest box installation would almost certainly be an ineffective restoration technique. Alternative E consists of the lethal control of avian predators of Pigeon Guillemots and their nests, including Common Ravens (*Corvus corax*), Northwestern Crows (*Corvus caurinus*), and Black-billed Magpies (*Pica pica*). This alternative would require a constant, persistent, and intensive effort to reduce populations of avian predators, and the resulting increase in survival of guillemot eggs and chicks is likely to be insignificant in comparison to the loss of eggs, chicks, and adults due to mink predation. Alternative F consisted of a combination of provisioning of nest boxes (Alternative D) and control of corvid (Alternative E) and mink (Alternative B) populations. This combination of alternatives is unlikely to be more effective than any of the alternatives implemented on its own. The current management strategy (Alternative G), involves no restoration action. Given the high predation pressure on guillemot nests at the Naked Island group, this alternative will almost certainly lead to a continued low (< 25 nesting pairs) breeding population or local extirpation of the guillemot breeding population at this site.

Eradication of mink was selected as the preferred alternative because it is most likely to facilitate the recovery of Pigeon Guillemots throughout PWS. This alternative is less expensive, both economically and in terms of the number of mink killed, compared to any effective, perennial culling effort. Other alternatives are either currently unavailable or unlikely to be effective. An effort to eradicate mink at the Naked Island group is likely to be successful in a relatively short period of time (10 years) due to both well-developed methods of eradication and the low likelihood of mink re-colonization. Although, the preferred alternative would be implemented to address the Pigeon Guillemot population decline in PWS, a suite of other seabird species, including Tufted Puffins, Horned Puffins, and Arctic Terns, with depressed breeding populations at the Naked Island group would also benefit. Mink eradication may also promote local increases in other populations of ground-nesting birds (e.g., waterfowl), small mammals, amphibians, and crustaceans.

Potential negative effects of the preferred alternative appear to be either negligible or largely avoidable. Proposed eradication methods include steps to minimize capture of non-target species (i.e., selection of trap type and use of artificial burrows in which to set traps). The restoration of guillemots at the Naked Island group will not have a significant negative impact on herring stocks because juvenile herring have never been an important part of the diet of guillemots nesting at this location. Eradication of mink at the Naked Island group would not adversely affect trappers in PWS because mink at the Naked Island group are rarely exploited for their fur and are remote to trappers in the region. Due to the fur farm ancestry of mink at the Naked Island group, this alternative would not injure the Sound-wide population of native mink. There is no concern over a potential detrimental population eruption by small introduced herbivores or omnivores, such as rabbits or rats, following mink eradication because no such species occur at the Naked Island group.

The population response of guillemots to mink eradication at the Naked Island group is measurable through the comparison of historical and recent guillemot population surveys completed at the Naked Island group and the Smith Island group (mink-free islands) using a Before–After–Control–Impact design. Although a precise prediction of the guillemot population response to mink eradication is not possible, the time expected to population recovery can be estimated. If the expected increase in guillemot productivity from mink eradication is realized and model assumptions are correct, guillemot population at the Naked Island group will double within 10 years following mink eradication and the Sound-wide population of Pigeon Guillemots will begin to increase within 15 years after eradication of mink at the Naked Island group.

CHAPTER 1: PURPOSE AND NEED FOR ACTION

INTRODUCTION

The Pigeon Guillemot (*Cepphus columba*) is now the only marine bird species injured by the 1989 *Exxon Valdez* oil spill (EVOS) that is listed as "not recovering" on the Exxon Valdez Oil Spill Trustee Council's Injured Resources List and has shown no sign of population recovery. Since 1989, the population of Pigeon Guillemots in Prince William Sound (PWS) has declined by an alarming 47%, and there is no sign of population stabilization (McKnight et al. 2008). Given this steady, long-term, and drastic trend, restoration action is warranted and in all probability necessary for the recovery of the Pigeon Guillemot population in PWS.

The Naked Island group is a logical location to focus restoration efforts for guillemots in PWS (Figure 1). These islands provide a unique opportunity to facilitate the recovery of a disproportionately large number of guillemots through restoration along a small portion (~2%) of the total PWS shoreline. The Naked Island group was historically the most important breeding location for guillemots in the Sound (Sanger and Cody 1994). Approximately one quarter of the guillemot population in PWS nested at the Naked Island group in 1989 in the aftermath of the EVOS (U.S. Fish and Wildlife Service, unpubl. data). Recovery of Pigeon Guillemots at the Naked Island group to the number counted just after the spill (Oakley and Kuletz 1996) would increase the Sound-wide population by nearly 45% (McKnight et al. 2008).

The Naked Island group is also the site where we have the most thorough understanding of mechanisms regulating Pigeon Guillemot populations in PWS. Data on population size, nesting success, and diet of guillemots has been collected at the Naked Island group during 15 years between 1978 and 2008 (Appendix A). The historical, ecological, and socioeconomic contexts of Pigeon Guillemots at the Naked Island group are presented below. This information provides the foundation crucial for the development and assessment of feasible restoration alternatives designed to facilitate the population recovery of Pigeon Guillemots in PWS.

HISTORICAL CONTEXT

The Naked Island group was the site of arctic fox (*Alopex lagopus*) fur farms for more than 50 years beginning in 1895 (Bailey 1993, Lethcoe and Lethcoe 2001). The foxes roamed free on the islands (Evermann 1914) and, as in other locations, likely relied on native small mammals (i.e., voles, shrews, and mice) and seabirds as a food source (Heller 1910, Bailey 1993). The populations of native fauna, including Pigeon Guillemots, almost certainly plummeted following the introduction of foxes to the Naked Island group, as they did across many formerly fox-free islands in Alaska (Bailey 1993). In fact, there were apparently no rodents or shrews on Storey Island and no shrews on Naked Island by 1908, within 15 years of the commencement of fox farming (Heller 1910). A variety of native species including salmon, herring, harbor seals, and even whales were killed to provide supplemental food for foxes in the Sound (Bailey 1993, Lethcoe and Lethcoe 2001, Wooley 2002), thereby altering the entire ecosystem. The depression of the 1930's, the end of World War II, and changes in women's fashions in Europe together caused fox farming to become unprofitable (Lethcoe and Lethcoe

2001). Upon closure of the fox farms, foxes in PWS either were removed by trapping or died of starvation; arctic foxes are no longer found in the PWS region (Bailey 1993).

Other historical developments in PWS that may have directly or indirectly impacted the nearshore habitat of the Naked Island group include mining, commercial fishing of salmon and herring, pink salmon hatcheries, marine mammal harvest, and logging (Lethcoe and Lethcoe 2001, Wooley 2002). The 1964 earthquake resulted in an uplift of about four feet at the Naked Island group and massively altered both the shoreline and shallow nearshore habitat (Hanna 1971) where guillemots nest and forage (Ewins 1993).

On 24 March 1989, the T/V *Exxon Valdez* ran aground at Bligh Reef in PWS resulting in the release of at least 44 million liters of Prudhoe Bay crude oil into PWS. The oil spread to the southwest through the Sound and into the northern Gulf of Alaska. An estimated 500 to 1,500 Pigeon Guillemots in PWS were immediately killed due to oil exposure (Piatt and Ford 1996). There was evidence that guillemots were exposed to residual oil for at least a decade after the spill (Golet et al. 2002). However, there was no longer indication of direct contact with oil in guillemots by 2004 (B. Ballachey, U.S. Geological Survey, pers. comm.).

Previous studies have demonstrated that EVOS and/or a climatic regime shift associated with the Pacific Decadal Oscillation may have indirectly affected Pigeon Guillemots in PWS (Agler et al. 1999, Golet et al. 2002). The decline in the number of guillemots in the Sound, which began prior to EVOS, has been associated with the 1976 shift in the Pacific Decadal Oscillation (Agler et al. 1999, Golet et al. 2002) that resulted in reduced abundance of schooling forage fish across the North Pacific Ocean (Anderson et al. 1997, Francis et al. 1998, Anderson and Piatt 1999). EVOS also apparently contributed to the decline in populations of schooling forage fish, specifically Pacific herring (*Clupea pallasi*) and Pacific sand lance (*Ammodytes hexapterus)* in Prince William Sound (Marty et al. 1999, Golet et al. 2002, Marty 2008). The prevalence of high-lipid schooling forage fish in the diet of guillemot chicks at the Naked Island group was significantly lower in the decade after EVOS than prior to EVOS (Oakley and Kuletz 1996, Golet et al. 2002). Low proportions of high-lipid schooling prey, particularly sand lance, in the diet of Pigeon Guillemot chicks have been associated with lower nestling survival, lower nestling growth rates, and lower overall nesting success (Golet et al. 2000, Litzow et al. 2002).

Top-down factors, such as predation, may also have limited the recovery of the Pigeon Guillemot population in PWS (Hayes 1995, Oakley and Kuletz 1996, Golet et al. 2002). Common potential predators of guillemot nests in PWS include Glaucous-winged Gulls (*Larus glaucescens*), Black-billed Magpies (*Pica hudsonia*), Northwestern Crows (*Corvus caurinus*), Common Ravens (*Corvus corax*), river otters (*Lontra canadensis*), and American mink (*Neovison vison*) (Oakley and Kuletz 1979, Ewins 1993, Hayes 1995, Oakley and Kuletz 1996). The level of predation on guillemot nests at the Naked Island group increased significantly during the late 1990s compared to earlier years (Golet et al. 2002).

CURRENT ECOLOGICAL CONTEXT

The Pigeon Guillemot is a pursuit-diving seabird that preys upon a variety of nearshore demersal fishes, schooling fishes, and, occasionally, crustaceans (Ewins 1993). Guillemots are semi-colonial members of the seabird family Alcidae that produce 1- or 2-egg clutches (Ewins 1993). Pigeon Guillemots usually nest in rock crevices or burrows along rocky shorelines but are also known to nest in crevices of anthropogenic structures such as piers, bridges, and wooden nest boxes (Ewins 1993). Guillemots nest along the coastline of western North America from the Bering Strait to Santa Barbara, California, and as far south as the Kurile Islands in the Russian Far East. The current number of Pigeon Guillemots is considered stable and estimated to be about 470,000 individuals range-wide (BirdLife International 2009). The species is regarded as "of least conservation concern" (BirdLife International 2009). The Pigeon Guillemot is however, susceptible to long-term local declines in breeding populations (Ewins 1993).

The availability of schooling forage fish may continue to limit the rate and extent of Pigeon Guillemot population recovery, both at the Naked Island group and in the Sound as a whole (Appendix A). The prevalence of schooling forage fish in the diet of Pigeon Guillemots at the Naked Island group has not recovered to pre-EVOS levels. In addition, the average group size of Pigeon Guillemots detected in surveys declined near the Naked Island group, but also across a number of other important guillemot nesting areas in central and western PWS, a pattern consistent with a region-wide reduction in food availability.

However, the weight of available evidence indicates that the primary limiting factor for guillemot reproductive success and population recovery at the Naked Island group is now predation by a recent colonizer of the islands, the American mink (Appendix A). The overall abundance of schooling forage fish at the Naked Island group has increased since the 1990s, suggesting that forage fish populations are recovering from EVOS. Despite improving prey resources, the guillemot breeding population at the Naked Island group has declined by more than 90% during the last 15 years. Guillemots, like many other seabirds, produce few offspring and their populations are sensitive to even small decreases in adult survival. The rate of egg and chick predation increased during the 1990s and caused the majority of nest failures during this period. By 1998, at least 60% of monitored guillemot nests and 4.5% of breeding adults at those nests were killed by mink. In 2008, we determined that the rate of nest predation at the Naked Island group was similar to the late 1990s, and mink were still able to locate guillemot nests and kill guillemot nestlings, despite few remaining nests (only 17 active guillemot nests found). The prevalence of guillemot nest sites in crevices on cliffs increased at the Naked Island group, while the prevalence of nests in crevices or burrows near the ground, presumably more accessible to mink, decreased compared to pre-spill. The guillemot population trend at the Naked Island group compared to elsewhere in PWS is also consistent with the hypothesis that mink predation is the primary limiting factor. Guillemot numbers were stable between 1990 and 2008 at nearby mink-free islands (Smith Island group), and guillemot population declines at the Naked Island group since EVOS have been much more severe than across the rest of PWS. The number of guillemots at the Naked Island group comprised about 25% of the total population in PWS just after the spill in 1989. But in 2008, the number of guillemots at the Naked Island group comprised just 1% of the total Sound-wide population.

Prior to the invasion of mink 15-30 years ago, the Naked Island group had the largest nesting colony of Parakeet Auklets (*Aethia psittacula*) in PWS and high densities of Tufted Puffins (*Fratercula cirrhata*), Horned Puffins (*Fratercula corniculata*), and Arctic Terns (*Sterna paradisaea*), in addition to supporting the highest numbers of nesting Pigeon Guillemots (Oakley and Kuletz 1979). Nest predation by mink likely caused declines in these other seabirds nesting at the Naked Island group. Arctic Terns and Parakeet Auklets have been extirpated as breeding species at the Naked Island group. Other seabirds currently nest in greatly reduced numbers (i.e., Tufted Puffins and Horned Puffins; KSB, pers. obs). The few remaining pairs of puffins nesting on the Naked Island group are restricted to the highest available shoreline cliffs (80 - 100 m) on the archipelago. Foraging humpback whales (*Megaptera novaeangliae*), minke whales (*Balaenoptera acutorostrata*), harbor seals (*Phoca vitulina*), and Steller sea lions (*Eumetopias jubatus*) along with large foraging flocks of piscivorous birds, including Marbled Murrelets (*Brachyramphus marmoratus*), Black-legged Kittiwakes (*Rissa tridactyla*), and Glaucous-winged Gulls (*Larus glaucescens*) still occurred in the nearshore waters of the Naked Island group in 2008 (KSB, pers. obs.). These aggregations of piscivorous marine birds and mammals near the Naked Island group provide supporting evidence that predation by mink, and not limited forage fish, have caused the decline in seabirds breeding at the site.

Mink are semi-aquatic, largely nocturnal, generalist carnivores that are native to the mainland and nearshore islands of PWS. The natural distribution of mink on the more isolated, offshore islands in PWS is less well known, however, due to two centuries of trapping of furbearers by non-Native Alaskans and 50 years of fur farms for foxes and mink (Appendix B; Lethcoe and Lethcoe 2001). All available observational data suggest that mink arrived on the islands 15-30 years ago (U.S. Fish & Wildlife Service, unpubl. data). Evidence from both mtDNA sequencing and nuclear microsatellite genotyping suggest that the mink on the Naked Island group are descended in part from fur farm mink (Appendix B). In addition, it seems likely that mink were introduced to the Naked Island group by humans. There is no evidence of a gradual natural immigration of individuals and the founding population size was about 5 pairs, larger than expected from a natural colonization event. Mink from the Naked Island group are most closely related to those that occur on Knight Island, the nearest island to the Naked Island group (6 km away). This distance exceeds by 2 km the longest recorded natural dispersal distance over open water by mink. Mink were intentionally introduced by federal and state agencies to at least one remote island in PWS (i.e., Montague Island) in order to provide a harvestable population (Paul 2009). There is also suggestive evidence of introductions of mink to islands in PWS by fox farmers (Appendix B) and fur trappers (R. Ellis, USDA-Wildlife Services, pers. comm.) to establish new harvestable populations.

American mink have escaped from fur farms or from been intentionally introduced across much of Europe (Bonesi and Palazon 2007) where they have caused rapid population declines in a variety of ground-nesting birds (Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, Banks et al. 2008), small mammals, amphibians (Banks et al. 2008), and crustaceans (Bonesi and Palazon 2007). These effects are especially apparent on islands (Banks et al. 2008). A long-term, large-scale American mink removal program on islands in the Baltic Sea demonstrated that 1) nearly all species of birds, mammals, and amphibians present on the islands were negatively affected by mink predation and 2) populations of most species increased following mink removal (Nordström et al. 2003, Banks et al. 2008). Mink eradication resulted in successful reversal of the population decline and local extirpation of Black Guillemots (*Cepphus grylle*), a close relative of Pigeon Guillemots, in this study (Nordström et al. 2003).

Although we are unaware of any examples of mink eradication programs within the breeding range of Pigeon Guillemots, introduced arctic foxes have been removed from multiple islands in the Alaska Maritime National Wildlife Refuge Complex (Byrd et al. 1997). At two of these islands, Simeonof and Chernabura islands in the Shumagin Islands, the population of Pigeon Guillemots increased by 275% and 150%, respectively, within just six years of fox removal (Byrd 2001).

Not all guillemot nesting failure on the Naked Island group is caused by mink predation and the diet of the few guillemots that continue to nest on the Naked Island group does not include as high a proportion of schooling forage fishes as pre-EVOS (Appendix A). Consequently, a precise estimate of the guillemot population response should mink be eradicated at the Naked Island group is not possible. However, all available evidence suggests that eliminating mink predation on guillemot nests and adults would likely result in a measureable increase in the Pigeon Guillemot breeding population and its productivity at the Naked Island group, as well as increases in the breeding populations of other seabirds at the Naked Island group.

SOCIOECONOMIC CONTEXT

Outside of one privately owned parcel of land on Peak Island, the Naked Island group is part of the publically owned Chugach National Forest (Oakley and Kuletz 1979). The islands are used periodically for camping, hiking, deer hunting, and fishing (Oakley and Kuletz 1979). The protected bays on the west and north sides of Naked Island provide safe anchorages for sailboats, fishing boats, and an oil spill response barge. Although frequently exploited for their fur in other parts of PWS, trapping of mink at the Naked Island group rarely occurs due to the low price of furs and the time and expense involved in traveling to the islands (R. Ellis, U.S. Department of Agriculture – Wildlife Services, pers. comm.). Although Pigeon Guillemots have little subsistence value, they contribute to the success of ecotourism in PWS. Guillemots are conspicuous, vocal, and charismatic and thus play a role in the auditory and visual experience of all who frequent the shoreline of PWS.

CHAPTER 2: AUTHORITY AND RESPONSIBILITY

U. S. FISH AND WILDLIFE SERVICE

The U.S. Fish and Wildlife Service mission is "to work with others to conserve, protect and enhance fish, wildlife and plants and their habitats for the continuing benefit of the American people." Along with other Federal, State, Tribal, local, and private entities, the Service protects migratory birds, endangered species, certain fish species, and wildlife habitat. The Service is the primary agency responsible for the conservation of the Pigeon Guillemot and its habitat as authorized by the Migratory Bird Treaty Act.

ALASKA DEPARTMENT OF FISH AND GAME

The mission of the Alaska Department of Fish and Game is to "protect, maintain, and improve the fish, game, and aquatic plant resources of the state, and manage their use and development in the best interest of the economy and the well-being of the people of the state, consistent with the sustained yield principle." The Department is responsible for maintaining a harvestable surplus of fish and wildlife species, including furbearers and marine forage fish.

U.S. DEPARTMENT OF AGRICULTURE FOREST SERVICE

The mission of the Forest Service is "to sustain the health, diversity, and productivity of the Nation's forests and grasslands to meet the needs of present and future generations." The Forest Service is responsible for the management of the 5.4 million acre Chugach National Forest that includes nearly all of the Naked Island group, along with most of the rest of the land area of Prince William Sound.

CHAPTER 3: ALTERNATIVES

INTRODUCTION

The restoration objective for Pigeon Guillemots in PWS is population recovery, in this case defined as a stable or increasing population (*Exxon Valdez* Oil Spill Trustee Council 1994). All reasonable potential restoration alternatives have been considered. The ability of each alternative to meet the restoration objective was assessed and the most effective approach was selected as the preferred alternative. The compliance of the preferred alternative with the policies and standards of restoration of the *Exxon Valdez* Oil Spill Trustee Council (*Exxon Valdez* Oil Spill Trustee Council 1994) are addressed in more detail in Appendices D and E.

DETAILED DESCRIPTION OF ALTERNATIVES

Alternative A - Eradication of Mink – PREFERRED ALTERNATIVE

Actions under this alternative aim to eradicate mink at the Naked Island group. We consider eradication "the complete removal of all the individuals of the population, down to the last potentially reproducing individual" (Courchamp et al. 2003). The suggested method is lethal trapping with body grip traps along the coastline, supplemented with hunting using dogs as necessary.

Trapping is the most practical and effective method available to control mink (Boggess 1994, Macdonald and Harrington 2003, Moore et al. 2003). Although lethal trapping is more successful (Boggess 1994, Moore et al. 2003), live trapping followed by euthanasia with an air pistol or shotgun has been utilized in a few mink eradication projects due to concern for non-target captures and public acceptance (Moore et al. 2003). Other methods of euthanasia were considered but rejected. Although toxicants (e.g., sodium fluoroacetate - compound 1080 and sodium cyanide - M44) and fumigants (e.g. carbon monoxide) are in use in the United States for carnivore control, there are currently no chemical agents registered by the U.S. Environmental Protection Agency for the control of mink (Boggess 1994, National Wildlife Research Center 2008). Further, poisoning or secondary poisoning of non-target species (Courchamp et al. 2003, Moore et al. 2003) such as river otters (*Lontra canadensis*) and Bald Eagles (*Haliaeetus leucocephalus*) would likely be unacceptable. Shooting as a method of killing mink is considered inefficient (Boggess 1994, Courchamp et al. 2003). Although a potentially important management tool in European countries (Macdonald and Harrington 2003, Bonesi and Palazon 2007), control of mink through enhancement of possible competitors (i.e., river otters) seems unlikely to be effective in PWS given the lack of evidence for niche overlap (BenDavid et al. 1996). Other means of biological control, such as virus vectored immune-contraception, have yet to be fully developed (Courchamp and Cornell 2000, Macdonald and Harrington 2003) and might pose an irreversible danger to the viability of mink and other closely-related native furbearers (e.g., American marten) outside of the Naked Island group.

Trapping success would be maximized through continuous effort for at least three months of the year during the mating (January to March), juvenile dispersal (August to October), and/or winter (November to December) seasons (Bonesi et al. 2007). The precise timing of trapping will be determined using an adaptive management approach (see below). Traps would be set along the coastline of the islands (see Appendix C for details). Although mink on the Naked Island group may occur along a few inland streams and small lakes, there is evidence that mink relocate to the coast as territories become available during the eradication program (Bodey et al. 2010). We suggest the use of experienced trappers (Macdonald and Harrington 2003) for the duration of the project and hunting dogs to locate the last few mink (Moore et al. 2003).

Although we do not know the total number of mink at the Naked Island group, there likely is between 70 and 200 mink in this population (Appendix B). We anticipate that successful eradication would likely require multiple years of effort (Macdonald and Harrington 2003), potentially up to five years. Carcasses would be donated to permanent archives in public museums to be made available to research organizations for further genetic study. Long-term monitoring of the islands would be conducted periodically when mink are most easily detected (i.e., during deep snow cover; Bonesi and Palazon 2007) and any mink discovered will immediately be trapped.

The geography of the Naked Island group improves the likelihood of successful mink eradication, should eradication be attempted. The islands are relatively small with gentle topography and access to safe anchorages (Courchamp et al. 2003, Bonesi and Palazon 2007). Because the Naked Island group is geographically isolated, it is unlikely to be re-colonized by mink (Nordström and Korpimäki 2004, Bonesi and Palazon 2007).

Mink eradication at the Naked Island group would likely be followed by a clear and dramatic increase in the guillemot breeding population, but the precise response of the guillemot population following mink eradication is unknown. Based on the best available information, however, we estimate that the productivity of guillemots at the Naked Island group will increase by 16% to 36%. If this change in productivity is realized and model assumptions are accurate, the Sound-wide population should begin to increase within 15 years following eradication (See Chapter 4).

Alternative B - Culling of Mink

Alternative B is similar to Alternative A, with the exception that in this alternative the aim of lethal trapping is the suppression of the mink population at the Naked Island group, rather than eradication. Methods used would be identical to Alternative A with two main differences; 1) hunting with dogs would not be necessary and, 2) lethal trapping would have to occur indefinitely and on an annual basis in order to maintain a low density of mink on the archipelago (Bonesi et al. 2007).

There are several drawbacks to this alternative. It is possible for the population of mink to remain stable even under a culling program, and the level of culling necessary to cause and sustain a reduction in population density is unknown (Bonesi and Palazon 2007). If the population of mink declines and is released from density-dependent limiting factors, the reproductive rate would likely increase, raising the trapping effort required to maintain a low density (Courchamp et al. 2003). In order to maintain a low density population of mink, culling must occur annually (Bonesi et al. 2007), thus the ultimate economic cost and the total number of animals killed under a culling program would far exceed that of eradication (Courchamp et al. 2003). And finally, because even a single mink can devastate a guillemot colony (U.S. Fish and Wildlife, unpubl. data), culling is unlikely to significantly reduce the level of guillemot nest predation or facilitate population recovery.

Alternative C – Enhance the Pigeon Guillemot Food Supply during the Nesting Season

Actions under Alternative C would include the release of hatchery-reared juvenile forage fish within PWS, preferably in close proximity to the foraging areas of Pigeon Guillemots nesting at the Naked Island group. Due to the importance of prey lipid content to the reproductive success of guillemots (Golet et al. 2000, Litzow et al. 2002), only high-lipid schooling forage fish would be released (i.e. herring and/or sand lance). An increase in the abundance of high-lipid prey might lead to increased productivity and survival in guillemots (Golet et al. 2000, Litzow et al. 2002). The enhancement of native stocks of forage fish in PWS might also have a positive impact on populations of a variety of other species of seabirds, fish, and mammals that prey upon them, including the ESA-listed humpback whale (*Megaptera novaeangliae*) and Steller sea lion (*Eumetopias jubatus*). There is currently no stock enhancement program for either herring or sand lance in PWS. The initiation of such a program requires further research in order to ensure no unexpected negative consequences to the ecosystem (*Exxon Valdez* Oil Spill Trustee Council 2009). Although this alternative might be an effective restoration technique in the future, it is not a viable solution to stem the current alarming population decline of guillemots. More importantly however, this alternative fails to address the primary cause of guillemot nesting failure at the Naked Island group, namely predation on eggs and chicks.

Other methods of supplementing the guillemot food supply have been considered and rejected. For instance, releases of dead herring or sand lance into waters adjacent to active nests are unlikely to be utilized by guillemots because there is no indication that this species currently exploits such potential food resources (i.e., offal discarded from fishing vessels; Ewins 1993). Supplementing the diet of chicks in the nest was rejected as well. Although studies suggest that the supplementation of prey to nests can significantly increase productivity of seabirds (Robb et al. 2008), Pigeon Guillemots are prone to nest abandonment when subjected to high rates of human disturbance at the nest (Ainley et al. 1990, Vermeer et al. 1993).

Alternative D - Provide Nest Boxes to Enhance Nest Site Availability

Under this alternative, nest boxes would be installed on cliff faces that appear to be inaccessible to mink. The boxes would be placed in the immediate vicinity of either current or historical nesting locations.

Other options to prevent mink from depredating guillemot adults, chicks, and eggs inside nests were considered but eliminated. For instance, fencing is highly unlikely to be effective at reducing predation of guillemot nests at the Naked Island group. The prevention of gaps larger than 1 inch (Boggess 1994) on talus slopes and cliffs is not feasible. There are no registered chemical repellents or known effective frightening devices to modify the behavior of mink near guillemot nests (Boggess 1994, National Wildlife Research Center 2008).

There is no evidence that Pigeon Guillemots at the Naked Island group are limited by the availability of nesting habitat (Appendix A). A few nest boxes were installed at the Naked Island group during the late 1990s, but there was low incidence of use (DBI; pers. obs), most likely because there was an abundance of natural cavities available. The population of Pigeon Guillemots at the Naked Island group is now significantly lower than it was during the late 1990s. Consequently, nest box installation would almost certainly be an ineffective restoration technique.

Alternative E - Control Avian Predators of Pigeon Guillemot Nests

Actions under Alternative E intend to prevent the predation of Pigeon Guillemot nests through reduction in population of native avian predators at the Naked Island group. Avian species targeted would include the Common Raven (*Corvus corax*), Northwestern Crow (*Corvus caurinus*), and Black-billed Magpie (*Pica pica*). Lethal population control would be attained by shooting avian nest predators throughout the guillemot nesting season, April through August.

There are no other feasible methods of lethal or non-lethal control available. Although there is a conditioned taste aversion chemical registered by the U.S. Environmental Protection Agency (methiocarb) for corvid control, it is limited in use for the protection of federally threatened or endangered species (National Wildlife Research Center 2008). Similarly, lethal control of corvids through a toxicant (i.e. DRC-1339 [3-chloro-4-methylbenzenamine HCL]) is not permitted for this application (National Wildlife Research Center 2008). Harassment techniques, such as auditory deterrents, were rejected because they would likely negatively affect guillemot nest attendance.

There are several flaws inherent to this alternative. Culling by shooting has a decreasing efficacy for corvid species through time (Liebezeit and George 2002) suggesting that each year of control would require more effort with less success. The program would need to be conducted annually and continue indefinitely due to the high dispersal capability of these species. Finally, because an increase in survival of chicks after culling avian predators is likely to be insignificant in comparison to the loss of eggs, chicks, and adults due to mink predation, it seems very unlikely that this alternative would change the current population trajectory of Pigeon Guillemots at the Naked Island group.

Alternative F - Combination of Nest Boxes and Control of Predator Populations

Under this alternative, nest predators of Pigeon Guillemots (i.e., mink, ravens, crows, and magpies) would be culled and nest boxes would be installed at the Naked Island group. Actions taken include all of those listed in Alternatives B, D, and E. Due to flaws in each action (see above) that will not be lessened by the combination of alternatives, the population trajectory of Pigeon Guillemots at the Naked Island group is unlikely to change significantly.

Alternative G - No Action – Current Management

No management action would be taken under this alternative. The current breeding population of Pigeon Guillemots at the Naked Island group is likely to remain either exceedingly low (< 25 nesting pairs) or decline to local extirpation in the absence of restoration action given the high rate of predation on guillemot nests and adults by mink.

RATIONALE FOR SELECTION OF ERADICATION OF MINK ON THE NAKED ISLAND GROUP AS THE PREFERRED ALTERNATIVE

Alternative A, eradication of mink, is the preferred alternative because it is the most effective method to elevate the productivity of Pigeon Guillemots at the Naked Island group and facilitate the recovery of the species in PWS. This alternative is less expensive, both financially and in number of mink killed, than any culling method (Courchamp et al. 2003). Other alternatives are either currently unavailable or unlikely to facilitate guillemot population recovery. Given the high level of guillemot egg and chick mortality at the Naked Island group, there is no evidence to suggest that the population will recover without such restoration action. Mink eradication at the Naked Island group is likely to be successful due to both well developed methods of eradication (Bonesi and Palazon 2007) and geographic isolation of the islands (Nordström and Korpimäki 2004). The removal of all mink at the Naked Island group can be achieved within a relatively short period of time (3-5 years). Although the population response of guillemots is difficult to predict precisely, mink eradication would result in an increase in adult survival, reproductive success, and population size at the Naked Island group. A suite of seabird species with depressed breeding populations at the Naked Island group (e.g., Arctic Terns, Parakeet Auklets, Tufted Puffins, and Horned Puffins) (KSB, pers. obs.; Oakley and Kuletz 1979) would also benefit from this restoration action. Mink eradication may promote local increases in other populations of ground-nesting birds (Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, Banks et al. 2008), small mammals, amphibians (Banks et al. 2008), and crustaceans (Bonesi and Palazon 2007).

Potential negative effects of the preferred alternative appear to be negligible or largely avoidable. The preferred alternative includes steps to minimize capture of non-target species (i.e., trap type and use of artificial burrows as trap sites; see Appendix C). There is no evidence to suggest that restoration of guillemots at the Naked Island group would have a significant negative impact on herring because they have never been an important part of the diet of guillemots at this site (Golet et al. 2000). Mink at the Naked Island group are rarely exploited for their fur (R. Ellis, U.S. Department of Agriculture – Wildlife Services, pers. comm.), and thus the eradication of mink at these islands would not adversely affect trappers in PWS. Due to fur farm ancestry, the preferred alternative would not have a negative impact on the Sound-wide population of mink. There is no concern of sudden destructive eruptions of small exotic herbivore or omnivore (e.g. rabbits, rats) populations (Bergstrom et al. 2009) following mink eradication because no such introduced species occur at the Naked Island group.

CHAPTER 4: MEASURES OF SUCCESS

REFERENCE SYSTEM

The Pigeon Guillemot population trajectory between 1989 and 2008 at the Naked Island group and at the nearby Smith Island group (mink-free islands) can be compared to population trends following eradication using a Before–After–Control–Impact design (Smith 2002).

CONSTRAINTS

A precise estimate of the guillemot population response to mink eradication at the Naked Island group is not possible because there is some uncertainty about the exact proportion of all nest predation events that are caused by mink (see Appendix A). Also there is some evidence that availability of preferred forage fish may limit guillemot population recovery in some parts of PWS. Consequently, the expected time until guillemot population recovery is an estimate based upon the best available information.

TIME FRAME

We estimated the response of Pigeon Guillemot populations using a Leslie population-projection matrix after Golet et al. (2002). The following equation was used to calculate the population multiplication rate (λ):

$$\lambda = ((P_F * F_X * P_A^2) + (N_X * P_A)) / N_X$$

We assumed that fledgling survival (P_F) is 0.75 and age-constant adult survival (P_A) is 0.9. The initial population size (N_X) is the current population at the Naked Island group, 101 individuals. The initial number of offspring produced (F_X) was calculated using the average clutch size at the Naked Island group (1.7 eggs), average productivity after EVOS (0.35 chicks fledged/egg laid) plus 16% to 36%, and an initial breeding population size of about 90 (~ 45 pairs). The estimated increase in productivity, 16% to 36%, following the removal of all mink at the Naked Island group was derived from 1) the 16% increase in mortality of all chicks and eggs from pre-EVOS to post-EVOS coinciding with the apparent arrival of mink and 2) the 36% increase in the rate of predation of guillemot eggs and chicks in the years after EVOS compared to prior years. If this change in productivity is realized and model assumptions are accurate, the guillemot population at the Naked Island group would double within 10 years following eradication (Figure 2). Assuming that the model assumptions are met, the Sound-wide population of Pigeon Guillemots will increase within 15 years after eradication of mink at the Naked Island group (Figure 3). This will occur despite inclusion in the model of a 1.2% per year guillemot population decline that was documented between 1989 and 2008 across the remainder of the Sound.

EXPERIMENTAL DESIGN

1. Mink eradication at the Naked Island group would require up to five years to accomplish via lethal trapping (Appendix C) and hunting with dogs.

2. A long-term monitoring program is integral to the success of this proposed restoration. The Naked Island group would be surveyed every 2-3 years for sign (tracks, scat) in snow, when mink are most easily detected (Bonesi and Palazon 2007). The population of guillemots would be censused at both the Naked Island group and the Smith Island group during late May/early June every 3-4 years using the protocol described in Oakley and Kuletz (1996).

3. The preferred alternative requires an adaptive management strategy. This technique requires that data collected during trapping (e.g., trapping success, sex of trapped animals) as well as Pigeon Guillemot censuses be reviewed regularly to assess the success of the actions and methods. If there is evidence that the specified objective is not being met, the restoration methods or actions should be altered.

ACKNOWLEDGEMENTS

We appreciate the invaluable assistance of the following capable and dedicated field technicians: Dan Cushing, Meg Duhr-Schultz, Nathan Jones, and Adam Peck-Richardson. Aerial surveys of forage fish abundance were conducted by Evelyn Brown. The success of this project is in large part due to the many individuals involved in prior years of research on guillemots at the Naked Island group. Some of these investigators, Kathy Kuletz, Greg Golet, and Lindsey Hayes, contributed advice on field methods and insight into guillemot population declines. The USFWS office staff in Anchorage especially Karen Brenneman, provided much needed assistance and logistical support. Kelsey Sullivan, Ali McKnight, and the rest of the Shoup Bay kittiwake crew offered valued support and entertainment in the field. We are grateful to the mink trapping crew, especially Matt Sorum, Rick Ellis, and Kent Wohl, for their assistance and expertise in trapping mink.

The Department of Fisheries and Wildlife staff, particularly Jane Toliver, Trish House, Kim Howard, and Jan Cyrus, provided administrative support and assistance throughout. The support and camaraderie provided by all of the members of the Roby Lab was deeply appreciated.

LITERATURE CITED

Agler, B. A., S. J. Kendall, D. B. Irons, and S. P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. Waterbirds 22:98-103.

Ainley, D. G., R. J. Boekelheide, S. H. Morrell, and C. S. Strong. 1990. Pigeon Guillemot. Pages 276-305 *in* D. G. Ainley and R. J. Boekelheide, editors. Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Stanford University Press, Stanford, CA.

Anderson, P. J., J. E. Blackburn, and B. A. Johnson. 1997. Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. Pages 531-543 *in* Forage Fishes in Marine Ecosystems. Proceedings of an International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No.97-01, Fairbanks, AK.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117-123.

Bailey, E. P. 1993. Introduction of foxes to Alaska Islands-history, effects on avifauna, and eradication. U.S. Department of the Interior, Fish and Wildlife Service Resource Publication 193, Washington, D.C.

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

Ben-David, M., R. T. Bowyer, and J. B. Faro. 1996. Niche separation by mink and river otters: Coexistence in a marine environment. Oikos 75:41-48.

Bergstrom, D. M., A. Lucieer, K. Kiefer, J. Wasley, L. Belbin, T. K. Pedersen, and S. L. Chown. 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46:73-81.

BirdLife International. 2009. Species factsheet: *Cepphus columba*. Downloaded from http://birdlife.org on 5/1/2010.

Bodey, T. W., S. Bearhop, S. S. Roy, J. Newton, and R. A. McDonald. 2010. Behavioral responses of invasive American mink *Neovison vison* to an eradication program, revealed by stable isotope analysis. Journal of Applied Ecology 47:114-120.

Boggess, E. K. 1994. Mink. *in* S. E. Hygnstrom, R. M. Timm, and G. E. Larson, editors. Prevention and Control of Wildlife Damage. University of Nebraska-Lincoln, Lincoln, NE.

Bonesi, L., and S. Palazon. 2007. The American mink in Europe: status impacts, and control. Biological Conservation 134:470-483.

Bonesi, L., S. P. Rushton, and D. W. Macdonald. 2007. Trapping for mink control and water vole survival: identifying key criteria using a spatially explicit individual based model. Biological Conservation 136:636-650.

Byrd, G. V. 2001. Wildlife surveys at Simeonof, Chernabura and nearby islands in the Outer Shumagin Islands in July 2001. U.S. Fish and Wildlife Service report, Alaska Maritime National Wildlife Refuge, Homer, Alaska.

Byrd, G. V., E. P. Bailey, and W. Stahl. 1997. Restoration of island populations of Black Oystercatchers and Pigeon Guillemots by removing introduced foxes. Colonial Waterbirds 20:253-260.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Courchamp, F., J. L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biological Review 78:347-383.

Courchamp, F., and S. J. Cornell. 2000. Virus-vectored immunocontraception to control feral cats on islands: a mathematical model. Journal of Applied Ecology 37:903-913.

Evermann, B. W. 1914. Alaska fisheries and fur industries in 1913. Department of Commerce, Bureau of Fisheries Document 797, Washington, D.C.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). *in* A. Poole and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

Exxon Valdez Oil Spill Trustee Council. 1994. *Exxon Valdez* oil spill restoration plan. Anchorage, AK.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7:1-21.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on Pigeon Guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Hanna, G. D. 1971. Introduction: biological effects of the earthquake as observed in 1965. Pages pp. 15-34 *in* The Great Alaska Earthquake of 1964. Vol. Biology. National Academy of Sciences., Washington, D. C.

Hayes, D. L. 1995. Recovery monitoring of Pigeon Guillemot populations in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Unpubl. Report, Anchorage, AK.

Heller, E. 1910. Mammals of the 1908 Alexander Alaska Expedition with descriptions of the localities visited and notes on the flora of the Prince William Sound region. University of California Publications in Zoology, Vol. 5, No. 11, pp. 321-360, Berkeley, CA.

Lethcoe, J., and N. Lethcoe. 2001. A history of Prince William Sound, Alaska, 2nd edition. Prince William Sound Books, Valdez, AK.

Liebezeit, J. R., and T. L. George. 2002. A summary of predation by corvids on threatened and endangered species in California and management recommendations to reduce corvid predation. California Department of Fish and Game, Sacramento, CA.

Litzow, M. A., J. F. Piatt, A. K. Prichard, and D. D. Roby. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286-295.

Macdonald, D. W., and L. A. Harrington. 2003. The American mink: the triumph and tragedy of adaptation out of context. New Zealand Journal of Zoology 30:421-441.

Marty, G. D. 2008. Effects of the *Exxon Valdez* oil spill on Pacific herring in Prince William Sound, Alaska. Pages 925-932 *in* R. T. D. Giulio and D. E. Hinton, editors. Toxicology of fishes. CRC Press, Boca Raton, FL.

Marty, G. D., M. S. Okihiro, E. D. Brown, D. Hanes, and D. Hinton. 1999. Histopathology of adult Pacific herring in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Canadian Journal of Fisheries and Aquatic Sciences 56:419-426.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Moore, N. P., S. S. Roy, and A. Helyar. 2003. Mink (*Mustela vison*) eradication to protect ground-nesting birds in the Western Isles, Scotland, United Kingdom. New Zealand Journal of Zoology 30:443-452.

National Wildlife Research Center. 2008. Vertebrate control products. *in* Wildlife damage management. http://www.aphis.usda.gov/wildlife_damage/nwrc/registration/control_products.shtml. U.S. Department of Agriculture, Animal and Plant Health Inspection Service. Accessed July 1, 2010.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Nordström, M., and E. Korpimäki. 2004. Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. Journal of Animal Ecology 73:424-433.

Oakley, K. L., and K. J. Kuletz. 1979. Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot. U.S. Fish and Wildlife Service, Office of Special Studies, Anchorage, AK.

Oakley, K. L., and K. J. Kuletz. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:759-769.

Paul, T. 2009. Game transplants in Alaska. Technical bulletin No. 4, second edition. Alaska Department of Fish and Game, Juneau, AK.

Piatt, J. F., and R. G. Ford. 1996. How many seabirds were killed by the *Exxon Valdez* oil spill? American Fisheries Society Symposium 18:712-719.

Robb, G. N., R. A. McDonald, D. E. Chamberlain, and S. Bearhop. 2008. Food for thought: supplementary feeding as a driver of ecological change in avian populations. Frontiers in Ecology and the Environment 6:476-484.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Smith, E. P. 2002. BACI design. Pages 141–148 *in* A. H. El-Shaarawi and W. W. Piegorsch, editors. Encyclopedia of environmetrics. Wiley, Chichester, England.

Vermeer, K., K. H. Morgan, and G. E. J. Smith. 1993. Nesting biology and predation of pigeon guillemots in the Queen Charlotte Islands, British Columbia. Colonial Waterbirds 16:119-127.

Wooley, C. 2002. The myth of the "pristine environment": past human impacts in Prince William Sound and the Northern Gulf of Alaska. Spill Science & Technology Bulletin 7:89-104.

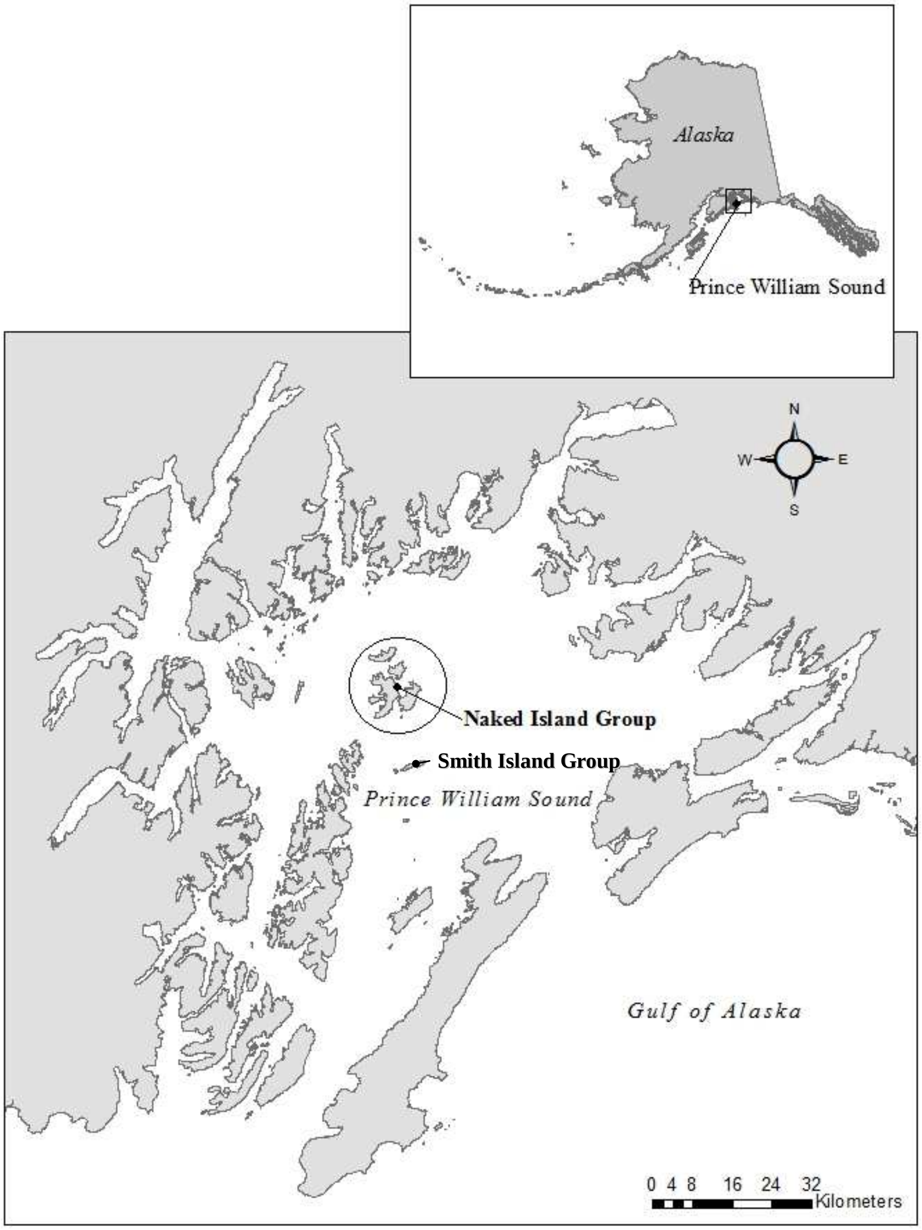


Figure 1. The location of Prince William Sound (inset map), the Naked Island group, and the nearby mink-free Smith Island group in Alaska.

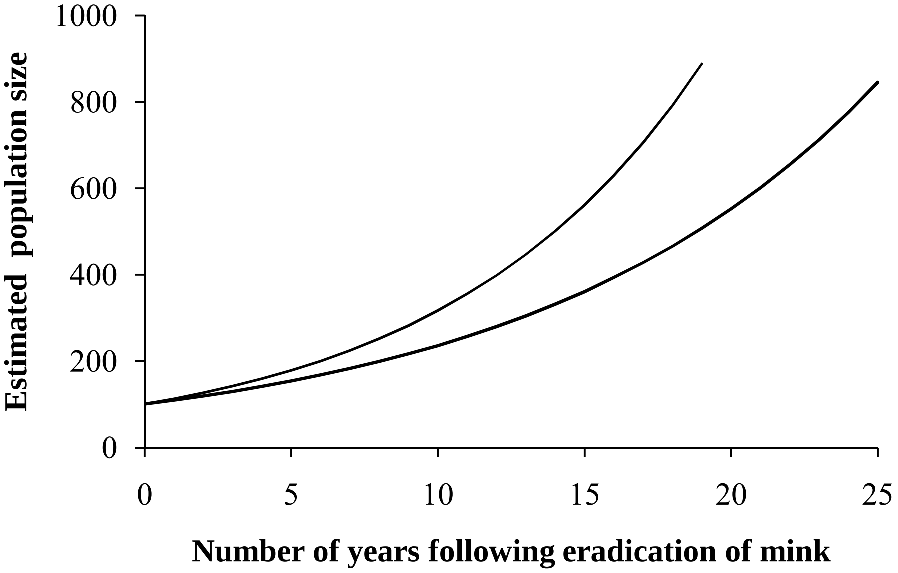


Figure 2. The maximum and minimum estimated Pigeon Guillemot population response at the Naked Island group in Prince William Sound, Alaska for 25 years after the eradication of American mink. The responses are calculated using a Leslie population-projection matrix after Golet et al. (2002). The two estimates are based upon an increase in productivity of 16% or 36% from the average productivity during the late 1990s, when the mink predation rate on guillemot nests was high at the Naked Island group.

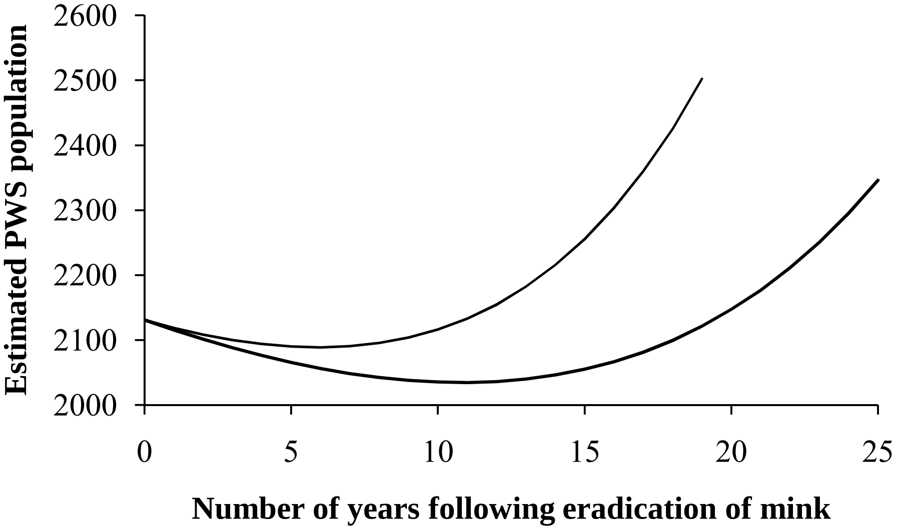


Figure 3. The maximum and minimum estimated Pigeon Guillemot population response in Prince William Sound, Alaska for 25 years after the eradication of American mink at the Naked Island group. The responses are calculated using a Leslie population-projection matrix after Golet et al. (2002). The two estimates are based upon a 16% or 36% increase from the average productivity at the Naked Island group during the late 1990s, when the mink predation rate on guillemot nests was high. Recovery of Pigeon Guillemots in Prince William Sound would occur despite the 1.2% mean decrease per annum in the population elsewhere in the Sound, as documented between 1989 and 2008.

APPENDIX A

Why Aren’t Pigeon Guillemots in Prince William, Sound, Alaska Recovering From the *Exxon Valdez* Oil Spill?

by
Kirsten S. Bixler

A THESIS

Submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented July 23, 2010
Commencement June 2011

Appendix A

AN ABSTRACT OF THE THESIS OF

Kirsten S. Bixler for the degree of Master of Science in Wildlife Science presented on July 27, 2010.
Title: Why Aren't Pigeon Guillemots in Prince William Sound, Alaska Recovering from the *Exxon Valdez* Oil Spill?

Abstract approved:

Daniel D. Roby

The Pigeon Guillemot (*Cepphus columba*) is now the only species of marine bird in Prince William Sound (PWS), Alaska that is listed as "not recovering" on the *Exxon Valdez* Oil Spill (EVOS) Trustee Council's Injured Resources List and has shown no sign of population recovery. During the 20 years since EVOS, the guillemot population in PWS has gradually declined by nearly 50% following the initial mortality event caused by direct contact with spilled oil. This decline has continued even though there is no longer evidence that guillemots are negatively affected by residual oil from EVOS. My objectives in this study were to (1) identify the primary factor now limiting Pigeon Guillemot population recovery at the Naked Island group, the most important historical breeding area for guillemots in PWS, and (2) determine whether guillemot population trends across PWS are consistent with my understanding of the primary limiting factor. I investigated two competing hypotheses for the lack of guillemot recovery at the Naked Island group: availability of high quality prey (i.e., schooling forage fish) and nest predation. The prevalence of schooling forage fish in

the diet of Pigeon Guillemots at the Naked Island group has not recovered to pre-EVOS levels. However, data from both aerial surveys and beach seines provided evidence of an increase in abundance of schooling forage fish near the Naked Island group since the late 1990s. Yet between 1990 and 2008, there was a precipitous 12% per annum decline in the guillemot population at the Naked Island group, where mink are present, while at the nearby mink-free Smith Island group guillemot numbers were stable. The mortality rate of guillemot eggs and chicks at the Naked Island group was high during the late 1990s, largely attributable to predation by mink. The weight of evidence indicates that predation by mink is now the primary factor limiting the reproductive success and population recovery of Pigeon Guillemots at the Naked Island group.

Differences in guillemot population trends between the Naked Island group and the remainder of PWS are also consistent with the mink predation hypothesis. The median decline in density of Pigeon Guillemots along transects at the Naked Island group was much greater (> 7 times) than the decline along transects throughout the remainder of PWS. The proportion of all guillemots in isolated pairs (as opposed to multi-pair groups) increased substantially only at the Naked Island group. This is consistent with the hypothesis that mink predation negatively affected guillemot colonies more than isolated nesting pairs; perhaps because guillemot nests in colonies were more apparent or more accessible to mink. At other high-density guillemot nesting areas in PWS, average group size of guillemots declined from 12 to 8 individuals suggesting that other factors may play a role in constraining of guillemots on a region-wide scale, perhaps availability of schooling forage fishes. Nevertheless, I conclude that the key to restoring the injured guillemot population at the Naked Island group is to eliminate mink predation pressure on guillemot eggs, nestlings, and attending adults.

Appendix A

Appendix A

Why Aren’t Pigeon Guillemots in Prince William Sound, Alaska Recovering from the *Exxon Valdez* Oil Spill?

by
Kirsten S. Bixler

A THESIS

Submitted to

Oregon State University

in partial fulfillment of
the requirements for the
degree of

Master of Science

Presented July 27, 2010
Commencement June 2011

Appendix A

Master of Science thesis of Kirsten S. Bixler presented on July 27, 2010.

APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my thesis will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my thesis to any reader upon request.

Kirsten S. Bixler, Author

Appendix A

ACKNOWLEDGEMENTS

I am very fortunate to have had the opportunity to participate in this research project, which offered insightful collaborators, a beautiful field site, interesting study species, and the potential to influence future management decisions. For funding, I thank the *Exxon Valdez* Oil Spill Trustee Council and the U.S. Fish and Wildlife Service. The project was largely designed and made possible through the efforts of David Irons and Dan Roby, my major advisor. I am sincerely grateful for their expertise, guidance, patience, and support. I am indebted to the capable and dedicated field technicians who worked with me in the field: Dan Cushing, Meg Duhr-Schultz, Nathan Jones, and Adam Peck-Richardson. Evelyn Brown collected data and provided advice on analysis of aerial survey data on forage fish abundance. The success of this project is in large part due to the many individuals involved in prior years of research on guillemots at the Naked Island group. Some of these investigators, Kathy Kuletz, Greg Golet, and Lindsey Hayes, provided advice on field methods and insight into guillemot population declines. Karen Brenneman and other USFWS office staff in Anchorage provided assistance and logistical support. Kelsey Sullivan, Ali McKnight, and the rest of the Shoup Bay kittiwake crew provided valued support and entertainment in the field.

Many people have contributed to this project and my education at Oregon State University. I am especially grateful for the statistical advice provided by Manuela Huso and Laurie Weitkamp. I thank my committee members, Robert Suryan and Matthew Betts, and graduate council representative Howard Gelberg. I am indebted to the Department of Fisheries and Wildlife staff, particularly Jane Toliver, Trish House, Kim Howard, and Jan Cyrus. The support and camaraderie provided by all of the members of the Roby Lab was deeply appreciated. For advice and discussion, I am particularly indebted to Jessica Adkins, Betsy Glenn, Karen Courtot, Nathan Hostetter, Don Lyons, Katie Moriarty, and Yasuko Suzuki.

My parents, sister, and friends, especially Sarah Stieg and Clara Fattor, provided invaluable encouragement and belief in my abilities. Their life paths are a continual source of inspiration. And finally, I thank Tim Lawes for his engaging companionship and generous support throughout this process.

Appendix A

CONTRIBUTION OF AUTHORS

The principal investigators, Dr. Daniel D. Roby (U.S. Geological Survey-Oregon Cooperative Fish and Wildlife Research Unit, Oregon State University, Corvallis, OR) and Dr. David B. Irons (U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK), acquired funding and made significant contributions to all aspects of this project, including study design, field work, interpretation of results, and preparation of manuscripts.

Appendix A

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

TABLE OF CONTENTS (Continued)

Appendix A

LIST OF FIGURES

LIST OF FIGURES (Continued)

Appendix A

LIST OF TABLES

Appendix A

Why Aren’t Pigeon Guillemots in Prince William Sound, Alaska Recovering from the *Exxon Valdez* Oil Spill?

CHAPTER 1

GENERAL INTRODUCTION

Kirsten S. Bixler

The Pigeon Guillemot (*Cepphus columba*) is currently the only avian species that is listed as "not recovering" on the *Exxon Valdez* Oil Spill Trustee Council's Injured Resources List and has shown no sign of population recovery (*Exxon Valdez* Oil Spill Trustee Council 2009). Before effective management can be implemented to restore the guillemot population in Prince William Sound, information on the factors that currently prevent population recovery must be obtained. Nearly a decade has passed, however, since research has been conducted on the causes of the guillemot population decline in Prince William Sound. I initiated this research to (1) identify the current primary factor limiting the recovery of the Pigeon Guillemot population at a historically important breeding location in Prince William Sound and (2) to determine whether guillemot population trends across Prince William Sound were consistent with our understanding of the primary limiting factor.

The Pigeon Guillemot is a pursuit-diving seabird that preys upon a variety of nearshore demersal fishes, schooling fishes, and, occasionally, crustaceans (Ewins 1993). Guillemots are semi-colonial members of the seabird family Alcidae that produce 1- or 2-egg clutches and can raise 1- or 2-chick broods each breeding season (Ewins 1993). Pigeon Guillemots usually nest in rock crevices or burrows along rocky shorelines, but are also known to nest in crevices of anthropogenic structures, such as piers, bridges, and wooden nest boxes (Ewins 1993). Pigeon Guillemots nest along the coastline of western North America from the Bering Strait, Alaska to Santa Barbara, California, and as far south as the Kurile Islands in the Russian Far East. The current range-wide population is considered stable at approximately 470,000 birds and is classified as "of least conservation concern" (BirdLife International 2009). Estimates of population size and trends are uncertain, however, because of the species' dispersed nesting distribution, concealed nest sites, inconsistencies in census techniques, and incomplete coverage during surveys (Ewins 1993).

Pigeon Guillemots are susceptible to local population declines following oil spills (Jewett et al. 1953, Ainley and Lewis 1974, Ewins 1993), such as that caused by the grounding of the T/V *Exxon Valdez* on 24 March 1989 at Bligh Reef in Prince William Sound, south-central Alaska. The subsequent oil spill released at least 44 million liters of Prudhoe Bay crude oil, which spread to the southwest through the Sound and into the northern Gulf of Alaska. An estimated 250,000 seabirds were killed due to direct contact with oil from the spill (Piatt and Ford 1996), including from 500 to 1,500 Pigeon Guillemots in Prince William Sound (Piatt et al. 1990). There were approximately 4,000 Pigeon Guillemots nesting in Prince William Sound (PWS) in 1989, after the *Exxon Valdez* oil spill (EVOS) (McKnight et al. 2008). At that time, about one fourth of the Sound-wide guillemot population nested at the Naked Island group, which consists of three main islands in central Prince William Sound: Naked Island (35 km^2), Storey Island (8 km^2), and Peak Island (5 km^2). Since 1989, the breeding population of Pigeon Guillemots in PWS has declined by approximately 47% (McKnight et al. 2008).

There is clear evidence that EVOS had a long-term negative effect on the population of Pigeon Guillemots in Prince William Sound during the decade after the spill (Murphy et al. 1997, Irons et al. 2000). Hepatic cytochrome P4501A, the most reliable indicator of exposure to residual oil in Pigeon Guillemots (Hovey 2002), was elevated in individuals nesting at the Naked Island group 10 years after the spill (Golet et al. 2002). Fifteen years after EVOS there was no longer evidence of exposure of Pigeon Guillemots in PWS to residual oil (B. Ballachey, U.S. Geological Survey, pers. comm.); nevertheless, the Pigeon Guillemot population in the Sound continued to decline.

The *Exxon Valdez* oil spill may continue to indirectly affect Pigeon Guillemots in PWS through reduced availability of high quality prey species (Golet et al. 2002). The spill may have contributed to the population decline of Pacific herring (*Clupea pallasi*) in PWS (Marty et al. 1999, Marty 2008), a schooling forage fish that was commercially harvested and the predominant prey for guillemots nesting in some parts of the Sound (Golet et al. 2002). Although causes are still disputed, Pacific herring in Prince William Sound have not recovered from a population crash in 1993, when herring spawned in 1989 failed to recruit to the adult population and just 25% of the expected number of adults returned (Brown and Carls 1998, *Exxon Valdez* Oil Spill Trustee Council 2010). Although there is no direct evidence available, EVOS possibly caused significant declines in Pacific sand lance (*Ammodytes hexapterus*) (Golet et al. 2002), another schooling forage fish that was an important prey type for guillemots nesting in Prince William Sound, especially at the Naked Island group (Golet et al. 2002). Schooling forage fish, including Pacific herring, Pacific sand lance, and smelt (Osmeridae spp.) generally have higher energy densities (~ 6 to 8 kJ g^{-1} fresh mass) than demersal fishes (< 5kJ g^{-1}; Anthony et al. 2000), and consequently are considered higher quality prey (Anthony et al. 2000, Rosen and Trites 2000, Romano et al. 2006). Low proportions of schooling prey in the diet of Pigeon Guillemot chicks have been associated with lower nestling survival, lower nestling growth rates (especially in beta chicks), higher incidence of brood reduction, and lower overall nesting success (Golet et al. 2000, Litzow et al. 2002). Significant reductions in the prevalence of schooling prey in the diet of guillemot chicks in the aftermath of EVOS were documented at the Naked Island group (Oakley and Kuletz 1996, Golet et al. 2002).

The decline in the breeding population of Pigeon Guillemots in PWS apparently began prior to EVOS (Oakley and Kuletz 1996, Agler et al. 1999), so it is likely that factors unrelated to the spill have contributed to the decline. A climatic regime shift associated with the Pacific Decadal Oscillation occurred in 1976, and was associated with changes in weather patterns, ocean circulation, and community composition in the North Pacific Ocean (Mantua et al. 1977, Anderson and Piatt 1999, Hare and Mantua 2000). Among other effects, the warm water regime following the 1976 shift in the Pacific Decadal Oscillation resulted in widespread declines in abundance of some schooling forage fishes, including capelin (*Mallotus villosus*), Pacific herring, and Pacific sand lance (Anderson et al. 1997, Francis et al. 1998, Agler et al. 1999, Anderson and Piatt 1999, Brown 2003). Although it is clear that the proportion of schooling forage fish in the diet of guillemots at the Naked Island group declined following EVOS, the relative contribution of EVOS and the Pacific Decadal Oscillation shift to those changes remains unresolved.

Top-down factors, such as predation, may also be limiting the recovery of the Pigeon Guillemot population in PWS. Potential predators of guillemots and their nest contents that are common throughout the Sound include Bald Eagles (*Haliaeetus leucocephalus*), Peregrine Falcons (*Falco peregrinus*), Glaucous-winged Gulls (*Larus glaucescens*), Black-billed Magpies (*Pica hudsonia*), Northwestern Crows (*Corvus caurinus*), Common Ravens (*Corvus corax*), river otters (*Lontra canadensis*), and American mink (*Neovison vison*) (Oakley and Kuletz 1979, Ewins 1993, Hayes 1995). In particular, there is considerable evidence that mink predation on guillemot nests increased dramatically at the Naked Island group during the decade following EVOS (Hayes 1995, Oakley and Kuletz 1996, Golet et al. 2002).

Mink are largely nocturnal, semi-aquatic, generalist predators that are native in Alaska and to the mainland and nearshore islands of PWS. Mink are less likely to occur on isolated offshore islands (Banks et al. 2008), but they are capable of open-water crossings of at least 4 km (Fleming and Cook 2010). There is documentation that mink have been introduced by federal and state agencies to at least one remote island in Prince William Sound where the species did not naturally occur (i.e., Montague Island) in order to provide a harvestable population of furbearers (Paul 2009). In addition, there is evidence of undocumented introductions of mink to islands in Prince William Sound by fox farmers (Lethcoe and Lethcoe 2001, Fleming and Cook 2010) and fur trappers (R. Ellis, USDA-Wildlife Services, pers. comm.) in order to establish new harvestable populations. The introduction and range expansion of mink has been documented to cause rapid population declines in a variety of ground-nesting birds (Cairns 1985, Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, Banks et al. 2008), small mammals, and amphibians (Banks et al. 2008), and potentially inter-tidal communities as well (Delibes et al. 2004), especially on islands (Banks et al. 2008). The natural distribution of mink on the more isolated, offshore islands in PWS is largely unknown, as trapping of furbearers by non-Native Alaskans began there more than two centuries ago and the Sound supported fur farms for more than 50 years during the first half of the 20th Century.

The majority of the data on population size, nesting success, and diet of Pigeon Guillemots in PWS comes from studies conducted at the Naked Island group over 13 nesting seasons during the period 1978 – 1999. This is because the Naked Island group has traditionally supported an order of magnitude higher (Sanger and Cody 1994) nesting densities than the rest of PWS. Although the Naked Island group comprises only about 2% of the total shoreline within PWS, about one quarter of all the breeding guillemots in the Sound were found along the shoreline of these islands in 1989, after EVOS (McKnight et al. 2008). Studies of Pigeon Guillemot nesting ecology have been conducted on only one other island in PWS (Jackpot Island), and only for four nesting seasons (Golet et al. 2002). Consequently, available data on the potential factors limiting recovery of the PWS population of Pigeon Guillemots, such as food availability and nest predation, are largely limited to the Naked Island group. No intensive research on Pigeon Guillemots nesting on the Naked Island group has been conducted since 1999, however, and there has been no evidence of direct exposure of guillemots to residual oil from the EVOS since 2000 (B. Ballachey, U.S. Geological Survey, pers. comm.).

In response to the lack of current information on the breeding population size of Pigeon Guillemots at the Naked Island group, as well as mechanisms limiting population recovery in the aftermath of EVOS, I studied the nesting ecology, diet, and nesting success of guillemots on these islands during 2007 and 2008. My first objective was to assess the relative importance of the two hypothesized limiting factors for recovery of the Pigeon Guillemot breeding population on the Naked Island group, namely availability of schooling forage fish and nest predation. I used data on guillemot population trends, the presence or absence of mink, the contribution of predation to egg and chick mortality, changes in guillemot nesting habitat, and availability of schooling forage fish at the Naked Island group and in surrounding areas. My second objective was to compare the population size, population trend, and nesting distribution of Pigeon Guillemots on the Naked Island group to the remainder of PWS. This comparison was undertaken to test the hypothesis that limiting factors for recovery of the guillemot population differed between the Naked Island group and other areas of the Sound. In order to determine population trends, I used data on the density of Pigeon Guillemots reported in previous studies by Irons et al. (2000) and McKnight et al. (2008), as well as population and group size data reported by Sanger and Cody (1994), in comparison with similar data collected in 2008 as part of the present study. My study was designed to provide crucial information for designing and implementing effective restoration actions for Pigeon Guillemots in PWS in the aftermath of EVOS.

LITERATURE CITED

Agler, B. A., S. J. Kendall, D. B. Irons, and S. P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. Waterbirds 22:98-103.

Ainley, D. G., and T. J. Lewis. 1974. The history of Farallon Island marine bird populations, 1854-1972. Condor 76:432-446.

Anderson, P. J., J. E. Blackburn, and B. A. Johnson. 1997. Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. Pages 531-543 *in* Forage Fishes in Marine Ecosystems. Proceedings of an International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No.97-01. Fairbanks, AK.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117-123.

Anthony, J. A., D. D. Roby, and K. R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248:53-78.

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

BirdLife International. 2009. Species factsheet: *Cepphus columba*. Downloaded from http://birdlife.org on 5/1/2010.

Brown, E. D. 2003. Stock structure and environmental effects on year class formation and population trends of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska. Ph.D. dissertation, University of Alaska Fairbanks, Fairbanks, AK.

Brown, E. D., and M. G. Carls. 1998. Pacific herring. Restoration Notebook. *Exxon Valdez* Oil Spill Trustee Council. Anchorage, AK.

Cairns, D. K. 1985. Ermine visitation to Black Guillemot colonies in northeastern Hudson Bay. Condor 87:144-145.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Delibes, M., M. Clavero, J. Prenda, M. D. C. Blázquez, and P. Ferreras. 2004. Potential impact of an exotic mammal on rocky intertidal communities of northwestern Spain. Biological Invasions 6:213-219.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). *in* A. Poole, and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

_____. 2010. *Exxon Valdez* oil spill restoration plan. Update on injured resources & services. May 2010. Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Fleming, M. A., and J. A. Cook. 2010. MtDNA and microsatellite DNA provide evidence of fur farm ancestry for mink populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project 070853. Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7:1-21.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on Pigeon Guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-145.

Hayes, D. L. 1995. Recovery monitoring of Pigeon Guillemot populations in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Unpubl. Report, Anchorage, AK.

Hovey, A. K. 2002. Effects of diet and crude oil ingestion on growth and biochemistry of captive-reared pigeon guillemots (*Cepphus columba*). Unpubl. M.S. Thesis, Oregon State University, Corvallis, OR.

Irons, D. B., S. J. Kendall, W. P. Erickson, L. L. McDonald, and B. K. Lance. 2000. Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska. Condor 102:723-737.

Jewett, S. G., W. P. Taylor, W. T. Shaw, and J. W. Aldrich. 1953. Birds of Washington State. University of Washington Press, Seattle, WA.

Lethcoe, J., and N. Lethcoe. 2001. A history of Prince William Sound, Alaska. 2nd edition. Prince William Sound Books, Valdez, AK.

Litzow, M. A., J. F. Piatt, A. K. Prichard, and D. D. Roby. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286-295.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1977. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079.

Marty, G. D. 2008. Effects of the *Exxon Valdez* oil spill on Pacific herring in Prince William Sound, Alaska. Pages 925-932 *in* R. T. D. Giulio, and D. E. Hinton, editors. Toxicology of fishes. CRC Press, Boca Raton, FL.

Marty, G. D., M. S. Okihiro, E. D. Brown, D. Hanes, and D. Hinton. 1999. Histopathology of adult Pacific herring in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Canadian Journal of Fisheries and Aquatic Sciences 56:419-426.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Murphy, S. M., R. H. Day, J. A. Wiens, and K. R. Parker. 1997. Effects of the *Exxon Valdez* oil spill on birds: Comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299-313.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Oakley, K. L., and K. J. Kuletz. 1979. Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot. U.S. Fish and Wildlife Service, Office of Special Studies, Anchorage, AK.

_____. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:759-769.

Paul, T. 2009. Game transplants in Alaska. Technical bulletin No. 4, second edition. Alaska Department of Fish and Game, Juneau, AK.

Piatt, J. F., and R. G. Ford. 1996. How many seabirds were killed by the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:712-719.

Piatt, J. F., D. W. Macdonald, C. J. Lensink, W. Butler, M. Kendziorek, and D. R. Nysewander. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107:387-397.

Romano, M. D., J. F. Piatt, and D. D. Roby. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. Waterbirds 29:407-414.

Rosen, D. A. S., and A. W. Trites. 2000. Pollock and the decline of Steller sea lions: testing the junk food hypothesis. Canadian Journal of Zoology 78:1243-1250.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

CHAPTER 2

FACTORS LIMITING POPULATION RECOVERY OF PIGEON GUILLEMOTS IN PRINCE WILLIAM SOUND, ALASKA: TOP-DOWN VS. BOTTOM-UP CONSTRAINTS

Kirsten S. Bixler[1], Daniel D. Roby[1], and David B. Irons[2]

[1]U.S. Geological Survey-Oregon Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University,
Corvallis, OR 97331 USA

[2]U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road,
Anchorage, AK 99503 USA

ABSTRACT

The Pigeon Guillemot (*Cepphus columba*) is now the only species of marine bird in Prince William Sound (PWS), Alaska that is listed as "not recovering" on the *Exxon Valdez* Oil Spill (EVOS) Trustee Council's Injured Resources List and has shown no sign of population recovery 20 years after the spill. The guillemot population in PWS has gradually declined since EVOS and, although there is no longer evidence that guillemots are negatively affected by residual oil from EVOS, the population is now about half its post-spill size. Our study objective was to test two competing hypotheses for the lack of population recovery in Pigeon Guillemots at the Naked Island group, historically the highest density breeding area for guillemots in PWS. We investigated the availability of preferred guillemot prey and predation on guillemot nests. The prevalence of schooling forage fish in the diet of Pigeon Guillemots at the Naked Island group has not recovered to pre-spill levels since EVOS. However, there is evidence that the abundance of forage fish near the Naked Island group was higher in 2008 than during the 1990s. The guillemot population at the Naked Island group, where mink are present, declined by 12% per annum between 1990 and 2008, whereas at the nearby mink-free Smith Island group guillemot numbers were stable. Rates of egg and chick mortality at the Naked Island group were high during this period and most of this mortality could be attributed to mink predation. The weight of evidence indicates that predation by mink is now the primary limiting factor for guillemot reproductive success and population recovery at the Naked Island group.

INTRODUCTION

The Pigeon Guillemot (*Cepphus columba*) is a piscivorous seabird that has declined by about 47% since the 1989 breeding season, immediately following the *Exxon Valdez* oil spill (EVOS) in Prince William Sound (PWS), Alaska (McKnight et al. 2008). A portion of this decline is attributable to chronic exposure to weathered crude oil during the decade following the spill (Seiser et al. 2000, Golet et al. 2002). Although there is no longer evidence that guillemots are exposed to residual oil from EVOS (B. Ballachey, U.S. Geological Survey, pers. comm.), the population in PWS continues to decline (McKnight et al. 2008). The Pigeon Guillemot is now the only species of marine bird in PWS that is listed as "not recovering" on the *Exxon Valdez* Oil Spill Trustee Council's Injured Resources List (*Exxon Valdez* Oil Spill Trustee Council 2009). Our objective in this study was to identify the primary factor now limiting Pigeon Guillemot population recovery at the Naked Island group, the most important historical breeding area for guillemots in PWS (Sanger and Cody 1994). We investigated the two current, most prominent hypotheses for the lack of guillemot recovery at the Naked Island group: availability of prey and nest predation. The results of this study will inform the selection of a preferred restoration action for the Pigeon Guillemot in PWS.

The grounding of the T/V *Exxon Valdez* in March of 1989 resulted in at least 44 million liters of Prudhoe Bay crude oil spreading across central and southwestern

PWS, and the immediate mortality of from 500 to 1,500 Pigeon Guillemots in the Sound (Piatt et al. 1990). There was an estimated population of 4,000 breeding Pigeon Guillemots remaining in PWS after EVOS in 1989 (Klosiewski and Laing 1994). At that time, about one quarter of all guillemots nesting along the shoreline of the Sound was at the Naked Island group. Immediately following the spill, guillemots declined more along the oiled shoreline in PWS than along the un-oiled shoreline (Oakley and Kuletz 1996, Irons et al. 2000). In addition, elevated levels of hepatic cytochrome P4501A in Pigeon Guillemots from PWS indicated that even a decade after the spill, individuals were still exposed to residual oil (Golet et al. 2002). By 2004, however, there was no longer evidence of direct oil exposure for guillemots in PWS (B. Ballachey, U.S. Geological Survey, pers. comm.).

One proposed explanation for the continued lack of recovery of Pigeon Guillemots in PWS is a reduction in the availability of schooling forage fishes as prey for guillemots, either due to long-term effects of EVOS, residual oil from the spill, or a climatic regime shift to unfavorable ocean conditions that was un-related to the spill (Golet et al. 2002). The decline in numbers of Pigeon Guillemots in PWS apparently began before the EVOS, and has been linked to changing marine communities associated with a shift in the Pacific Decadal Oscillation in 1976 (Agler et al. 1999, Golet et al. 2002). This shift to a positive Pacific Decadal Oscillation was a widespread climatic phenomenon in the North Pacific that was associated with a long-term reduction in schooling forage fishes (i.e., herring [*Clupea pallasi*], capelin [*Mallotus villosus*]) in the northern Gulf of Alaska and subsequent population declines of multiple seabird species (Francis et al. 1998, Anderson and Piatt 1999). Regardless of the cause, the proportion of schooling forage fish in the diet of guillemots at the Naked Island group declined following the oil spill, and the proportion of this prey type in nestling diets is positively correlated with chick growth rates and overall guillemot reproductive success (Golet et al. 2002).

In addition to changes in availability of prey for guillemots in the aftermath of the spill, there is also evidence for increased predation rates on guillemot nests at the Naked Island group (Hayes 1996, Oakley and Kuletz 1996, Golet et al. 2002). Known nest predators for Pigeon Guillemots at the Naked Island group include avian species such as Bald Eagles (*Haliaeetus leucocephalus)*, Peregrine Falcons (*Falco peregrinus)*, Glaucous-winged Gulls (*Larus glaucescens)*, Black-billed Magpies (*Pica hudsonia)*, Northwestern Crows (*Corvus caurinus)*, and Common Ravens (*Corvus corax*); and mammalian predators such as the northern river otter (*Lontra canadensis)*, and American mink (*Neovison vison)* (Oakley and Kuletz 1979, Hayes 1996, Oakley and Kuletz 1996). In particular, mink predation rates on guillemot nests increased appreciably at the Naked Island group during the 1990s (Hayes 1996, Oakley and Kuletz 1996, Golet et al. 2002).

In this study, we investigated the potential factors that may currently preclude population recovery of Pigeon Guillemots at the Naked Island group: food availability (bottom-up control) and nest predation (top-down control). To test these competing hypotheses, we collected data on numbers, distribution, and habitat use of nesting guillemots; guillemot nesting success and factors causing guillemot nest failure; guillemot diet composition and the abundance of schooling forage fishes; and the presence or absence of mink on the Naked Island group and other islands in central PWS, specifically the Smith Island group to the south of the Naked Island group and Fool Island to the west. These two areas were selected for comparison with the Naked Island group because guillemots have historically nested on these islands and mink have not been reported from either island. Our objective was to identify the primary factor currently limiting population recovery of Pigeon Guillemots at the Naked Island group through a "weight of evidence" approach, and to assess whether management actions can be implemented that would contribute to Pigeon Guillemot recovery over 20 years after the *Exxon Valdez* oil spill.

METHODS

Study Area

Prince William Sound is a sub-arctic, inland sea connected to the Gulf of Alaska. The Sound is approximately 10,000 km^2 in area and is bounded by the Chugach and Kenai mountains (Figure 2.1; Niebauer et al. 1994). The terrestrial vegetation at sea level is dominated by spruce-hemlock forest (Cooper 1942). The Sound is adjacent to the relatively shallow (< 200 m) continental shelf of the northern Gulf of Alaska, with which water exchanges primarily through Montague Strait and Hinchinbrook Entrance (Niebauer et al. 1994, Vaughan et al. 2001). PWS is a complex fjord estuarine system with about 5,000 km of coastline, high levels of freshwater input, and bathymetry ranging from shallow glacial moraines and tidal flats to deep fjords and basins (maximum depth > 800 m; (Niebauer et al. 1994, Vaughan et al. 2001). Water circulation is generally cyclonic, but wind and precipitation cause significant deviations (Vaughan et al. 2001). Productivity in PWS is affected by exchange of water with the Gulf of Alaska, which can influence inflow, outflow, and retention of phytoplankton, zooplankton, and planktonic fish larvae (Brown et al. 1999, Kline 1999, Eslinger et al. 2001, Norcross et al. 2001, Vaughan et al. 2001).

Pigeon Guillemots are distributed throughout PWS during the breeding season, which extends from late May to late August. The Naked Island group, our primary study area, includes three main islands; Naked, Storey, and Peak. We collected data on numbers of Pigeon Guillemots at the Naked Island group and the Smith Island group (Smith Island and Little Smith Island; ~10 km south of the Naked Island group) in 2008 and compared these results to counts conducted in the same areas during 1990-1996 (Oakley and Kuletz 1996, Golet et al. 2002) and 2007.

Guillemot prey items were identified at nests at the Naked Island group and at Fool Island (approximately ~25 km to the west of the Naked Island group) in 2008, and compared with diet composition data collected at Naked Island during 1979-1981, 1989-1990, and 1994-1999 (Golet et al. 2000, Golet et al. 2002). Studies of guillemot nesting ecology have not previously occurred on Fool Island, but the island supported the highest known nesting density of guillemots in PWS in 2007-2008.

Aerial surveys for schooling forage fishes (herring, sand lance) were conducted at the Naked Island group and the Smith Island group in 2008, and compared with similar survey data collected during 1998 and 1999 (Brown and Moreland 2000, Ainley et al. 2003, Suryan et al. 2006). Beach seining as a means to assess forage fish availability was conducted at three sites on Naked Island in 2008, and compared with beach seine data collected at the same sites in 1996 and 1997 (G. Golet, U.S. Fish and Wildlife Service, unpubl. data).

Pigeon Guillemot Population Size

Pigeon Guillemot numbers were assessed along the shorelines of Naked, Storey, Peak, Smith, and Little Smith islands by means of nearshore boat-based surveys (Figure 2.1). Surveys were conducted at speeds of 10 to 20 km h^{-1} from either 3.7-m inflatable boats or 7.7-m hard-hulled skiffs maintained at a distance of 50 m to 100 m from shore using standard U.S. Fish and Wildlife Service methods (Irons et al. 1988). Two observers counted Pigeon Guillemots within 100 m on either side of, ahead of, and above the vessel. Guillemots on shoreline rocks and cliffs were counted as well. Surveys were limited to periods of good conditions for observation, when wave heights were less than 0.6 m, but usually surveys were conducted when wave heights were less than 0.3 m. Data collection was centered on the egg-laying stage of the nesting cycle and early morning high tides when guillemot colony attendance is least variable (Vermeer et al. 1993a). Guillemot surveys were conducted between 0400 and 1000 hours during the last week of May and the first week of June.

Presence/Absence of Mink

To assess whether mink were present on Naked, Storey, Peak, Smith, Little Smith, Fool, and Seal islands in central PWS (Figure 2.1), we set Oneida Victor® Conibear® 110 and 120 traps baited with herring and ground beaver castor lure inside black plastic mail tubes just above high tide line along the shoreline. Traps were set at an average frequency of 1.5 traps km^{-1} of shoreline on each island (range = 0.5 to 3.3 traps km^{-1}; Table 2.1). Traps were checked once per day or as weather conditions permitted. We assumed that an island was mink-free for the duration of the study if no mink were captured during the trapping effort, which was conducted between 28 April and 28 May 2008.

Aerial Surveys for Schooling Forage Fish

Using aerial surveys, we measured the relative abundance of surface-schooling forage fishes in central Prince William Sound. Surveys were conducted by Dr. E. Brown who conducted similar surveys in 1998 and 1999 (Brown and Moreland 2000), using a float plane traveling approximately 204 km h^{-1} and at a 30° banking angle. The target survey altitude was 305 m (actual altitude range = 274 to 366 m), resulting in a transect width of about 455 m (range = 410 to 501 m). Each survey included a strip transect < 1 km from shore encircling Naked, Peak, Storey, Smith, and Little Smith islands (Figure 2.1). Transects ran parallel to shore, although the pilot circled as necessary to provide additional time for data collection. The surveyor counted schools of forage fish near the surface and measured the horizontal surface area per school using a calibrated cylinder. To ensure that schools within approximately the upper 20 m of the water column were visible, surveys were conducted only when visibility conditions were optimal (i.e., high cloud cover, little or no precipitation, no white capping on water surface). The effort per survey was similar across the three years when aerial survey data were collected (1998, 1999, 2008), although the number of surveys per year differed among years (Table 2.2). Aerial surveys were conducted during the Pigeon Guillemot chick-rearing period in July and August of each of the three survey years.

Aerial surveys are the best available method for assessing the relative abundance of both juvenile herring and sand lance in PWS (Brown and Moreland 2000). Guillemots

(Kuletz 1983), sand lance (Robards and Piatt 1999), and juvenile herring (Carlson 1980, Norcross et al. 2001) are all associated with nearshore water (< 1 km from shore). At Naked Island, most (> 75%) sand lance transported by guillemots to their nests were obtained in water less than 15 m deep (Kuletz 1983). Acoustic surveys indicate that the majority of schools of juvenile herring in nurseries in PWS were located within 20 m of the surface (Brown and Moreland 2000). Aerial surveys sample both shallow and surface water where a large portion of the juvenile herring and sand lance population tends to reside, areas inaccessible to boat-based bio-acoustic surveys (Brown and Moreland 2000). Aerial surveys are also immune to bias caused by vertical and horizontal vessel avoidance by herring (Misund and Aglen 1992, Fréon et al. 1993, Misund et al. 1996, Churnside et al. 2003) and sand lance (Pitcher and Wyche 1983, Logerwell and Hargreaves 1997). Aerial surveys are also capable of sampling a relatively wide transect swath (> 400 m) across the entire study area within hours. The aerial survey data provide an index of herring and sand lance density and cannot be converted to a biomass estimate without a measure of the depth distribution for these species. Our index does not include schools > 20 m in depth, and thus underestimates what is potentially available to foraging guillemots.

Beach Seine Sampling for Forage Fish

We measured the relative abundance of nearshore forage fish by seining at three beaches on Naked Island during the 2008 nesting season (Figure 2.1). The three beaches (Fuel, Inside Outside, and McPherson North) were selected because they were seined in 1996 and 1997 (G. Golet, U.S. Fish and Wildlife Service, unpubl. data). These sites were originally selected in 1996 because they were considered suitable for seining (i.e., sand or cobble beach with a shallow slope and minimal current) and because of their proximity to guillemot colonies during the mid-1990s. We calculated the proportion of the total catch that consisted of each prey type (percent species composition) and catch per unit effort (CPUE) of individuals of each prey type in seine hauls conducted in 2008, and compared these results to the comparable data collected in 1996 and 1997.

Beach seining is an effective method to sample relative abundance of nearshore forage fishes (Cailliet et al. 1986, Litzow et al. 2004). At Naked Island, Kuletz (1983) found that about 70% of all prey items and > 90% of all schooling prey items that Pigeon Guillemots delivered to nests were retrieved from shallow, nearshore dives (< 25 m in depth, < 600 m from shore). Further, the species composition of beach seine catches has been shown to be correlated with the diet composition of guillemot chicks, as well as measures of reproductive success (Litzow et al. 2000, Litzow and Piatt 2003).

We seined using a 37 m long variable-mesh net, 0.5 m wide at the ends and 2.4 m wide in the center, with a 6-mm mesh bunt. The seine was set parallel to shore using a 3.7-m inflatable boat. Sampling occurred opportunistically through the study period, within 1.5 h of low tide. We seined between 4 June and 17 August 2008 (n = 14 seine samples per site), during the guillemot chick-rearing period; seining in 1996 (n = 6 samples) and 1997 (n = 2 samples) also occurred during this period.

All fish captured in beach seines were separated by species, counted, and then species grouped into larger prey categories consisting of either schooling forage fishes (i.e., Pacific sand lance, Pacific herring, and smelt [Osmeridae; i.e., capelin, surf smelt, and rainbow smelt]) or demersal fishes. The demersal fish category was further subdivided into two groups: (1) gadids (Gadidae; i.e., juvenile walleye pollock [*Theragra chalcogramma*], juvenile Pacific cod [*Gadus macrocephalus*], juvenile Pacific tomcod [*Microgadus proximus*]) and (2) "other," including pricklebacks (Stichaeidae), gunnels (Pholidae), ronquils (Bathymasteridae), sculpins (Cottidae), juvenile rockfish (*Sebastes* spp.), juvenile greenling (*Hexagrammos* spp.), and juvenile salmon (*Oncorhynchus* spp.).

Guillemot Diet Composition

We determined the diet composition of Pigeon Guillemots during the chick-rearing period by identifying prey being transported to the nest site by adults provisioning young. Observers in either a small anchored skiff or an on-shore blind identified individual prey items using binoculars or spotting scopes. The guillemot prey items, which are held crosswise in the bill, were identified to species, if possible, but otherwise the lowest possible taxonomic group. As with the beach seine samples, identified guillemot prey items were classified as either schooling forage fish (sand lance, herring, and smelt) or demersal fish (pricklebacks, gunnels, sculpins, gadids, etc.). A minimum of 10 prey items were identified at each active nest ($\bar{x} =$ 33.1 prey items; range = 10 to 163). Observations were conducted at each nest over multiple days (= 5 sampling days; range = 2 to 14) to avoid bias due to short-term prey preferences and to represent chick diet composition over a range of chick ages (8 to 30 days post-hatch). Data from 2008 were compared to previously published data collected during 1979-1981, 1989-1990, and 1994-1999 (Golet et al. 2000; Golet et al. 2002).

Growth and Condition of Guillemot Nestlings

We measured total body mass (g) and flattened wing chord (mm) of each accessible guillemot nestling at least twice during the linear phase of growth, generally between 8 and 18 days post-hatch (Emms and Verbeek 1991, Ewins 1993, Golet et al. 2000), at the Naked Island group in 2008 (Figure 2.1). Our procedure was the same as that followed during 1978-1981, 1989-1990, and 1994-1998 at the Naked Island group (Golet et al. 2000, Golet et al. 2002). For nestlings measured at least twice between ages 8 and 18 days post-hatch during 2008, growth rates were calculated as Δ mass (g) day^{-1}. For nests where nestling age was not known, age was estimated based on flattened wing chord and the regression of wing chord on age based on known-age chicks measured during earlier studies of guillemots on the Naked Island group (Golet et al. 2000, Golet et al. 2002):

$$\text{age} = (\text{wing chord (mm)} + 1.179084) / 4.435389$$

Because the sample size of nestling growth rates available in 2008 was small, use of inferential statistics to compare chick growth rates among years was precluded. Instead, an index of chick condition was created after Benson et al. (2003) to compare the condition of chicks in 2008 with those measured in previous years. A single measure of chick condition (body mass and wing chord) was randomly selected for each chick for which growth rates were calculated between 1978 and 2008. Chicks from both the Naked Island group and Fool Island that were only measured once during the linear growth phase (due to either chick death or our inability to recapture chicks) were added to the sample from 2008.

Egg and Chick Mortality

Contents of active Pigeon Guillemot nests were monitored during the chick-rearing stage through either fledging or nest failure at the Naked Island group and at Fool Island in 2008 (Figure 2.1). Nest contents were checked a minimum of two times and nest activity (prey deliveries) monitored at least every five days during the nestling period; these observations were used to calculate overall chick mortality rates. Eggs or chicks were considered depredated if they disappeared prior to hatching/fledging or if found with signs of predation (e.g., puncture wounds, partially consumed). The cause of nest failure was recorded as “other” if chicks were found dead in the nest crevice without signs of predation. Chicks were considered fledged if they survived in the nest until at least 30 days post-hatch. Chicks were removed from the analysis if the entire nest crevice could not be searched. Similar data on guillemot nesting success were collected during 13 years between 1978 and 1999 at the Naked Island group, with the difference that previous studies monitored nests during the egg stage as well as the nestling stage and nest contents were checked at least every 5 days (Golet et al. 2000, Golet et al. 2002). Comparison of chick survival in 2008 to that in previous years was precluded by the small sample size (Hensler and Nichols 1981). In order to determine the primary factors responsible for egg and chick mortality at the Naked Island group and Fool Island, the present study reports causes of guillemot egg and/or chick mortality, as opposed to overall productivity (chicks fledged/egg laid) and rate of nest predation previously published by Golet et al. (2000, 2002).

Guillemot Nest Types

We described and classified the sites of active Pigeon Guillemot nests throughout the Naked Island group during the 2008 nesting season, regardless of accessibility to researchers (Figure 2.1). The nests were found by searching suitable nesting habitat, following adults transporting chick meals to their nest site, and opportunistically during collection of other data (e.g., marine bird censuses, shoreline habitat mapping, guillemot nest monitoring). We classified each active nest site into one of three nest types described by Oakley and Kuletz (1979) on the Naked Island group: (1) talus, (2) cliff face, and (3) cliff edge. The talus type was defined as a nest located amidst rocks or boulders at the base of or on a ledge of a cliff, and usually consisting of a nest chamber relatively close to the surface. The cliff face nest type was defined as a nest on a cliff, and varied from a narrow crack extending several meters into a cliff face to a narrow cliff ledge concealed by vegetation. Cliff edge nests were usually at the end of burrows in soil at the top of a cliff or steep rocky bank, often among tree roots and usually a meter or more deep. Comparable data on guillemot nest types were collected using the same methods across the Naked Island group during 1978 (Oakley and Kuletz 1979).

Statistical Analysis

We used multiple linear regression analysis to detect differences in guillemot population trends between islands with mink and those without mink (Ramsey and Schafer 2002). To meet assumptions of normality and equal variance, assessed using residual plots, the response variable (number of birds counted) was log transformed.

We used permutation tests (Ramsey and Schafer 2002) to compare the surface area density of fish (as measured during aerial surveys) between 1998-1999 and 2008 for both the Naked Island group and the Smith Island group and to compare these two island groups in 2008 because the data did not meet assumptions of parametric tests and our sample sizes were small. We used a Wilcoxon rank sum test with normal approximation and continuity correction (Ramsey and Schafer 2002), where sample sizes permitted, to compare the surface area density of fish between 1998 and 1999 for both island groups, as well as between island groups during 1998-1999.

To assess the spatial and temporal differences in composition and CPUE of fish caught per seine, we used two multivariate techniques. A one-way analysis of similarities (ANOSIM; Clarke 1993) was used to compare seine catches between months and years (1996 vs. 1997). A two-way ANOSIM (Clarke 1993) was used to compare seine catches between time periods (1996-1997 vs. 2008) and among the three seined beaches. We assessed the percent contribution of each fish category (schooling vs. demersal) to the dissimilarity of seine catches between 1996-1997 and 2008 using a similarity percentage breakdown analysis (SIMPER; Clarke and Warwick 2001).

Logistic regression was used to estimate the odds of a nest receiving a meal delivery of schooling fish (sand lance, herring, or smelt) between years and between locations (Naked Island group vs. Fool Island). A single measure of chick condition (body mass and wing chord) was randomly selected for each chick for which growth rates were calculated between 1978 and 2008. To maximize our sample size in 2008, we included data for chicks measured a single time. We regressed total body mass (g) on wing chord length (mm) for nestlings and then divided the residuals by predicted values to produce an index of guillemot chick condition expressed as a percentage of predicted body mass for each chick (Benson et al. 2003). A one-way analysis of variance was utilized to compare these chick condition indices, both spatially (Naked Island group vs. Fool Island) and temporally (1978-1981, 1989-1999, and 2008).

Due to small sample sizes, permutation tests were use to compare the overall egg/chick mortality, mortality caused by predation, and mortality due to other causes between years and locations. A Fisher's Exact test was used to compare the number of active guillemot nests at the Naked Island group that were assigned to each nest type category between 1978 and 2008 (Ramsey and Schafer 2002).

Differences in responses between groups were distinguished using two-sided tests. If directionality (i.e., greater or less than) of a difference was indicated in permutation or Wilcoxon Rank Sum tests, a one-sided test was used. We used the conventional *a priori* $\alpha = 0.05$. Results were considered statistically significant if $P \leq 0.05$ and suggestive if $0.05 < P \leq 0.10$. We present global R-statistics and/or R-statistics for ANOSIM comparisons of seine catches between years, months, and beaches, that range from -1 to +1 (no separation to complete separation of groups). Multivariate analysis was completed using Primer-E software (Clarke and Green 1988). All other analyses were conducted using SAS 9.2 software (SAS Institute 2008).

RESULTS

Guillemot Population Trends

In 2008, only 17 Pigeon Guillemot nests were found at the Naked Island group: eight at Storey Island, two at Peak Island, and seven at Naked Island. Because guillemot nests are cryptic, the number of nests found is a minimum estimate of the number of active nests present. A small number of additional nests may not have been discovered prior to fledging or failure. We estimate that the actual number of Pigeon Guillemot nests at the Naked Island group in 2008 was likely between 17 and 22 nests (0.16 to 0.21 nests/km of shoreline). Although the total number of guillemot nests across the Naked Island group in years prior to 2008 is unknown, 124 active nests within 19 colonies across Naked and Storey islands were recorded in 1997 (G. Golet, U. S. Fish and Wildlife Service, unpubl. data). Only four active guillemot nests were found within this same area in 2008, a 96.8% decline from 1997.

The total number of active Pigeon Guillemot nests at Fool Island was estimated to be between 18 and 23 nests in 2008 (18 nests found). Although the number of nests found was similar, the density of nests at Fool Island (10 to 12.78 nests/km of shoreline) was more than 60 times greater than that at the Naked Island group in 2008.

Average trapping effort was 126 trap nights per island at islands where mink were captured (range = 14 to 323 trap nights) and 165 trap nights per island at islands where mink were not captured (range = 90 to 300 trap nights). Mink were captured at Naked, Storey, and Peak islands in 2008 (n = 323, 42, and 14 trap nights respectively; Table 2.1). The average trapping effort for each mink captured was 14.7 trap nights at Naked Island, 21.0 trap nights at Storey Island, 2.8 trap nights at Peak Island. No mink were captured at Smith, Little Smith, Fool, or Seal islands in 2008 (n = 300, 90, 174, and 96 trap nights, respectively), and we therefore assumed that mink were not present on these islands.

The change in median guillemot population size at islands with mink (Naked Island group) between 1990 and 2008 was significant ($t = -19.83$, $P < 0.0001$), and guillemot numbers declined by an estimated 11.8% per year (95% CI = -13.0% to -10.7%; Figure 2.2). The count of guillemots at the Naked Island group declined from 1,124 to 101 individuals (- 91%) between 1990 and 2008. There was no evidence of a change in median guillemot population size at the Smith Island group, islands near the Naked Island group without mink ($t = -0.52$, $P = 0.605$; estimated annual population decline = - 0.4%, 95% CI = -2.0% to 1.2%). The estimated annual decline in median guillemot population size at the Naked Island group (islands with mink) was significantly greater than at the Smith Island group (mink-free islands; $t = 15.03$, $P = 0.0001$).

Abundance of Guillemot Prey

There was no evidence of a difference between 1998 and 1999 in surface area density of schooling fish (based on aerial surveys) at either the Naked Island group (z = 0.99, P = 0.323) or the Smith Island group (z = - 0.38, P = 0.702) and data from these two years were combined in further analyses (Figure 2.3). At the Naked Island group, there was a highly significant increase (s = 62.0, P = 0.006) in the mean surface area density of schooling fish from 1998-1999 (mean = 18.0 m^2 km^{-2}; range = 0.3 to 104.9 m^2 km^{-2}) to 2008 (mean = 66.6 m^2 km^{-2}; range = 39.0 to 94.4 m^2 km^{-2}). In striking contrast, there was no statistical difference (s = 30.5, P = 0.726) in surface area density of schooling fish at the Smith Island group between 1998-1999 and 2008. At the Smith Island group, there was a mean surface area density of 41.0 m^2 km^{-2} of schooling fish during 1998-1999 (range = 0 to 146.5 m^2 km^{-2}) and a mean of 32.2 m^2 km^{-2} during 2008 (range = 0 to 66.9 m^2 km^{-2}). The surface area density of schooling fish at the Smith Island group was significantly greater than that at the Naked Island group during 1998-1999 (z = 1.90, P = 0.029). In 2008, although the mean surface area density of schooling fish at the Naked Island group was higher than at the Smith Island group, the difference was not significant (s = 13.0, P = 0.200).

A total of 6,465 fish were caught in 14 beach seine hauls completed in 2008; 787 fish were caught in eight beach seine hauls conducted during 1996 and 1997 (G. Golet, U.S. Fish and Wildlife Service, unpubl. data). There was no difference between 1996 and 1997 in catch composition (*R* = 0.07, *P* = 0.393) or CPUE (*R* = -0.12, *P* = 0.643), and data from these two years were combined in further analyses (Table 2.3). There were also no differences among months (June, July, and August) in either catch composition (global *R* = 0.02, *P* = 0.347) or CPUE (global *R* = -0.05, *P* = 0.698) for the two fish categories, and this explanatory variable was not included in further analyses.

Of all fish captured by seining during the two sampling periods, 6.4% were categorized as schooling fish and 93.6% were categorized as demersal fish. The majority (68.9%) of captured fish in the demersal category consisted of gadids. There was a significant difference among seining beaches in both catch composition (global *R* = 0.21, *P* = 0.022) and CPUE (global *R* = 0.13, *P* = 0.058) of seine catches. The composition of catches at Fuel Beach was different from that at Inside Outside Beach (*R* = 0.45, *P* = 0.025) and McPherson North Beach (*R* = 0.17, *P* = 0.031). CPUE at Fuel Beach was also different from that at Inside Outside Beach (*R* = 0.34, *P* = 0.077), but not that at McPherson North Beach (*R* = 0.09, *P* = 0.126). We found no evidence of a difference between Inside Outside Beach and McPherson North Beach in either catch composition (*R* = -0.01, *P* = 0.436) or CPUE (*R* = 0.004, *P* = 0.43). The average composition of fish captured at Fuel Beach was 21.3% schooling fishes (range = 0 to 66.2%), 19.9% gadids (range = 0 to 78.0%), and 58.8% other demersal fishes (range = 16.3 to 100%). The average composition of fish at both other beaches was 19.0%

schooling fishes (range = 0 to 92.3%), 41.1% gadids (range = 0 to 91.4%), and 39.9% other demersal fishes (range = 7.5 to 100%). At Fuel Beach, the average CPUE was 19.0 schooling fish (range = 0 to 103), 21.1 gadids (range = 0 to 124), and 65.4 other demersal fishes (range = 4 to 311). At both other beaches, the average CPUE was 23.0 schooling fishes (range = 0 to 93), 404.3 gadids (range = 0 to 3191), and 126.5 other demersal fishes (range = 1 to 772).

When both seining site and sampling period (1996-1997 vs. 2008) were considered together, there was suggestive evidence of a difference in CPUE between seining sites (global R = 0.15, *P* = 0.10). We did not detect a statistical difference in CPUE between sampling periods (global R = 0.10, *P* = 0.185), although the average total CPUE was 4.69 times higher in 2008 than during 1996-1997. During 1996-1997, the average CPUE was 13.4 schooling fish (range = 0 to 85), 55.1 gadids (range = 0 to 417), and 29.9 other demersal fishes (range = 4 to 145). In 2008, the average CPUE was 25.4 schooling fishes (range = 0 to 103), 302.7 gadids (range = 0 to 3,191), and 133.7 other demersal fishes (range = 1 to 772). The average total CPUE increased from 98.4 fish (range = 7 to 456) during 1996-1997 to 461.8 fish (range = 1 to 3,968) in 2008. When both explanatory variables were included in the analysis there was evidence of a difference in catch composition among seining sites (global R = 0.20, *P* = 0.050), but not sampling periods (global R = 0.15, *P* = 0.114). The average composition of fish captured in 1996-1997 was 18.9% schooling fishes (range = 0 to

92.4%), 18.9% gadids (range = 0 to 91.4%), and 62.2% other demersal fishes (range = 7.6 to 100%). The average composition of fish in 2008 was 21.4% schooling fishes (range = 0 to 86.1%), 42.1% gadids (range = 0 to 87.3%), and 36.5% other demersal fishes (range = 7.6 to 100%).

Guillemot Diet Composition

There was no evidence of a difference between 2008 and 1989-1999 in the odds that a Pigeon Guillemot delivered a schooling fish to its nest at Naked Island ($\chi^2 = 0.25$, $P = 0.620$; $\bar{x} = 1.3$, 95% CI = 0.4 to 4.2; Figure 2.4). The odds that a Pigeon Guillemot at Naked Island delivered a schooling fish to its nest during 1979-1981 (pre-EVOS) were about 3.4 times greater than during 1989-1999 (95% CI = 2.2 to 5.3 times; $\chi^2 = 29.10$, $P < 0.001$) and about 4.6 times greater than during 2008 (95% CI = 1.5 to 14.0 times; $\chi^2 = 6.98$, $P = 0.008$). Over the past three decades, the average percentage schooling forage fish of all fish delivered by adults to nests at Naked Island declined from 46.7% (95% CI = 40.1% to 53.5%) in 1979-1981 to 20.5% (95% CI = 15.3% to 26.8%) during 1990-1999 and 16.2% (95% CI = 6.08% to 36.5%) in 2008.

The odds that a guillemot adult delivered a schooling fish to its nest at Fool Island in 2008 were about 7.2 times greater than at the Naked Island group in the same year (95% CI = 2.6 to 20.0 times; $\chi^2 = 14.45$, $P = 0.0001$; Figure 2.5). In 2008, only 12.8% of all fish delivered by adults to nests at the Naked Island group (including Peak and

Storey islands) were schooling fishes (95% CI = 5.7% to 26.5%). At Fool Island in 2008, 51.5% of all fish delivered by adults to nests were schooling fishes (95% CI = 39.5% to 63.3%).

Guillemot Chick Growth and Condition

The mean growth rate of guillemot chicks at the Naked Island group was 18.0 g/day in 2008, but the sample size was very small (n = 2, sd = 0.8). Mean chick growth rate during 1978-1981 was 20.0 g/day (n = 43, sd = 5.0, range in yearly means = 19.2 to 22.1 g/day), while mean chick growth rate during 1989-1998 was 17.9 g/day (n = 120, sd = 5.68, range in yearly means = 15.7 to 20.9 g/day; Golet et al. 2002). Golet et al. (2002) found suggestive evidence that chick growth rates at the Naked Island group during 1989-1998 were lower than during 1978-1981 ($U = 5$, $P = 0.089$). Although the sample size of chick growth rates in 2008 precluded any statistical comparisons, the average was within the post-spill range of yearly means and below the pre-spill range of yearly means.

There was no significant difference in the condition indices of guillemot chicks between the Naked Island group (n = 6) and Fool Island (n = 7) in 2008 (mean difference = 5.5, 95% CI = -18.8 to 29.8; $t = 0.58$, $P = 0.937$; Figure 2.6). There was no significant difference in the condition index of chicks from the Naked Island group in 2008 compared to chicks from the Naked Island group during 1989-1999 (mean = -

5.0, 95% CI = - 23.1 to 13.2; t = -0.71, P = 0.893) or during 1978-1981 (mean = 12.6, 95% CI = - 7.6 to 32.7; t = 1.62, P = 0.371). Similarly, there was no significant difference in chick condition indices between Fool Island chicks in 2008 and Naked Island chicks during either 1989-1999 (mean = - 10.4, 95% CI = - 27.3 to 6.4; t = -1.60, P = 0.379) or 1978-1981 (mean = 7.1, 95% CI = - 11.9 to 26.1; t = 0.97, P = 0.766). We found strong evidence, however, of a difference in chick condition index at the Naked Island group among the periods 1978-1981 (n = 22), 1989-1999 (n = 163), and 2008, and at Fool Island in 2008 ($F_{3, 197}$ = 7.60; $P < 0.0001$). This difference was due to the higher condition index of chicks at the Naked Island group during 1978-1981 compared to during 1989-1999 (mean = 17.5, 95% CI = 7.6 to 27.5; t = 4.58, $P < 0.0001$).

Guillemot Egg and Chick Mortality

The mortality rate of guillemot chicks at the Naked Island group in 2008 (n = 22 chicks monitored) was 31.8%. Most (86%; n = 6) of this chick mortality was due to predation. These results represent a minimum estimate of mortality for 2008 because they do not include mortality during the egg stage and, in several cases, the early chick-rearing stage. However, the percentage of all chicks that died due to predation in 2008 was similar to the mean percentage of chicks and eggs depredated during 1989-1999 and 14.2 times greater than the mean percentage of chicks and eggs depredated during 1978-1984. No dead adult guillemots were found in nests at Naked Island during 2008. There was no mortality of chicks (n = 7) or adults in nests at Fool Island in 2008.

Based on our analysis of data reported by Golet et al. (2000, 2002), there was suggestive evidence that the overall mortality of guillemot eggs and chicks on the Naked Island group increased from 1978-1984 to 1989-1999 ($S = 16.0$, $P = 0.08$; Figure 2.7). During 1978-1984 the mean mortality rate for guillemot eggs and chicks was 50.1% (range = 38.2% to 71.4%, n = 4 years) and during 1989-1999 the mean mortality rate was 66.3% (range = 45.8% to 93.4%, n = 7 years). For the period 1978-1984, egg and chick mortality rates due to predation (mean = 1.9%, range = 0.0% to 5.7%) was lower ($S = 10.0$, $P = 0.014$) than that due to other causes (mean = 48.2%, range = 36.4% to 65.7%). During 1989-1999, however, there was no evidence ($S = 61.0$, $P = 0.318$) of a significant difference between mortality rates caused by predation (mean = 38.0%, range = 22.0% to 60.5%) and other causes (mean = 28.3%, range = 12.5% to 41.5%). The predation rate on eggs and chicks increased significantly at the Naked Island group between 1978-1984 and 1989-1999 ($S = 10.0$, $P = 0.003$). The rate of egg and chick mortality due to other causes decreased significantly between 1978-1984 and 1989-1999 ($S = 37.0$, $P = 0.006$). The majority (56.6%) of all egg and chick mortality was due to predation during 1989-1999. Carcasses of adult guillemots that showed signs of having been depredated in the nest were first observed in 1996 (D. L. Hayes, U.S. Fish and Wildlife Service, unpubl.

data). During that breeding season, a dead adult was found in 5% of monitored nests (2 of 44 nests). Depredated adults were found in 0% (0 of 56 nests), 9% (6 of 66 nests), and 4% (2 of 49 nests) of monitored nests in 1997, 1998, and 1999, respectively (G. Golet, U.S. Fish and Wildlife Service, unpubl. data).

Guillemot Nest Type Use

The number of active guillemot nests at the Naked Island group declined dramatically between 1978 and 2008 (see above). Nevertheless, there was a proportionately much greater decline in the number of guillemot nests in the talus nest type compared to the cliff nest type ($P = 0.0008$; Table 2.4). There was also a proportionately greater decline in the number of nests in the cliff edge nest type compared to the cliff nest type ($P = 0.0013$). In 2008, no active nests were found in the talus nest type, whereas in 1978 24.7% of active nests were in the talus nest type. Of all active nests found in 2008 ($n = 17$), 11.8% were cliff edge nests, whereas in 1978 ($n = 146$ active nests), 39.7% were cliff edge nests. Finally, in 2008, 88.2% of active nests were the cliff nest type, whereas in 1978, only 35.6% were the cliff nest type.

DISCUSSION

The Pigeon Guillemot population at the Naked Island group continued to show no sign of recovery in 2008, 19 years after the *Exxon Valdez* oil spill. Instead, numbers of breeding guillemots at the Naked Island group have continued to decline, and are now at a very low level compared to either pre- or immediately post-EVOS. A portion of this population decline, which began prior to 1989, has been attributed to the 1976 shift in the Pacific Decadal Oscillation. Our study provided evidence that forage fish abundance near the Naked Island group is now greater than during the 1990s, although guillemot diet composition indicates that lower availability of high-lipid schooling fish, due either to oil effects or unrelated factors (i.e. Pacific Decadal Oscillation), may have continued to limit recovery in 2008, as demonstrated during the 1990s (Golet et al. 2000, Golet et al. 2002). However, our data suggest that mink predation currently limits the recovery of Pigeon Guillemots at the Naked Island group more than food availability.

Forage Fish Availability and Abundance

A greater proportion of high-lipid schooling forage fish in the diet of Pigeon Guillemot chicks has been correlated with higher nestling survival, higher productivity, higher chick growth rates (especially in beta chicks), and less brood reduction (Golet et al. 2000, Litzow et al. 2002). In these studies, the rate of delivery of prey to the nest and prey size did not vary, even with large shifts in abundance and availability of prey. This indicates that a higher percentage of low-lipid demersal prey in chick diets results in lower reproductive success for Pigeon Guillemots (the "junk food" hypothesis; Rosen and Trites 2000, Romano et al. 2006). Studies investigating the effects of low-lipid prey on other seabirds indicate that low-lipid diets result in smaller lipid reserves and elevated levels of corticosteroids that could potentially reduce survival of fledglings and adults (Kitaysky et al. 1999, Romano et al. 2006)

The proportion of schooling fish in chick diets and chick growth rates were lower during the 1990s compared to 1978-1981 (Golet et al. 2002). We demonstrated that the proportion of schooling fish in guillemot diets at the Naked Island group during 2008 had not recovered to pre-spill levels (1978-1981). We did not detect a difference in average chick condition index between 2008 and 1979-1981, however, likely due to both the weakness of this measure (Benson et al. 2003) and limited sample size in 2008. Mean chick condition index in 2008 was higher than during the 1990s, but the difference was not significant, again likely due to small sample sizes. Nevertheless, the percentage of schooling forage fish in guillemot chick diets and chick growth rates at the Naked Island group in 2008 (as well as during most of the 1990s) were higher than that documented in previous studies of guillemots at four locations outside Alaska (see Golet et al. 2000). At one of those locations, Ainley et al. (1990) documented a stable guillemot population during the six years when chick growth rates were calculated. This suggests that diet quality and growth rates of chicks at the Naked Island group during the 1990s and in 2008, while not as favorable as during 1978-1981, were not likely to have caused the drastic population declines observed since the spill. Availability of schooling prey was apparently greater at the Naked Island group during 1978-1981 than during the 1990s and 2008. At Jackpot Island

(Golet et al. 2002) and Fool Island (this study) in Prince William Sound and at inner Kachemak Bay in Cook Inlet, Alaska (Litzow et al. 2002) chick growth rates (where measured) and the percentage of schooling fish in chick diets were also relatively high, similar to that at the Naked Island group prior to the *Exxon Valdez* oil spill.

The overall beach seine CPUE was more than 4.5 times higher in 2008 than in 1996-1997, suggesting that guillemot prey abundance may be recovering following EVOS. Between 1996-97 and 2008, Pigeon Guillemot colonies adjacent to the beach seining sites disappeared and the total breeding population of guillemots on Naked Island declined by more than 90%. This strongly suggests that the availability and species composition of forage fish were not responsible for the dramatic declines in the guillemot breeding population at Naked Island. Our inability to detect a statistically significant difference in abundance of schooling or demersal forage fish between beach seines conducted in 2008 and in earlier study years was likely due to the small sample and high variability of seine catches.

Based on aerial surveys, we found strong evidence of an increase in surface area density of schooling forage fish from 1998-1999 to 2008 at the Naked Island group. The density of schooling fish remained stable, however, at the Smith Island group. The mean surface area density of schooling forage fish at the nearby Smith Island group (all three years) was significantly greater than the mean at the Naked Island group in 1998/1999, but significantly less than the mean at the Naked Island group in 2008. Although the apparent increase in abundance of schooling fish at the Naked Island group from 1998-99 to 2008 was not reflected in the diet composition of guillemot chicks in this area, it suggests that schooling forage fish stocks at the Naked Island group may be recovering from the low levels observed during 1998-99.

Mink Predation

There was a strong association between the presence/absence of mink at islands in central Prince William Sound and Pigeon Guillemot population trends between 1990 and 2008. Guillemots declined by nearly 12% per year at islands with mink (Naked Island group), but remained stable at mink-free islands (Smith Island group), suggesting that currently mink strongly limit population recovery at the Naked Island group. These different population trajectories between island groups with and without mink suggest that two potentially important limiting factors are unlikely to be the cause of continued guillemot population declines. First, both island groups were oiled following the *Exxon Valdez* oil spill (Neff et al. 1995). Second, if food availability were currently a limiting factor, we would expect a similar or lower density of schooling prey at the Naked Island group in 2008 compared to the late 1990s, rather than the significant increase observed (Figures 2.2 and 2.3). Differing guillemot population trends in relation to the presence or absence of mink were corroborated on a larger scale throughout western Prince William Sound. Between 1993 and 2008, the only observed increase in guillemot populations at high-density guillemot areas in western Prince William Sound occurred on islands where we confirmed the absence of mink: the Smith Island group (combined) and Seal Island (see Chapter 3).

High predation rates on guillemot (*Cepphus* spp.) nests have been attributed to a variety of predators, including Northwestern Crows (Emms and Verbeek 1989, Vermeer et al. 1993a), garter snakes (*Thamnophis elegans*; Emms and Verbeek 1989), raccoons (*Procyon lotor*; Vermeer et al. 1993a), ermine (*Mustela ermine*; Cairns 1985), and American mink (Nordström et al. 2003). Extensive predation of nesting adult guillemots by ermine (Cairns 1985), mink (Nordström et al. 2003), and raccoons (Vermeer et al. 1993b) has been documented as well. The magnitude of nest predation at guillemot colonies ranges from negligible (Oakley and Kuletz 1979, Ainley et al. 1990) to extremely high (57% of eggs and chicks; Vermeer et al. 1993a). The magnitude of impact to guillemot populations is particularly high when the predator is a non-native invasive species. For example, the range expansion of non-native mink (escaped from fur farms) coincided with the extirpation of Black Guillemots (*Cepphus grylle*) as a nesting species on islands in the Baltic Sea where mink control was not implemented (Nordström et al. 2003).

Observations during intensive studies of Pigeon Guillemot nesting ecology at the Naked Island group since 1978 strongly suggest that mink first arrived at the Naked

Island group after 1981, about 15-30 years ago (K. Kuletz, unpubl. data; Hayes 1995). These long-term studies and mink trapping in 2008 both indicate that other mammalian predators, such as American marten (*Martes americana),* whose sign (scat, tracks, inter-canine distance of wounds in prey remains) are likely to be indistinguishable from mink, are not present at the Naked Island group. Although there was insufficient evidence to positively identify the predator in most cases where predation was considered the cause of guillemot mortality, records of mink predation increased at the Naked Island group through the 1990s. The highest mink predation rate on guillemot nests at the Naked Island group was recorded in 1998, when the failure of 60% of the monitored guillemot nests (n = 66) was attributed to mink. Also during that year, an adult guillemot was found depredated by mink inside or near the nest crevice at 9% of all monitored guillemot nests (n = 6 nests).

The percentage of all guillemot eggs and chicks that were depredated was higher during the 1990s compared to earlier years. During the 1990s, the majority (approx. 57%) of all guillemot chick and egg mortality was caused by predation, although the level of predation was not significantly greater than all other causes of mortality combined. Golet et al. (2002) found that overall productivity during this period was significantly related to the rate of nest predation at Naked Island. Mink predation was confirmed as a cause of mortality of both chicks at one nest at the Naked Island group in 2008 (Alaska Veterinary Pathology Services, unpublished data), despite the extremely low number of active guillemot nests (17-22 breeding pairs). In 2008, the majority (86%) of chick mortality was again attributed to predation. Evidence from Fool Island in 2008 provides further support of the importance of mink predation to guillemot nesting success. In contrast to the Naked Island group, there was no chick mortality and a relatively high guillemot nesting density at Fool Island, where mink did not occur.

The nesting ecology of Pigeon Guillemots may make this species particularly vulnerable to predation by mink. Crevice-nesting and the vulnerability of adults, as well as eggs and chicks, have been correlated to more severe impacts of predation on seabird colonies (Jones et al. 2008). Lack of a predator attack response by breeding guillemots in defense of eggs or nestlings (perhaps due to the potential for adults to become trapped in their nest crevice by invading predators) may make eggs and chicks more susceptible to mink predation, as demonstrated in other birds (Sargeant et al. 1973, Ferreras and MacDonald 1999, Clode and MacDonald 2002). Predation on adult guillemots has a disproportionate impact on the population due to their K-selected life history traits (i.e., high annual adult survival, low reproductive rates; (i.e., high annual adult survival, low reproductive rates; Terborgh 1974, i.e., high annual adult survival, low reproductive rates; McKinney 1997, Groom et al. 2006).

There is some evidence that nest site selection by Pigeon Guillemots varies among areas with the susceptibility to nest predation (Emms and Verbeek 1989), and thus guillemots may respond to an increase in predation pressure by selecting nest sites that afford greater protection from nest predators, as has been demonstrated in other birds (Frostmeier and Weiss 2004, Eggers et al. 2006). We found a correlation between the onset of nest predation by mink and changes in use of different types of nest sites at the Naked Island group, suggesting that increasing predation pressure from mink caused a major shift in the type of nest sites used. Between 1978 and 2008, the proportion of nest sites that were likely inaccessible to mink (cliff face nests) increased, while the proportion of nest sites likely accessible to mink (talus and cliff edge nests) decreased. In 2008, not a single active nest of the talus type was found, although in 1978, 25% of all active nests on Naked Island were located in talus. Talus nest sites, located on relatively moderate slopes with easy access for quadrupeds, were all likely readily accessible to mink. Mink were potentially able to access cliff edge nests in soil burrows, either via the burrow entrance(s) located on moderate slopes or by digging an access hole to the nest chamber. A higher proportion of cliff nests were likely completely inaccessible to mink, especially when guillemot nest crevices were not adjacent to a ledge.

We assumed that nest sites were not limiting for Pigeon Guillemots nesting at the Naked Island group in 2008 because of the large decline in population size compared to previous years. Surveys indicate that the guillemot population on the Naked Island group was even larger during the early 1970s (Isleib and Kessel 1973) then during the late 1970s, suggesting that nest sites were not limited during either 1978 or 2008. Further, we found no evidence of a reduction in available guillemot nesting habitat in 2008. In addition, because both surveys were designed to find all nests regardless of type or accessibility to researchers, we have no reason to suspect a systematic bias in the data on nest type.

Increased nest predation by mink may have negatively affected other seabirds nesting at the Naked Island group. Arctic Terns (*Sterna paradisaea*) were the only surface-nesting seabirds breeding at the Naked Island group in 1978, but the species no longer nested there by 2008. Other crevice- or burrow-nesting seabirds, totaling more than 1,000, present at the Naked Island group in 1978 (Oakley and Kuletz 1979) either no longer nest there (i.e., Parakeet Auklet, *Aethia psittacula*) or nest in greatly reduced numbers (i.e., Tufted Puffins, *Fratercula cirrhata,* and Horned Puffins, *Fratercula corniculata*) (KSB, pers. obs). The few pairs of puffins that still nest on Naked Island are confined to the tallest cliffs (80 - 100 m) on the island. Large foraging flocks of piscivorous birds, including Marbled Murrelets (*Brachyramphus marmoratus*), Black-legged Kittiwakes (*Rissa tridactyla*), and Glaucus-winged Gulls (*Larus glaucescens*) still occurred along the shoreline of the Naked Island group in 2008, as did foraging humpback whales (*Megaptera novaeangliae*), minke whales (*Balaenoptera acutorostrata*), harbor seals (*Phoca vitulina*), and Steller sea lions (*Eumetopias jubatus*) (KSB, pers. obs.). These aggregations of piscivorous marine birds and mammals near the Naked Island group suggest that forage fish are plentiful in the area.

The weight of evidence suggests that in 2008 predation by mink was the primary limiting factor for guillemot nesting success and population recovery at the Naked Island group. Although the utilization of schooling forage fish by Pigeon Guillemots nesting at the Naked Island group has not returned to the levels observed prior to the *Exxon Valdez* oil spill, there was evidence that food availability and forage fish abundance have increased since the 1990s. The rapid decline in the guillemot breeding population at the Naked Island group between 1990 and 2008 compared with the stable breeding population at the nearby mink-free Smith Island group can best be explained by local top-down control of the guillemot population at the Naked Island group. Mortality rates of guillemot eggs and chicks in the nest during this period were higher than pre-EVOS, and the majority of this mortality was apparently due to predation. Mink evidently arrived at the Naked Island group between 1981 and 1994, and by 1998 mink predation rates on guillemot nests at the Naked Island group were at least 60%, and associated predation rates on nesting adult guillemots were at least 4.5% (G. Golet, U.S. Fish and Wildlife Service, unpubl. data). The recent colonization of the Naked Island group by mink, the rapid increase in the size of the mink population, and the associated high predation rates on guillemot nests and breeding adults is the most parsimonious explanation for the crash of the guillemot breeding population at the Naked Island group. Even if there was a resurgence in the availability of schooling forage fish in the nearshore of the Naked Island group to levels last seen pre-EVOS, it is very unlikely that the guillemot breeding population will be able to recover as long as mink are present in their current numbers.

LITERATURE CITED

Agler, B. A., S. J. Kendall, D. B. Irons, and S. P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. Waterbirds 22:98-103.

Ainley, D. G., R. J. Boekelheide, S. H. Morrell, and C. S. Strong. 1990. Pigeon Guillemot. Pages 276-305 *in* D. G. Ainley, and R. J. Boekelheide, editors. Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Stanford University Press, Stanford, CA.

Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology 84:709-723.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117-123.

Benson, J., R. M. Suryan, and J. F. Piatt. 2003. Assessing chick growth from a single visit to a seabird colony. Marine Ornithology 31:181-184.

Brown, E. D., and S. M. Moreland. 2000. Ecological factors affecting the distribution and abundance of forage fish in Prince William Sound, Alaska; an APEX synthesis product, Restoration Project 00163T. Anchorage, AK.

Brown, E. D., J. Wang, S. L. Vaughan, and B. L. Norcross. 1999. Identifying seasonal spatial scale for the ecological analysis of herring and other forage fish in

Prince William Sound, Alaska. *in* Proceedings of Lowell Wakefield Fisheries Symposium: Ecosystem approaches in fisheries management AK-SG-99-01, Fairbanks, AK.

Cailliet, G. M., M. S. Love, and A. W. Ebeling. 1986. Fishes: A field and laboratory manual on their structure, identification, and natural history. Wadsworth Publishing, Belmont, CA.

Cairns, D. K. 1985. Ermine visitation to Black Guillemot colonies in northeastern Hudson Bay. Condor 87:144-145.

Carlson, H. R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, Southeastern Alaska. Transactions of the American Fisheries Society 109:71-78.

Churnside, J. H., D. A. Demer, and B. Mahmoudi. 2003. A comparison of lidar and echosounder measurements of fish schools in the Gulf of Mexico. ICES Journal of Marine Science 60:147-154.

Clarke, K. R. 1993. Nonparametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18:117-143.

Clarke, K. R., and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Marine Ecology Progress Series 46:213-226.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition, PRIMER-E, Plymouth, UK.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Cooper, W. S. 1942. Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. Ecological Monographs 12:2-22.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in Siberian jay. Proceedings of the Royal Society B: Biological Sciences 273:701-706.

Emms, S. K., and N. A. M. Verbeek. 1989. Significance of the pattern of nest distribution in the pigeon guillemot (*Cepphus columba*). Auk 106:193-202.

_____. 1991. Brood size food provisioning and chick growth in the pigeon guillemot *Cepphus columba*. Condor 93:943-951.

Eslinger, D. L., R. T. Cooney, C. P. McRoy, A. Ward, T. C. Kline, E. P. Simpson, J. Wang, and J. R. Allen. 2001. Plankton dynamics: observed and modeled responses to physical conditions in Prince William Sound, Alaska. Fisheries Oceanography 10:81-96.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). *in* A. Poole, and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7:1-21.

Fréon, P., F. Gerletto, and O. A. Misund. 1993. Consequences of fish behaviour for stock assessment. ICES Journal of Marine Science 196:190-195.

Frostmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487-499.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on pigeon guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Groom, M. J., G. K. Meffe, and C. R. Carroll. 2006. Principles of conservation biology. 3rd edition. Sinauer, Sunderland, MA.

Hayes, D. L. 1995. Recovery monitoring of Pigeon Guillemot populations in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Unpubl. Report, Anchorage, AK.

_____. 1996. A comparison of the breeding and feeding ecology of Pigeon Guillemots at Naked and Jackpot islands in Prince William Sound, APEX: 95163 F. U.S. Fish and Wildlife Service, Anchorage, AK.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42-53.

Irons, D. B., S. J. Kendall, W. P. Erickson, L. L. McDonald, and B. K. Lance. 2000. Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska. Condor 102:723-737.

Irons, D. B., D. R. Nysewander, and J. L. Trapp. 1988. Prince William Sound waterbird distribution in relation to habitat type. U.S. Fish and Wildlife Service, Anchorage, AK.

Isleib, M. E. P., and B. Kessel. 1973. Birds of the north Gulf Coast - Prince William Sound region, Alaska. Biological Papers of the University of Alaska 14:1-149.

Jones, H. P., B. R. Tershy, E. S. Zavaleta, D. A. Croll, B. S. Keitt, M. E. Finkelstein, and G. R. Howald. 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22:16-26.

Kitaysky, A. S., J. F. Piatt, J. C. Wingfield, and M. Romano. 1999. The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. Journal of Comparative Physiology B 169:303-310.

Kline, T. C., Jr. 1999. Temporal and spatial variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in pelagic biota of Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:94-117.

Klosiewski, S. P., and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. U.S. Fish and Wildlife Service, Anchorage, AK.

Kuletz, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. Unpubl. M.Sc. thesis in Biological Sciences, University of California, Irvine, CA.

Litzow, M. A., and J. F. Piatt. 2003. Variance in prey abundance influences time budgets of breeding seabirds: Evidence from pigeon guillemots *Cepphus columba*. Journal of Avian Biology 34:54-64.

Litzow, M. A., J. F. Piatt, A. A. Abookire, A. K. Prichard, and M. D. Robards. 2000. Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with pigeon guillemot (*Cepphus columba*) diets. ICES Journal of Marine Science 57:976-986.

Litzow, M. A., J. F. Piatt, A. A. Abookire, and M. D. Robards. 2004. Energy density and variability in abundance of pigeon guillemot prey: support for the quality-variability trade-off hypothesis. Journal of Animal Ecology 73:1149-1156.

Litzow, M. A., J. F. Piatt, A. K. Prichard, and D. D. Roby. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286-295.

Logerwell, E. A., and N. B. Hargreaves. 1997. Seabird impacts on forage fish: populations and behavioral interactions. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. University of Alaska Sea Grant Program Report 97-01, Fairbanks, AK.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495-516.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Misund, O. A., and A. Aglen. 1992. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. ICES Journal of Marine Science 49:325-334.

Misund, O. A., J. T. Ovredal, and M. T. Hafsteinsson. 1996. Reactions of herring schools to the sound field of a survey vessel. Aquatic Living Resources 9:5-11.

Neff, J. M., E. H. Owens, S. W. Stoker, and D. M. McCormick. 1995. Shoreline oiling conditions in Prince William Sound following the *Exxon Valdez* oil spill. *in* P. G. Wells, J. N. Butler, and J. S. Hughes, editors. *Exxon Valdez* oil spill: fate and effects in Alaskan waters. ASTM Special Technical Publication no. 1219, American Society of Testing Materials, Philadelphia, PA.

Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99:14113-14126.

Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline, D. M. Mason, E. V. Patrick, A. J. Paul, and K. D. E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10:42-57.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Oakley, K. L., and K. J. Kuletz. 1979. Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot. U.S. Fish and Wildlife Service, Office of Special Studies, Anchorage, AK.

_____. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:759-769.

Piatt, J. F., D. W. Macdonald, C. J. Lensink, W. Butler, M. Kendziorek, and D. R. Nysewander. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107:387-397.

Pitcher, T. J., and C. J. Wyche. 1983. Predator-avoidance behaviors of sand-eel schools: why schools seldom split. Dr. W. Junk Publishers, Boston, MA.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, CA.

Robards, M. D., and J. F. Piatt. 1999. Biology of the genus Ammodytes, the sand lances. U. S. Department of Agriculture Forest Service Pacific Northwest Research Station Research Paper:1-16.

Romano, M. D., J. F. Piatt, and D. D. Roby. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. Waterbirds 29:407-414.

Rosen, D. A. S., and A. W. Trites. 2000. Pollock and the decline of Steller sea lions: testing the junk food hypothesis. Canadian Journal of Zoology 78:1243-1250.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Sargeant, A. B., G. A. Swanson, and H. A. Doty. 1973. Selective predation by mink, *Mustela vison*, on waterfowl. American Midland Naturalist 89:208-214.

Seiser, P. E., L. K. Duffy, A. D. McGuire, D. D. Roby, G. H. Golet, and M. A. Litzow. 2000. Comparison of pigeon guillemot, *Cepphus columba*, blood parameters from oiled and unoiled areas of Alaska eight years after the *Exxon Valdez* oil spill. Marine Pollution Bulletin 40:152-164.

Suryan, R. M., D. B. Irons, E. D. Brown, P. G. R. Jodice, and D. D. Roby. 2006. Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. Progress in Oceanography 68:303-328.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. Bioscience 24:715-722.

Vaughan, S. L., C. N. K. Mooers, and S. M. Gay. 2001. Physical variability in Prince William Sound during the SEA study (1994-98). Fisheries Oceanography 10:58-80.

Vermeer, K., K. H. Morgan, and G. E. J. Smith. 1993a. Colony attendance of pigeon guillemots as related to tide height and time of day. Colonial Waterbirds 16:1-8.

_____. 1993b. Nesting biology and predation of pigeon guillemots in the Queen Charlotte Islands, British Columbia. Colonial Waterbirds 16:119-127.

Table 2.1. Number of traps, trap density, and trapping effort for study islands in central Prince William Sound, Alaska during 2008 to determine presence or absence of American mink (*Neovison vison*).

Location	Number Traps Set	Effort (trap nights)	Shoreline Length (km)	Density (traps/km)	Mink Captured
Fool Island	6	174	1.8	3.3	0
Seal Island	4	96	2.5	1.6	0
Little Smith Island	3	90	2.7	1.1	0
Smith Island	10	300	12.7	0.8	0
Storey Island	21	42	17.5	1.2	2
Peak Island	7	14	14.2	0.5	5
Naked Island	124	323	72.8	1.7	22

Table 2.2. Average and standard deviation (SD) of effort (km^2) per aerial survey and number (n) of aerial surveys completed during 1998, 1999, and 2008 to estimate abundance of schooling forage fish at the Naked Island group and the Smith Island group in Prince William Sound, Alaska.

			Effort/Survey (km^2)	
Island Group	Year	n	Average	SD
Naked Island Group	1998	11	51.5	4.9
	1999	9	54.9	3.0
	2008	3	63.1	2.1
Smith Island Group	1998	10	10.0	2.7
	1999	9	8.1	1.8
	2008	3	11.2	0.3

Table 2.3. Catch per unit effort (CPUE) and percent contribution of schooling fish and demersal fish to the relative composition of beach seine catches during 1996-1997 and 2008 at three sites on Naked Island, Prince William Sound, Alaska. Schooling fishes included Pacific sand lance *Ammodytes hexapterus*, Pacific herring *Clupea pallasi,* and smelt Osmeridae spp. Demersal fishes were subdivided into (1) Gadids and (2) Other, which included all remaining fish species.

			Schooling fishes	Demersal fishes	
Parameter	Year(s)	n		Gadids	Other
Composition	1996-1997	8	18.9%	18.9%	62.2%
	2008	14	21.4%	42.1%	36.5%
CPUE	1996-1997	8	13.4	55.1	29.9
	2008	14	25.4	302.7	133.7

Table 2.4. Number and percent of active Pigeon Guillemot nests in different nest site types on the Naked Island group, Prince William Sound, Alaska in 1978 and 2008. Guillemot nests were classified as one of three types: (1) cliff, located in a crevice on a cliff face; (2) cliff edge, in overhanging soil at a cliff top; and (3) talus, under boulders at the base of a cliff or amidst rocks on a cliff ledge.

	1978		2008	
Nest Type	Number	Percent	Number	Percent
Cliff	52	35.6%	15	88.2%
Cliff Edge	58	39.7%	2	11.8%
Talus	36	24.7%	0	0.0%
Total	146	100.0%	17	100.0%

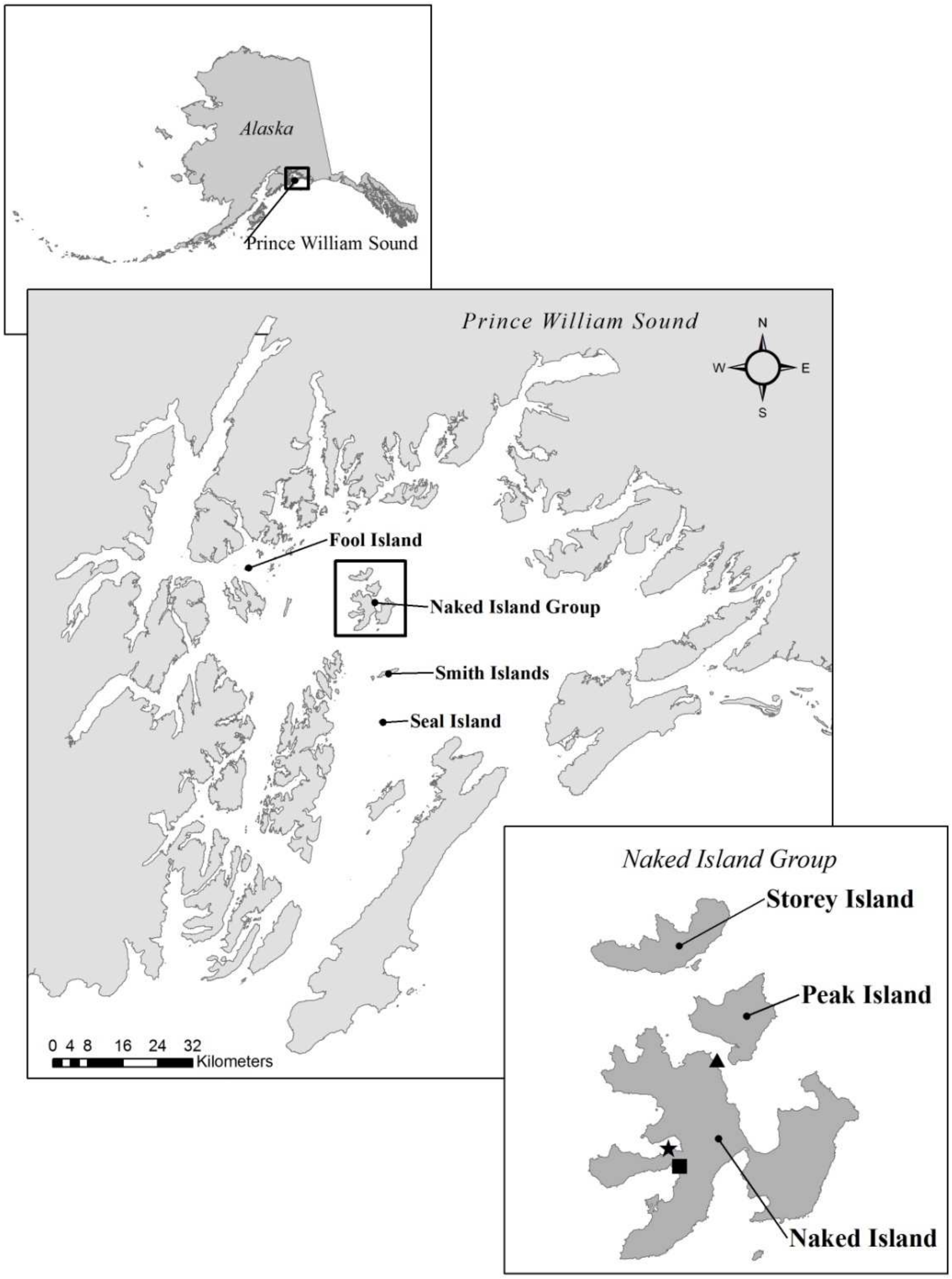


Figure 2.1. Inset map showing the location of Prince William Sound in Alaska, study islands within Prince William Sound, and the locations of three beaches that were seined at Naked Island during 1996, 1997 (G. Golet, U.S. Fish and Wildlife Service, unpubl. data) and 2008. McPherson North Beach, Fuel Beach, and Inside Outside Beach represented by a triangle, star, and square, respectively.

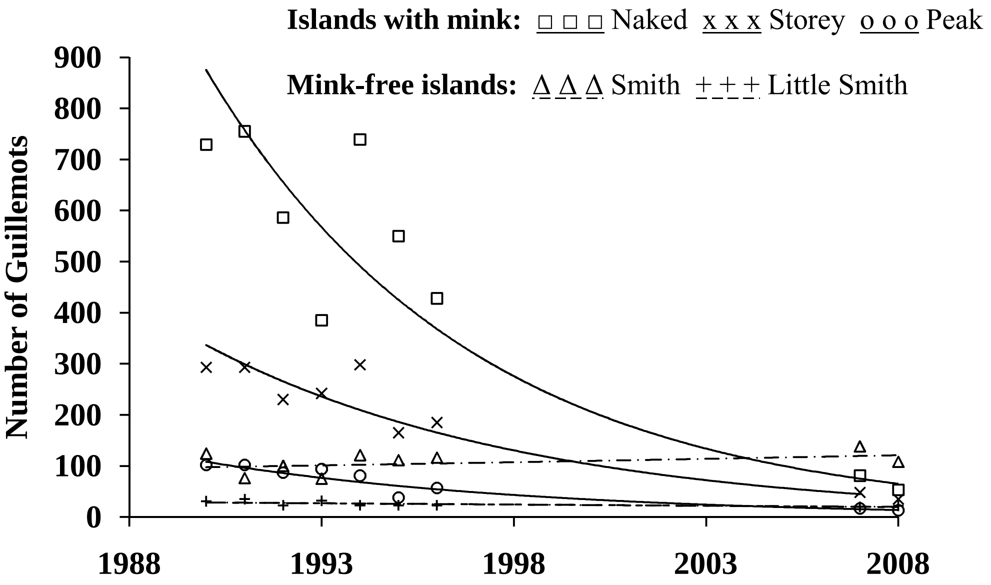


Figure 2.2. Size of Pigeon Guillemot breeding populations at islands with mink (Naked, Storey, and Peak islands) and islands without mink (Smith and Little Smith islands) in central Prince William Sound, Alaska from 1990 to 2008. Data from 1990 to 1999 are from Golet et al. (2002).

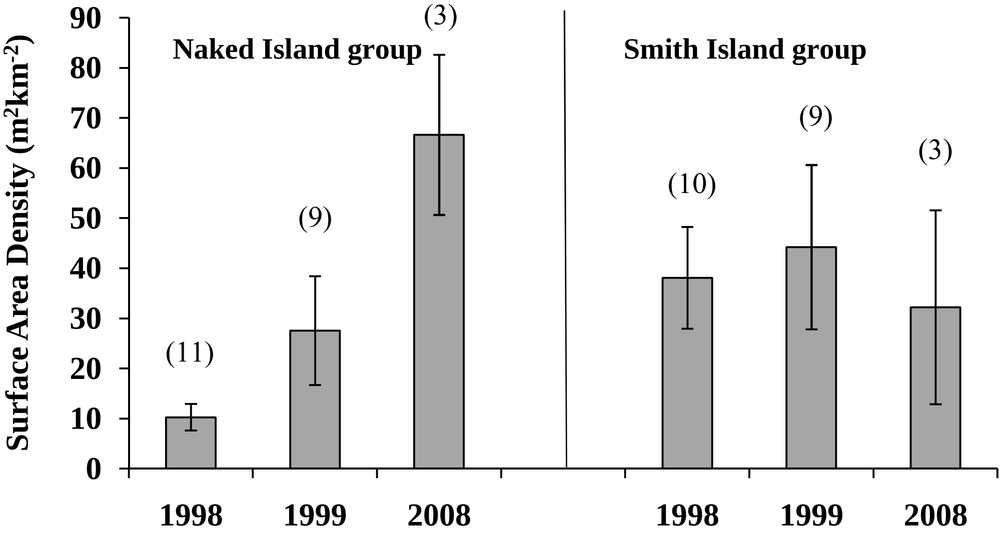


Figure 2.3. Mean and standard error of surface area density (m^2 km^{-2}) of schooling forage fishes visible during aerial surveys at the Naked Island group and the Smith Island group during July - August in 1998, 1999, and 2008. The numbers of aerial surveys completed are shown in parentheses. Data from 1998 and 1999 are from Brown and Moreland (2000).

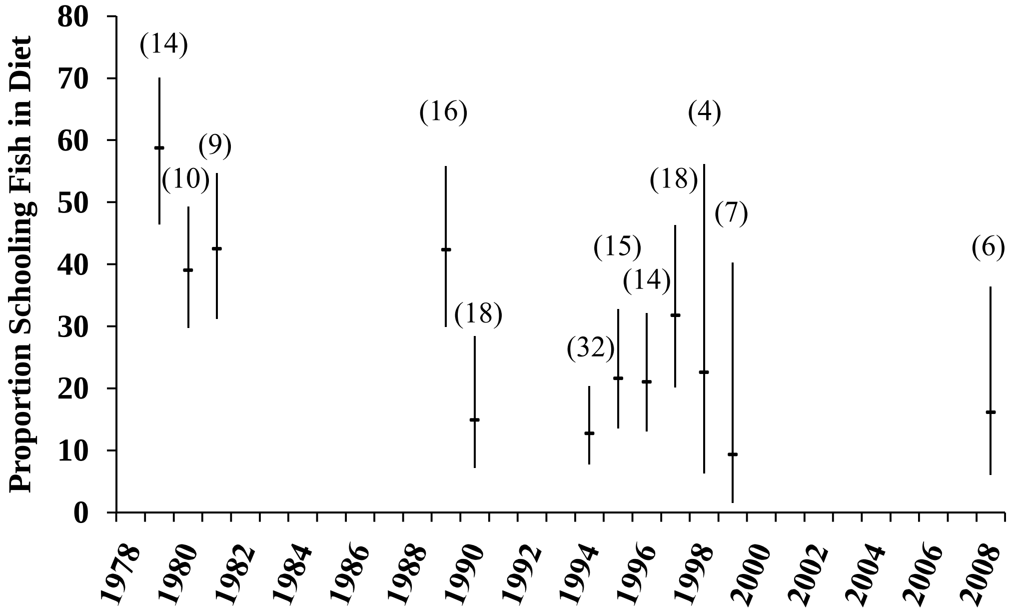


Figure 2.4. The mean and 95% confidence interval of the proportion of prey delivered to Pigeon Guillemot nests at Naked Island that were schooling fishes (sand lance, herring, and smelt spp.) from 1979 to 2008. The numbers of nests where prey items were identified are shown in parentheses. Data from 1978 to 1999 are from Golet et al. (2002).

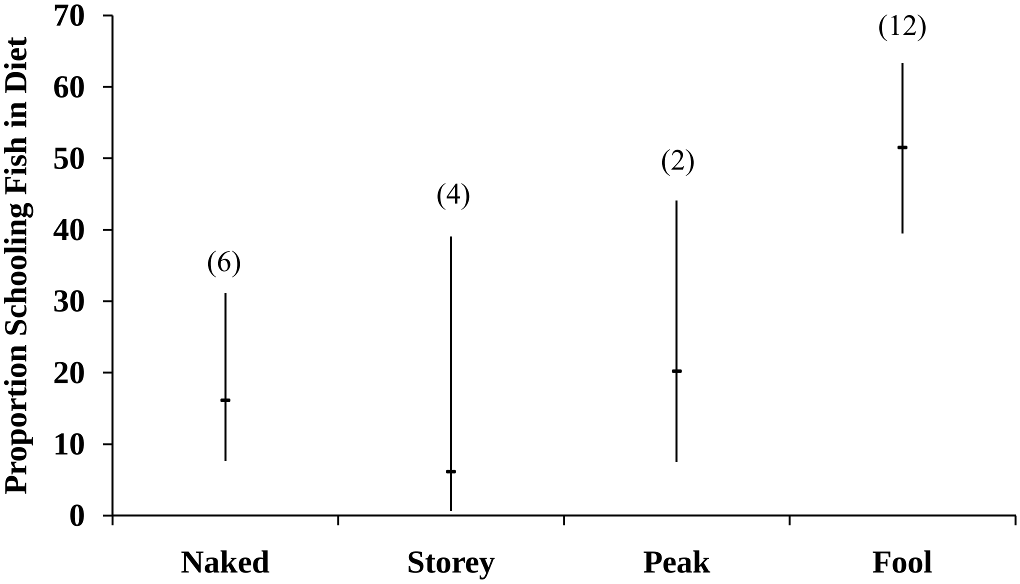


Figure 2.5. The mean and 95% confidence interval of the proportion of all prey delivered to Pigeon Guillemot nests at the Naked Island group (Naked, Storey, and Peak islands) and Fool Island that were schooling fishes (sand lance, herring, and smelt spp.) in 2008. The numbers of nests where prey items were identified are shown in parentheses.

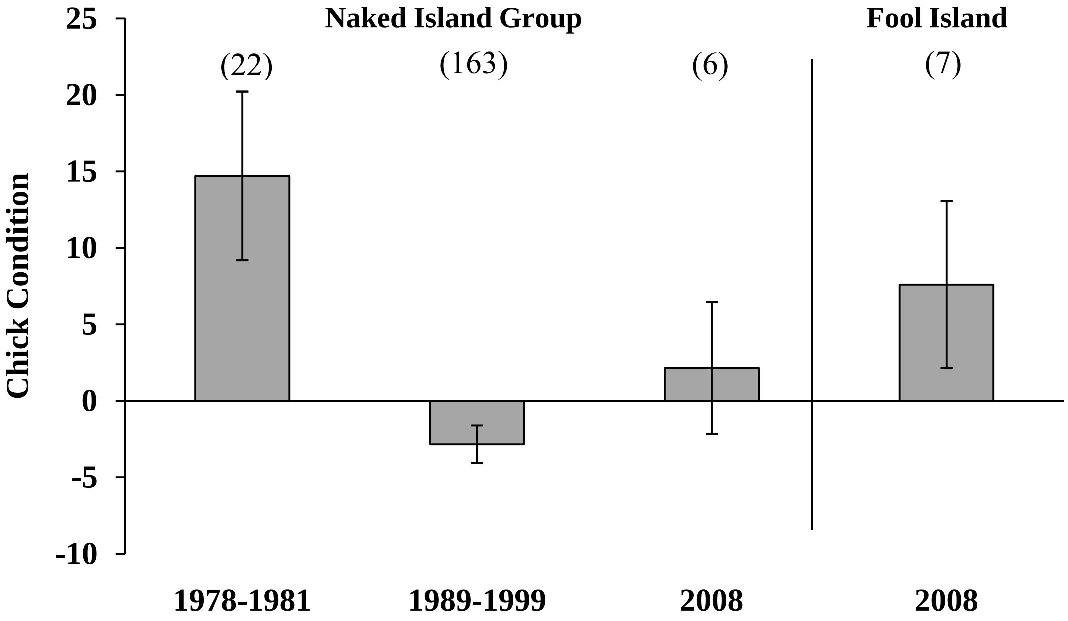


Figure 2.6. Condition indices for Pigeon Guillemot chicks in Prince William Sound, Alaska based on one-time measurements of body mass and wing chord length during the linear growth phase (8 to 18 days post-hatch) at the Naked Island group in 1978-1981, 1989-1999, and 2008, and at Fool Island in 2008. Chick condition indices are the residuals of the regression of body mass on wing chord length, presented as the percent of predicted body mass. Bars represent the mean (± 1 standard error) chick condition index. Sample sizes are presented in parentheses. Data from 1978 to 1999 are from Golet et al. (2002).

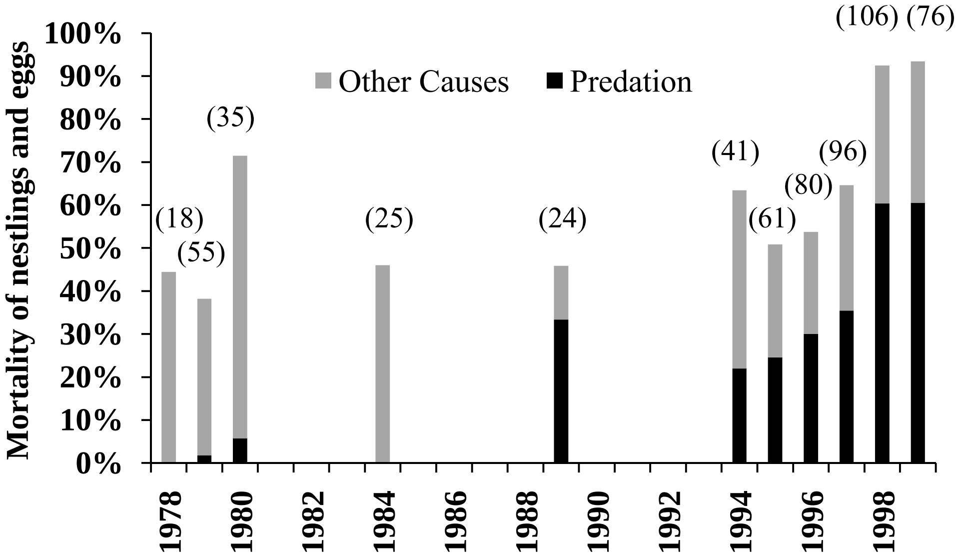


Figure 2.7. Percent mortality of Pigeon Guillemot eggs and chicks caused by predation and other factors for nests monitored between 1978 and 1999 at the Naked Island group, central Prince William Sound, Alaska. Data are from Golet et al. (2002).

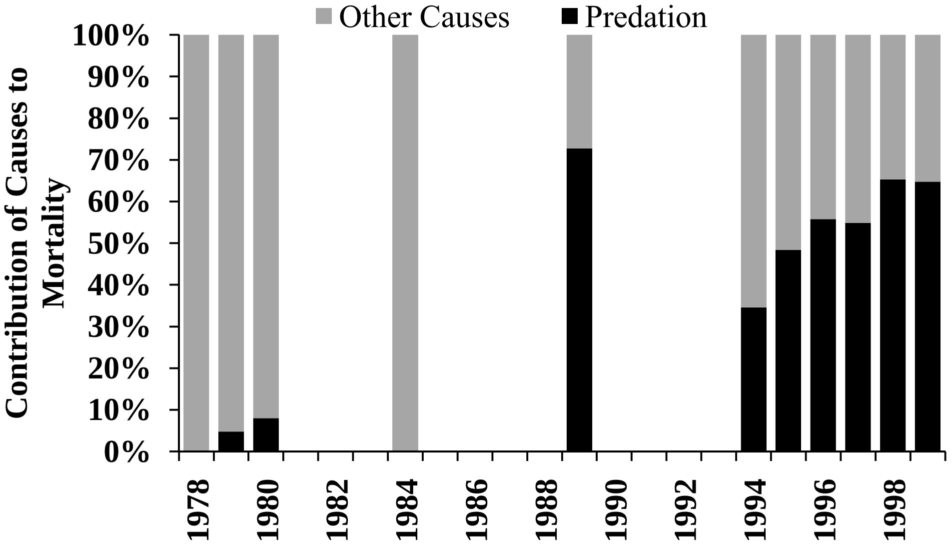


Figure 2.8. The relative contribution of predation and other causes to the mortality of all Pigeon Guillemot eggs and chicks in nests monitored between 1978 and 1999 at the Naked Island group, central Prince William Sound, Alaska. Data are from Golet et al. (2002).

CHAPTER 3

POPULATION TRENDS OF PIGEON GUILLEMOTS IN PRINCE WILLIAM SOUND, ALASKA: CONTINUED DECLINE 20 YEARS AFTER THE *EXXON VALDEZ* OIL SPILL

Kirsten S. Bixler[1], Daniel D. Roby[1], and David B. Irons[2]

[1]U.S. Geological Survey-Oregon Cooperative Fish and Wildlife Research Unit,
Department of Fisheries and Wildlife, 104 Nash Hall, Oregon State University,
Corvallis, OR 97331 USA

[2]U.S. Fish and Wildlife Service, Migratory Bird Management, 1011 East Tudor Road,
Anchorage, Alaska 99503 USA

ABSTRACT

The Pigeon Guillemot (*Cepphus columba*) is the only seabird species that is listed as "not recovering" on the *Exxon Valdez* Oil Spill Trustee Council's Injured Resources List and has shown no sign of population recovery from damages caused by the 1989 *Exxon Valdez* oil spill (EVOS) in Prince William Sound (PWS), Alaska. Pigeon Guillemot numbers in PWS are 47% lower than following the initial mortality event caused by direct contact with EVOS oil and, although there is no evidence since 2000 that guillemots have been exposed to residual oil from EVOS, the population continued to decline. A portion of this population decline, which began prior to 1989, has been attributed to lower prey abundance following the 1976 regime shift in the Pacific Decadal Oscillation. In this study, we assessed trends in guillemot populations across PWS to test the hypothesis that nest predation by mink is currently the primary factor limiting recovery of Pigeon Guillemots at the Naked Island group, despite regional declines in guillemots attributed to reductions in food availability. The post-spill decline in median density of Pigeon Guillemots at the Naked Island group (12.5% per annum) was more than seven times that of the remainder of PWS (1.5% per annum). From 1993 to 2008, the number of guillemots at the Naked Island group declined by more than 2.5 times that of all other high-density guillemot nesting areas in central and western PWS. The proportion of guillemots counted on surveys that were in isolated pairs increased at the Naked Island group, but did not change elsewhere in PWS, suggesting that nest predation by mink had a higher impact on

guillemot colonies than on isolated guillemot nests, perhaps through increased attraction or greater accessibility to mink. Average group size of Pigeon Guillemots in surveys declined by a third (from 12 to 8 individuals per group) across all high-density guillemot areas in Prince William Sound, suggesting that availability of schooling forage fishes may also limit guillemot numbers regionally. Differences in guillemot population trends between the Naked Island group and the remainder of Prince William Sound are consistent with the hypothesis that nest predation by mink is the primary factor causing the continued decline of guillemots nesting at the Naked Island group.

INTRODUCTION

The Pigeon Guillemot (*Cepphus columba*) is a semi-colonial piscivorous seabird that suffered significant direct mortality from the 1989 *Exxon Valdez* oil spill (EVOS) in Prince William Sound (PWS), Alaska (*Exxon Valdez* Oil Spill Trustee Council 2009). Populations of all other species of marine birds injured by the spill and whose recovery status is known, have either fully recovered or nearly so (*Exxon Valdez* Oil Spill Trustee Council 2009). The population of Pigeon Guillemots, however, has declined by about 47% since the direct acute mortality from EVOS (McKnight et al. 2008). Although there is no longer evidence that guillemots are being exposed to residual oil from EVOS (B. Ballachey, U.S. Geological Survey, pers. comm.), the population exhibits no signs of either stabilization or recovery (McKnight et al. 2008). Mechanisms that could potentially prevent population recovery have been investigated at the Naked Island group in central PWS, historically the most important breeding area for Pigeon Guillemots in PWS (see Chapter 2). The primary factor limiting recovery of guillemots nesting at these islands now appears to be local: increased nest predation and adult mortality following the recent establishment of American mink (*Neovison vison*) on the islands. Declines in availability of schooling forage fishes, such as sand lance (*Ammodytes hexapterus*) and juvenile herring (*Clupea pallasi*), may also limit guillemot recovery, but on a larger regional scale. Reduced availability of schooling forage fish is considered a cause of guillemot population decline across PWS (Agler et al. 1999, Golet et al. 2002, McKnight et al. 2008).

In this study, we investigated population trends of Pigeon Guillemots at the Naked Island group and in other areas of PWS to test the hypothesis that predation by a recently established mink population is the primary factor limiting recovery of guillemots at the Naked Island group. We reasoned that if the guillemot population at the Naked Island group was experiencing a more severe and persistent decline than at other areas in PWS, this would support the role of local mink predation in the decline.

Direct exposure to oil in the immediate aftermath of the EVOS killed an estimated 500 to 1,500 guillemots in PWS (Piatt et al. 1990). Pigeon Guillemot numbers continued to decline in PWS through 2007 (McKnight et al. 2008), and this decline was greater in the oiled portion of PWS than in un-oiled areas through at least 1998 (Irons et al. 2000). Elevated levels of hepatic cytochrome P4501A, an indicator of exposure of guillemots to crude oil (Hovey 2002), were detected in Pigeon Guillemots from the oiled portion of PWS through 2000, but not in 2004, suggesting that guillemots no longer experience direct negative effects of residual oil from the EVOS (B. Ballachey, U.S. Geological Survey, pers. comm., Seiser et al. 2000, Golet et al. 2002).

The EVOS may have negatively affected the abundance of certain schooling forage fishes, notably sand lance and herring (Golet et al. 2002, Marty 2008), and the availability of these forage fishes has been linked to reproductive success in Pigeon

Guillemots (Golet et al. 2002). A higher percentage of high-lipid schooling forage fish in guillemot chick diets has been associated with higher chick growth rates, as well as higher peak mass and fledging mass of chicks, all presumably enhancing post-fledging survival of guillemots, as in other seabirds (Gaston 1997, Sagar and Horning 1998, Stienen and Brenninkmeijer 2002). Golet et al. (2002) found a lower percentage of schooling forage fish in the diet of chicks from an oiled area (the Naked Island group) when compared to an un-oiled area (Jackpot Island) in PWS. In addition, the diet of chicks at the Naked Island group included fewer schooling forage fish (sand lance) after EVOS then prior to EVOS (Golet et al. 2002).

These indirect effects of EVOS were likely an important driving factor in the decline of the Pigeon Guillemot population throughout PWS, but the magnitude of these effects from EVOS is uncertain. Confounding the effects of EVOS on the forage fish base was the regime shift in the Pacific Decadal Oscillation during 1976. This ocean climate shift resulted in lower abundance of schooling forage fishes (e.g., sand lance, herring, capelin [*Mallotus villosus*]) and increased abundance of demersal fishes in the Gulf of Alaska (Francis et al. 1998, Anderson and Piatt 1999, Brown 2003). The decline in the population of Pigeon Guillemots apparently began prior to EVOS, and ostensibly in association with changes in relative abundance of forage fishes due to the Pacific Decadal Oscillation regime shift (Agler et al. 1999, Golet et al. 2002).

In 2008, the proportion of schooling fish in the diet of Pigeon Guillemot chicks at the Naked Island group had still not returned to the levels observed prior to the EVOS (Chapter 2). There was evidence, however, that forage fish availability and abundance were higher in 2008 than during the 1990s (Golet et al. 2002), suggesting that the drastic decline in Pigeon Guillemots at the Naked Island group was not due to food supply. Although the availability of schooling forage fish plays a role in the productivity of guillemots in PWS, it does not now appear to be the major factor limiting population recovery at the Naked Island group (Chapter 2).

Predation on guillemot nests, a local factor apparently unrelated to EVOS, gradually increased during the 1990s and appeared to be the primary limiting factor for nest success and population recovery at the Naked Island group in 2008 (Chapter 2). The gradual increase in predation rates on guillemot nests followed the first reports of mink at the Naked Island group in the early 1990s. This semi-aquatic, generalist predator is native to the mainland and nearshore islands of PWS, but is not present on all offshore islands in the Sound (Paul 2009). The mink at the Naked Island group, which are in part descended from fur farm stock, may well have been introduced by humans (Fleming and Cook 2010). Several studies have documented rapid and severe population declines in several species of birds, including the closely-related Black Guillemot (*Cepphus grylle*), following range expansion or introduction of American mink to islands (Cairns 1985, Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, Banks et al. 2008).

In this study, we compare the population trends of Pigeon Guillemots at the Naked Island group with those in other areas of PWS. We collected data on guillemot abundance and distribution during the 2007 and 2008 breeding seasons, and compared these data to guillemot densities reported in previous studies by Irons et al. (2000) and McKnight et al. (2008), as well as guillemot population and group size data reported by Sanger and Cody (1994). We hypothesized that if mink predation, a local issue, is the primary limiting factor for population recovery of Pigeon Guillemots at the Naked Island group, then the population decline there is likely to be much more severe than elsewhere in PWS. However, if availability of schooling forage fish, a region-wide factor, is preventing recovery, then guillemot population trends are likely to be similar across PWS.

METHODS

Study Area

Prince William Sound is a sub-arctic, inland sea approximately 10,000 km^2, adjacent to the northern Gulf of Alaska, and bounded by the Chugach and Kenai mountains (Niebauer et al. 1994). Terrestrial vegetation at sea level is dominated by spruce-hemlock forest (Cooper 1942). The Sound is connected with the relatively shallow (<

200 m), continental shelf in the Gulf of Alaska, primarily through Montague Strait and Hinchinbrook Entrance (Niebauer et al. 1994, Vaughan et al. 2001). Prince William Sound is a complex fjord estuarine system with about 5,000 km of coastline, high levels of freshwater input, and bathymetry ranging from shallow glacial moraines and tidal flats to deep fjords and basins (maximum depth > 800 m) (Niebauer et al. 1994, Vaughan et al. 2001). Marine circulation in PWS is generally cyclonic, although wind and precipitation can cause significant deviations (Vaughan et al. 2001). Productivity in PWS is affected by exchange of water with the Gulf of Alaska, which influences inflow, outflow, and retention of phytoplankton, zooplankton, and planktonic fish larvae (Brown et al. 1999, Kline 1999, Eslinger et al. 2001, Norcross et al. 2001, Vaughan et al. 2001).

Pigeon Guillemots are distributed throughout Prince William Sound during the breeding season, which extends from late May to late August. These semi-colonial seabirds generally nest in isolated pairs or in small colonies, usually less than 25 pairs, but occasionally up to 500 pairs (Ewins 1993). The Pigeon Guillemot population at the Naked Island group in central PWS was the primary focus of this study, and this archipelago includes three main islands: Naked Island (38.6 km^2), Storey Island (7.2 km^2), and Peak Island (6.1 km^2). We collected data on guillemot population densities in 2008, and compared these data to those collected during 10 different nesting seasons post-EVOS (1989, 1990, 1991, 1993, 1996, 1998, 2000, 2004, 2005, and

2007) along transects distributed randomly across Prince William Sound (Irons et al. 2000, McKnight et al. 2008). During the 2008 nesting season, we collected data in the field on the numbers of guillemots and their group sizes in areas that supported relatively high densities of Pigeon Guillemots in 1993 to investigate potential changes over the intervening 15 years (Sanger and Cody 1994). These areas of high guillemot density in PWS included coastal fjords (i.e., Passage Canal, Port Bainbridge) and islands (i.e., Fool, Lone, Naked, Storey, Peak, Smith, Little Smith, Seal, Jackpot, and the Pleiades islands).

Sound-wide Guillemot Densities

The densities of Pigeon Guillemots at the Naked Island group and across Prince William Sound were determined using nearshore boat-based surveys. The area within 200 m of land in Prince William Sound (820.74 km^2) was split into 772 transects of variable length (mean = 6 km) (Irons et al. 2000). In 1989, 187 transects were randomly selected and an additional 25 transects were randomly selected in 1990 (Klosiewski and Laing 1994). During each subsequent survey, these 212 transects, which encompassed 29% of the total nearshore area within Prince William Sound, were re-sampled. Surveys were completed over approximately three weeks in July, using equivalent methods. Surveys were conducted while traveling at 10 to 20 km h^{-1} in 7.7-m Boston Whalers piloted 100 m from shore. Two observers counted Pigeon Guillemots, as well as other birds and mammals, within 100 m on either side of, ahead of, and above the vessel. Birds and mammals on land within 100 m of shore were counted as well. Surveys were limited to periods of good observation conditions, when wave height was less than 0.6 m, but usually surveys were conducted when wave height was less than 0.3 m. A few transects in some surveys were not completed due to poor weather conditions. For a more detailed description of survey methodology see Klosiewski and Laing (1994), Irons et al. (2000), and McKnight et al. (2008).

We removed transects from the sample that was analyzed if, throughout the duration of the study, guillemots were never counted along the transect (n = 28, 26.95 km^2). The remaining sample included six transects at the Naked Island group and 178 transects across the remainder of Prince William Sound, covering 21.9% and 25.5% of the available nearshore area, respectively (Figure 3.1). Transects in Prince William Sound, excluding those at the Naked Island group, were post-stratified into two categories following Klosiewski and Laing (1994), Irons et al. (2000), and McKnight et al. (2008). Transects within the general *Exxon Valdez* oil spill area were considered oiled, and if outside of this area were considered un-oiled. This stratification assumes that (1) birds within the general spill area were affected by oil even though there were sections of shoreline within the spill path that remained un-oiled (see Irons et al. 2000) and (2) that there was no movement of guillemots between oiled and un-oiled areas. Oiling categorization was based upon Shoreline Cleanup Assessment Team data from 1989, considered the highest quality data available (Irons et al. 2000).

Areas of High Guillemot Density

We conducted a separate nearshore boat-based survey to determine the number of Pigeon Guillemots at the Naked Island group and several other areas with high guillemot densities in Prince William Sound. This survey was designed specifically to maximize the count of Pigeon Guillemots, rather than all birds and mammals as in the previous survey, and consequently there are several methodological differences between them. In this survey, we collected data along the coast of entire islands/fjords during two nesting seasons, as opposed to randomly selected transects spread across Prince William Sound during 10 years.

Short stretches of shoreline with relatively high densities of Pigeon Guillemots were identified in 1993 during a boat-based survey for Pigeon Guillemots that covered 98% of the Prince William Sound shoreline (Sanger and Cody 1994). In 2008, we re-sampled 12 of the 14 islands or coastal fjords that supported high guillemot densities in 1993: Passage Canal, Port Bainbridge, and Naked, Storey, Peak, Fool, Lone, Smith, Little Smith, Seal, Jackpot, and the Pleiades islands (Figure 3.2). We did not survey the two high-density guillemot areas that Sanger and Cody (1994) found in eastern Prince William Sound, Bligh and Hinchinbrook islands, due to logistic constraints. At the time of the Sanger and Cody (1994) survey, 46% of all guillemots counted in PWS occurred at the 12 islands or coastal fjords in central and western Prince William

Sound that supported high guillemot densities, along 357 km of shoreline (7% of the total shoreline in PWS). Although there were differences in shoreline lengths, guillemot numbers, and guillemot densities among the 12 high-density areas, the total length of shoreline surveyed was similar between the Naked Island group and other high-density areas surveyed in 1993. Also, the proportion of all guillemots counted that were at the Naked Island group (23.6%) in 1993 was similar to the proportion counted at all other high-density areas combined (22.3%; Sanger and Cody 1994).

Sound-wide surveys for waterbirds were conducted over three weeks in July in 2007 during any time of day (McKnight et al. 2008). Data collection during guillemot surveys was limited to the pre-egg-laying, egg-laying, and early incubation stages of the guillemot nesting cycle, and to early morning high tides when guillemot colony attendance is the least variable (Vermeer et al. 1993a). The guillemot surveys were performed between 05:00 and 10:00 h ADT on days with an early morning high tide, and on other days within one hour of high tide. Guillemot surveys were conducted from 9 May to 14 June in 1993 (Sanger and Cody 1994) and from 29 May to 13 June in 2008. The mean difference in date of survey for particular high-density guillemot areas was 14.3 days (range = 1 to 30 days).

Guillemot surveys were conducted from either 3.7-m inflatable boats or 7.7-m Boston Whalers. Vessels were piloted between 50 m and 100 m from shore, up to 50 m closer to shore than in the general waterbird surveys. During guillemot surveys, the maximum travel speed was 5 km h^{-1} slower (survey speed, 10 to 15 km h^{-1}) and the width of the strip sampled adjacent to the shoreline was 100 m narrower (100-m wide) than in the previous survey. As with the general waterbird previous surveys, two observers counted all guillemots within the sampling strip as well as on shoreline rocks and cliffs. However, in guillemot surveys, the size and coordinates of all guillemot groups were recorded using a global positioning system (GPS) receiver, with the exception of groups composed of less than four individuals in 1993 (Sanger and Cody 1994).

Guillemots were considered a group based upon a combination of physical proximity and behavior during observation periods of up to 30 min. If observers could not position themselves between the birds without disturbing them (i.e., causing flushing or escape diving), then they were considered part of a group. Courtship behavior, such as duet whistles and “water games” (Ewins 1993) indicated group membership as well. We considered a group of four or more individuals an indicator of multiple breeding pairs (i.e., a colony) and a group of less than four individuals to be an isolated breeding pair (Sanger and Cody 1994). Following Ewins (1985) and Sanger and Cody (1994), guillemots were considered as belonging to different groups if an observer could potentially position themselves onshore between the groups without disturbing either group. Although we did not attempt to find active nests and verify the presence of eggs or chicks, we believe that our guillemot groups were an accurate indicator of breeding activity and colony size. We observed behaviors that strongly suggested breeding (e.g., flying into or out of a crevice, copulation, circling between water and land) for the majority of multi-pair groups (76.5% in 1993 and 74.5% in 2008). Although we did not observe these behaviors in about a quarter of the multi-pair groups, we included these groups in our analysis because during the laying and incubation periods breeding guillemots often remain near their nests but access them infrequently. For a more detailed description of survey methodology, see Sanger and Cody (1994).

Statistical Analysis

To detect differences in population density trends on transects (sampling unit) at the Naked Island group compared to the remainder of Prince William Sound, we used multiple linear regression analysis with repeated measures (10 years sampled) (Ramsey and Schafer 2002). Ordinal date of survey for each transect was included as an explanatory variable to account for possible changes in attendance patterns during the 3-week survey period. To meet assumptions of normality and equal variance, assessed using residual plots, the response (number of birds km^{-2} $transect^{-1}$) was log transformed. We compared toeplitz, unstructured, compound symmetry, and autoregressive covariance structures (Jennrich and Schluchter 1986) and selected a structure (toeplitz 5) based upon the minimum Akaike's Information Criterion (AIC) value (Akaike 1974). We selected a model after removing all non-significant explanatory variables using a backwards-model-selection technique (Ramsey and Schafer 2002). We completed a second multiple linear regression analysis identical to the first, with the exception that transects at the Naked Island group were compared to only those transects elsewhere in PWS that were considered oiled following EVOS.

We compared the change in response variables at the Naked Island group with other high-density guillemot areas in western Prince William Sound between 1993 and 2008, including the percent change in number of guillemots, percent change in number of multi-pair groups, and change in proportion of all guillemots in isolated pairs. Due to violations of parametric test assumptions and small sample sizes, we used permutation tests (Ramsey and Schafer 2002). We used a Wilcoxon Rank Sum test with normal approximation and continuity correction (Ramsey and Schafer 2002) to compare size of multi-pair guillemot groups between the Naked Island group and other high-density areas.

Results were considered statistically significant if $P \leq 0.05$ and suggestive if $0.05 < P \leq 0.10$. Although several other studies comparing population trends in oiled and un-oiled areas used either an $\alpha = 0.10$ (McKnight et al. 2008) or an $\alpha = 0.20$ (Wiens et al. 1996, Day et al. 1997, Murphy et al. 1997, Irons et al. 2000, McKnight et al. 2008), we used the conventional *a priori* $\alpha = 0.05$ because detecting a difference between oiled and un-oiled transects was of secondary importance to our analysis. All analyses were conducted using SAS 9.2 software (SAS Institute 2008).

RESULTS

Sound-wide Guillemot Densities

There was no evidence that transect survey date influenced the density of Pigeon Guillemots on transects ($t = 1.52$, $P = 0.22$), and this factor was not included in subsequent analyses. The density of guillemots along shoreline transects declined between 1989 and 2008 at both the Naked Island group ($t = -9.13$, $P < 0.0001$) and elsewhere in Prince William Sound ($t = -5.61$, $P < 0.0001$; Figure 3.3). However, the decline in guillemot density on-transect was much greater at the Naked Island group than in the remainder of Prince William Sound ($t = -7.95$, $P < 0.0001$). The median annual decline in density of guillemots along Naked Island group transects was 12.5% (95% CI = 10.0% to 15.0%). Elsewhere in the Sound, the median annual decline was only 1.5% (95% CI = 1.0% to 2.0%). The guillemots at the Naked Island group comprised about 25% of the total guillemot population in Prince William Sound during the 1989 nesting season, immediately after EVOS, but this declined to about 1% in 2007. There was suggestive evidence of a decline in guillemot density along oiled transects ($t = -1.91$, $P = 0.056$) in Prince William Sound (exclusive of transects at the Naked Island group; $\bar{x} = -0.83\%$, 95% CI = -1.67% to 0.02%).

Areas of High Guillemot Densities

Both the 1993 survey (Sanger and Cody 1994) and our survey in 2008 ended in mid-June, during the incubation period. However, the 1993 survey started about three weeks earlier than the 2008 survey, prior to egg-laying. Vermeer et al. (1993) reported higher but more variable peak colony counts during the pre-laying period than during incubation. There was no difference, however, in percent change from 1993 to 2008 for counts of guillemots that were completed during this first three weeks of the 1993 survey versus the last two weeks ($P = 0.788$).

There was no difference in the trend of guillemot numbers at high-density guillemot areas between oiled and un-oiled parts of PWS (two-sided permutation test, $P = 0.792$). If direct effects of lingering oil from EVOS were the sole cause of the decline in guillemot density at the Naked Island group, then we would also expect population declines at other high-density guillemot areas that were heavily oiled by EVOS. Further, we would expect stable or increasing populations in areas that were not oiled. Instead, there were population declines at all surveyed islands and fjords outside of the oil spill area. The only population increases between 1993 and 2008 occurred within the EVOS area at Seal Island and the Smith Island group (Figure 3.3), the latter of which was considered one of the most heavily oiled sites in the Sound following EVOS (Neff et al. 1995).

Between 1993 and 2008, there was a significantly greater decline in the number of guillemots at the Naked Island group than at other high-density guillemot areas in central and western Prince William Sound ($P = 0.042$; Table 3.1). The number of guillemots at Naked, Storey, and Peak islands declined significantly ($P = 0.050$; $\bar{x} = -211$; range = -80 to -338), while at other high-density guillemot areas in central and western Prince William Sound, there was only a suggestion of a decline ($P = 0.097$) in number of guillemots per area ($\bar{x} = -29.3$, range = -92 to 30). The relative contribution of guillemots at the Naked Island group to the total population of guillemots at all high-density areas in central and western Prince William Sound declined from 51.4% in 1993 to just 15.8% in 2008.

Only two high-density guillemot areas in western PWS had higher guillemot numbers in 2008 compared to 1993, and both were islands where we confirmed that mink were absent: the Smith Island group and Seal Island. Conversely, the only high-density guillemot area where a more severe decline in guillemot numbers occurred than at the Naked Island group was at Lone Island, where guillemots were completely absent in 2008. Unfortunately, there are no data on the presence or absence of mink on Lone Island in either 1993 or 2008, nor are there data on the relative abundance of schooling forage fish at this location.

There was a significant decline from 1993 to 2008 in the number of multi-pair guillemot groups counted at Naked, Storey, and Peak islands ($\bar{x}$ = -13; range = -6 to -24; P = 0.050). There was a greater percentage decline from 1993 to 2008 in the number of multi-pair guillemot groups counted at the Naked Island group than at the other high-density guillemot areas in central and western Prince William Sound (P = 0.023; Figure 3.4). There was no evidence of a decline in the number of multi-pair groups per area at other high-density guillemot areas ($\bar{x}$ = 0.1; range = -5 to 9; P = 0.294). There was no evidence, however, of a greater change between 1993 and 2008 in the size of multi-pair groups at the Naked Island group compared to other high-density guillemot areas (P = 0.251; Figure 3.5). There was also no evidence of a difference in average guillemot group size between the Naked Island group and other high-density guillemot areas either in 1993 (P = 0.388) or in 2008 (P = 0.848). But when group size data from all high-density guillemot areas were combined (including those from the Naked Island group), there was a significant difference (P = 0.0002) in average size of multi-pair groups between 1993 ($\bar{x}$ = 12.4, range = 4 to 48) and 2008 ($\bar{x}$ = 7.6, range = 4 to 19; Figure 3.6).

There was a significant increase from 1993 to 2008 in the percentage of all guillemots that were found in isolated pairs at Naked, Storey, and Peak islands ($\bar{x}$ = 44.3% change; range = 25.3% to 81.7%; P = 0.050). There was no evidence of a change in percentage of birds that were found in isolated pairs at other high-density guillemot areas ($\bar{x}$ = 13.0% change, range = -38.0% to 42.38%; *P* = 0.116). There was suggestive evidence of a difference between the Naked Island group and other high-density guillemot areas in the change between 1993 and 2008 in percentage of guillemots that were found in isolated pairs (*P* = 0.092; Figure 3.7).

DISCUSSION

We demonstrated, using data collected by Irons et al. (2000) and McKnight et al. (2008), that between 1989 and 2007 the median density of Pigeon Guillemots along transects at the Naked Island group declined at a much higher rate compared to the remainder of Prince William Sound. During this 18-year period, the median number of Pigeon Guillemots per km of shoreline at the Naked Island group decreased from having an order of magnitude more birds than elsewhere in PWS to a similar density. This occurred despite a significant decline in the median number of guillemots per km elsewhere in the Sound during the same period. The remarkable magnitude of the guillemot population decline at the Naked Island group cannot be attributed solely to the direct and indirect effects of EVOS, given the large difference in population trends at the Naked Island group compared to oiled transects across the remainder of PWS. These results provide strong support for our hypothesis that recent changes in predation pressure on guillemot nests, caused by the arrival of mink at the Naked Island group, prevented recovery of Pigeon Guillemots in that area, and eclipsed the more widespread effects of reduced availability of schooling forage fish.

We demonstrated that the decline in the size of the Pigeon Guillemot population between 1993 and 2008 was significantly greater at the Naked Island group than in other relatively high-density areas for guillemots in central and western PWS. As with the transect surveys, these results are consistent with our hypothesis that the recent advent of mink predation at the Naked Island group prevents recovery of Pigeon Guillemots more than the more widespread, region-wide effect of reduced availability of schooling forage fish.

There was an increase in the percentage of all counted guillemots that were in isolated pairs, as well as a proportionately greater decline in the number of multi-pair guillemot groups at the Naked Island group compared to other high-density guillemot areas. This may be explained in part by the greater decline in guillemot numbers at the Naked Island group. Unlike the Naked Island group, we did not detect a change in number of multi-pair groups or the percent of all guillemots found in isolated pairs at all other high-density guillemot areas. This indicates that declines in guillemots nesting in multi-pair groups (colonies) at the Naked Island group, but not at other high-density guillemot areas, were more responsible for overall guillemot declines than those nesting in isolated pairs. One of the costs of coloniality may be enhanced attraction of predators (Lack 1968, Burger 1984, Wittenberger and Hunt 1985), and several studies have demonstrated the rate of predation (Munro and Bédard 1977, Burger 1984, Brunton 1999) and predation risk (Brown and Brown 1996) can increase with colony size. Alternatively, nest sites at guillemot colony locations may be more accessible to mink than those of isolated breeding pairs.

The size of multi-pair groups of guillemots in PWS (Naked Island group and other high-density guillemot areas combined) declined from an average of about 12 birds in 1993 to about eight in 2008. Approximately 14% of all guillemot groups in 1993 contained ≥ 20 individuals, and maximum group size was 48 individuals. In 2008, however, no guillemot groups were found with ≥ 20 guillemots, and maximum group size was 19. This shift indicates that factors limiting populations across all high-density guillemot areas in PWS, regardless of location, were greater for larger colonies (≥ 20 birds) than for smaller ones (< 20 birds), a pattern consistent with a region-wide reduction in food availability, in particular schooling forage fishes. Larger colonies may experience greater reductions in local prey availability (Forero et al. 2002, Ainley et al. 2003, Ainley et al. 2006, Ballance et al. 2009) and lower breeding performance (Hunt et al. 1986, Suryan et al. 2000, Forero et al. 2002), particularly in years of lower overall food availability (Ainley et al. 2004), that in turn may negatively affect population growth (Lewis et al. 2001).

Our estimates of average guillemot densities along transects are somewhat higher than those of McKnight et al. (2008) and we found only suggestive evidence of a continued decline in the density of guillemots in the oiled area of PWS. This discrepancy can be explained by differences in data analysis, including: (1) our *a priori* α was 0.05, not α = 0.10, (2) we excluded offshore transects from the analysis, (3) we excluded transects at the Naked Island group from our analysis, and (4) we excluded transects where guillemots were never seen from our analysis.

Tide height, time of day, tide direction, reproductive stage, and weather all may affect the attendance of Pigeon Guillemots at colonies, although there is variation in the relative influence of these explanatory factors among locations (Kuletz 1983, Vermeer et al. 1993a). Surveys of guillemot density along transects were only conducted during good viewing conditions (i.e., low wind, wave height, and precipitation), when guillemot colony attendance is highest. Surveys were completed over about three weeks during the chick-rearing period (McKnight et al. 2008), and we found no evidence of a relationship between guillemot densities on transects and date of survey. Although other potentially significant explanatory factors were not standardized (McKnight et al. 2008), we have no reason to suspect a systematic bias in survey data between transects at the Naked Island group and those elsewhere in the Sound.

In summary, patterns in guillemot population trends across PWS were consistent with our hypothesis that increased predation of Pigeon Guillemot nests following a recent range expansion by mink is the primary factor limiting population recovery at the

Naked Island group, and a more significant local limiting factor than the apparent regional decline in availability of schooling forage fish. The decline in median density of Pigeon Guillemots along transects at the Naked Island group between 1989 and 2007 was more than seven times greater than that of the remainder of PWS. The population size of guillemots at the Naked Island group declined by more than 2.5 times that of all other high-density guillemot areas across central and western PWS between 1993 and 2008. The prevalence of coloniality in Pigeon Guillemots, indicated by the presence of multi-pair groups, declined at the Naked Island group, but remained stable across other high-density guillemot areas in PWS during this period, potentially due to a greater risk of mink predation for guillemots nesting in colonies compared to isolated pairs. The average group size of Pigeon Guillemots declined across Prince William Sound, however, from an average of 12 individuals to eight individuals per group, suggesting that a regional factor, such as availability of schooling forage fish, may also regulate the guillemot population in PWS. Nonetheless, the trends indicate that mink predation is the primary factor limiting recovery of Pigeon Guillemots at the Naked Island group, which has historically supported the largest number of breeding guillemots in Prince William Sound.

LITERATURE CITED

Agler, B. A., S. J. Kendall, D. B. Irons, and S. P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. Waterbirds 22:98-103.

Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. Ecology 87:2080-2093.

Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology 84:709-723.

Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adélie Penguin populations: overlap in colony-specific foraging areas. Ecological Monographs 74:159-178.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transaction on Automatic Control 19:716-723.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117-123.

Ballance, L. T., D. G. Ainley, G. Ballard, and K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. Journal of Avian Biology 40:279-288.

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

Brown, C. R., and M. B. Brown. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, IL.

Brown, E. D. 2003. Stock structure and environmental effects on year class formation and population trends of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska. Ph.D. dissertation, University of Alaska Fairbanks, Fairbanks, AK.

Brown, E. D., J. Wang, S. L. Vaughan, and B. L. Norcross. 1999. Identifying seasonal spatial scale for the ecological analysis of herring and other forage fish in Prince William Sound, Alaska. *in* Proceedings of Lowell Wakefield Fisheries Symposium: Ecosystem approaches in fisheries management AK-SG-99-01, Fairbanks, AK.

Brunton, D. 1999. "Optimal" colony size for Least Terns: an inter-colony study of opposing selective pressures by predators. Condor 101:607-615.

Burger, J. 1984. Colony stability in Least Terns. Condor 86:61-67.

Cairns, D. K. 1985. Ermine visitation to Black Guillemot colonies in northeastern Hudson Bay. Condor 87:144-145.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Cooper, W. S. 1942. Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. Ecological Monographs 12:2-22.

Day, R. H., S. M. Murphy, J. A. Wiens, G. D. Hayward, E. J. Harner, and L. N. Smith. 1997. Effects of the *Exxon Valdez* Oil Spill on habitat use by birds in Prince William Sound, Alaska. Ecological Applications 7:593-613.

Eslinger, D. L., R. T. Cooney, C. P. McRoy, A. Ward, T. C. Kline, E. P. Simpson, J. Wang, and J. R. Allen. 2001. Plankton dynamics: observed and modeled responses to physical conditions in Prince William Sound, Alaska. Fisheries Oceanography 10:81-96.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). *in* A. Poole, and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Fleming, M. A., and J. A. Cook. 2010. MtDNA and microsatellite DNA provide evidence of fur farm ancestry for mink populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project 070853. Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM.

Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic penguins. Ecology 83:3466-3475.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7:1-21.

Gaston, A. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. Ibis 139:673-678.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on Pigeon Guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Hunt, G. L., Z. A. Eppley, and D. C. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. Auk 103:306-317.

Irons, D. B., S. J. Kendall, W. P. Erickson, L. L. McDonald, and B. K. Lance. 2000. Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska. Condor 102:723-737.

Jennrich, R. I., and M. D. Schluchter. 1986. Unbalanced repeated-measures models with structured covariance matrices. Biometrics 42:805-820.

Kline, T. C., Jr. 1999. Temporal and spatial variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in pelagic biota of Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:94-117.

Klosiewski, S. P., and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. U.S. Fish and Wildlife Service, Anchorage, AK.

Kuletz, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. Unpubl. M.Sc. thesis in Biological Sciences, University of California, Irvine, CA.

Lack, D. 1968. Ecological adaptations for breeding birds. Methuen, London.

Lewis, S., T. N. Sherratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412:816-819.

Marty, G. D. 2008. Effects of the *Exxon Valdez* oil spill on Pacific herring in Prince William Sound, Alaska. Pages 925-932 *in* R. T. D. Giulio, and D. E. Hinton, editors. Toxicology of fishes. CRC Press, Boca Raton, FL.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Munro, J., and J. Bédard. 1977. Gull predation and creching behaviour in the Common Eider. Journal of Animal Ecology 46:799-810.

Murphy, S. M., R. H. Day, J. A. Wiens, and K. R. Parker. 1997. Effects of the *Exxon Valdez* oil spill on birds: Comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299-313.

Neff, J. M., E. H. Owens, S. W. Stoker, and D. M. McCormick. 1995. Shoreline oiling conditions in Prince William Sound following the *Exxon Valdez* oil spill. *in* P. G. Wells, J. N. Butler, and J. S. Hughes, editors. *Exxon Valdez* oil spill: fate and effects in Alaskan waters. ASTM Special Technical Publication no. 1219, American Society of Testing Materials, Philadelphia, PA.

Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99:14113-14126.

Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline, D. M. Mason, E. V. Patrick, A. J. Paul, and K. D. E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10:42-57.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Paul, T. 2009. Game transplants in Alaska. Technical bulletin No. 4, second edition. Alaska Department of Fish and Game, Juneau, AK.

Piatt, J. F., D. W. Macdonald, C. J. Lensink, W. Butler, M. Kendziorek, and D. R. Nysewander. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107:387-397.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, CA.

Sagar, P. M., and D. S. Horning. 1998. Mass-related survival of fledgling Sooty Shearwaters *Puffinus griseus* at The Snares, New Zealand. Ibis 140:329-339.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Seiser, P. E., L. K. Duffy, A. D. McGuire, D. D. Roby, G. H. Golet, and M. A. Litzow. 2000. Comparison of pigeon guillemot, *Cepphus columba*, blood parameters from oiled and unoiled areas of Alaska eight years after the *Exxon Valdez* oil spill. Marine Pollution Bulletin 40:152-164.

Stienen, E. W. M., and A. Brenninkmeijer. 2002. Variation in growth in Sandwich Tern chicks *Sterna sandvicensis* and the consequences for pre- and post-fledging mortality. Ibis 144:567-576.

Suryan, R. M., D. B. Irons, and J. Benson. 2000. Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect on reproductive success. Condor 102:374-384.

Vaughan, S. L., C. N. K. Mooers, and S. M. Gay. 2001. Physical variability in Prince William Sound during the SEA study (1994-98). Fisheries Oceanography 10:58-80.

Vermeer, K., K. H. Morgan, and G. E. J. Smith. 1993. Colony attendance of pigeon guillemots as related to tide height and time of day. Colonial Waterbirds 16:1-8.

Wiens, J. A., T. O. Crist, R. H. Day, S. M. Murphy, and G. D. Hayward. 1996. Effects of the *Exxon Valdez* oil spill on marine bird communities in Prince William Sound, Alaska. Ecological Applications 6:828-841.

Wittenberger, J. F., and G. L. Hunt. 1985. The adaptive significance of coloniality in birds. Volume 8.Academic Press, San Diego, CA.

Table 3.1. The area surveyed (km^2), the total number of Pigeon Guillemots counted in 1993 and in 2008, and the percent change in number of guillemots between years at three islands in the Naked Island group and eight islands/coastal fjords elsewhere in central and western Prince William Sound, Alaska that were identified by Sanger and Cody (1994) as high-density guillemot areas in 1993.

Location	Island/Fjord	Area Surveyed (km^2)	Total # Guillemots 1993	Total # Guillemots 2008	Percent Change
Naked Island Group	Naked Island	7.6	383	45	-88.3
	Storey Island	2.0	240	25	-89.6
	Peak Island	1.4	93	13	-86.0
	Total	11.1	716	83	-88.4
Western PWS	Passage Canal	2.7	70	30	-57.1
	Fool Island	0.2	65	55	-15.4
	Lone Island	1.2	92	0	-100.0
	Smith Island Group	1.7	107	137	+28.0
	Seal Island	0.4	62	74	+19.4
	Pleiades Islands	0.4	48	13	-72.9
	Jackpot Island	0.1	78	22	-71.8
	Port Bainbridge	6.6	155	112	-27.7
	Total	13.4	677	443	-34.6

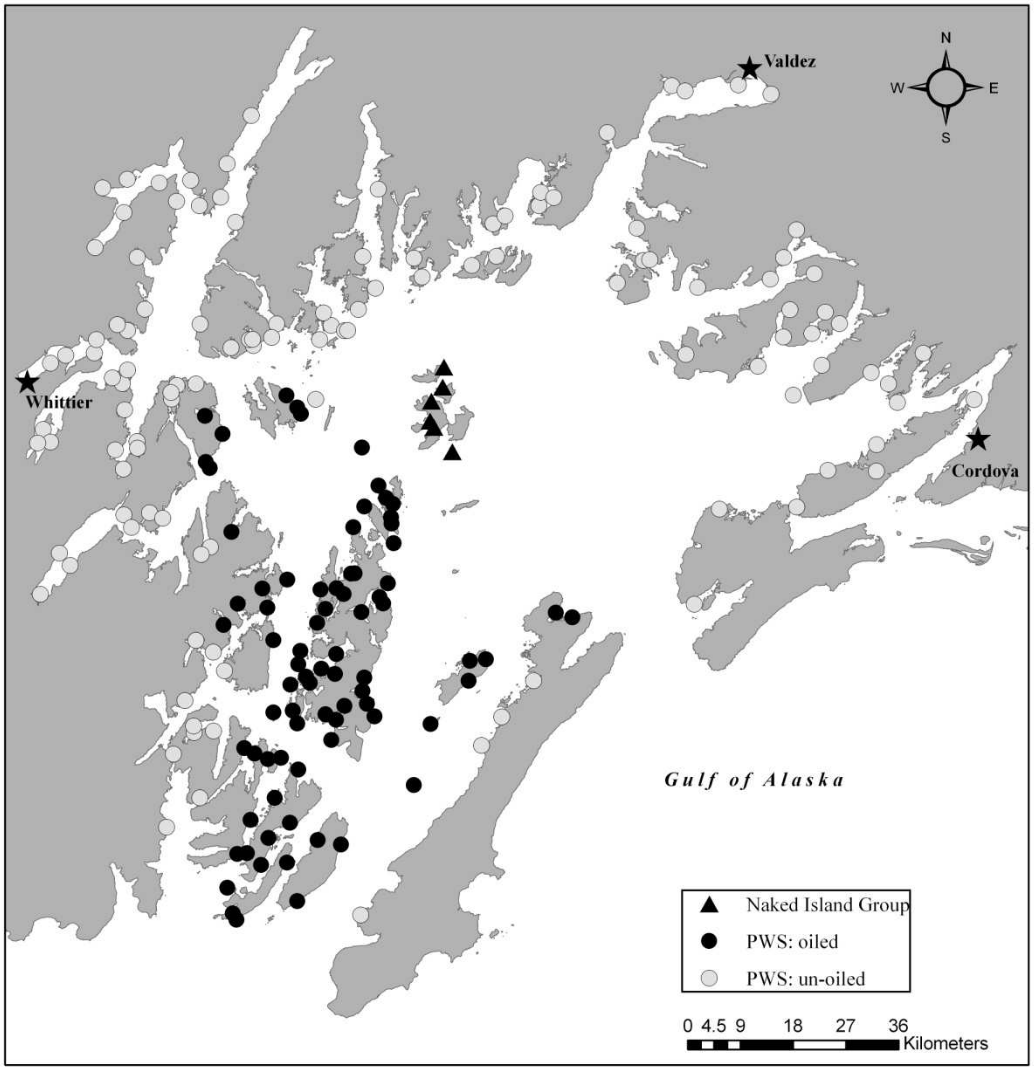


Figure 3.1. Locations of shoreline transects across Prince William Sound, Alaska where data were collected on Pigeon Guillemot densities during 10 years between 1989 and 2007 by Irons et al. (2000) and McKnight et al. (2008). Black circles indicate locations of transects that were oiled following the 1989 *Exxon Valdez* oil spill. Grey circles indicate the locations of un-oiled transects. Black triangles indicate transects located at the Naked Island group, regardless of oiling.

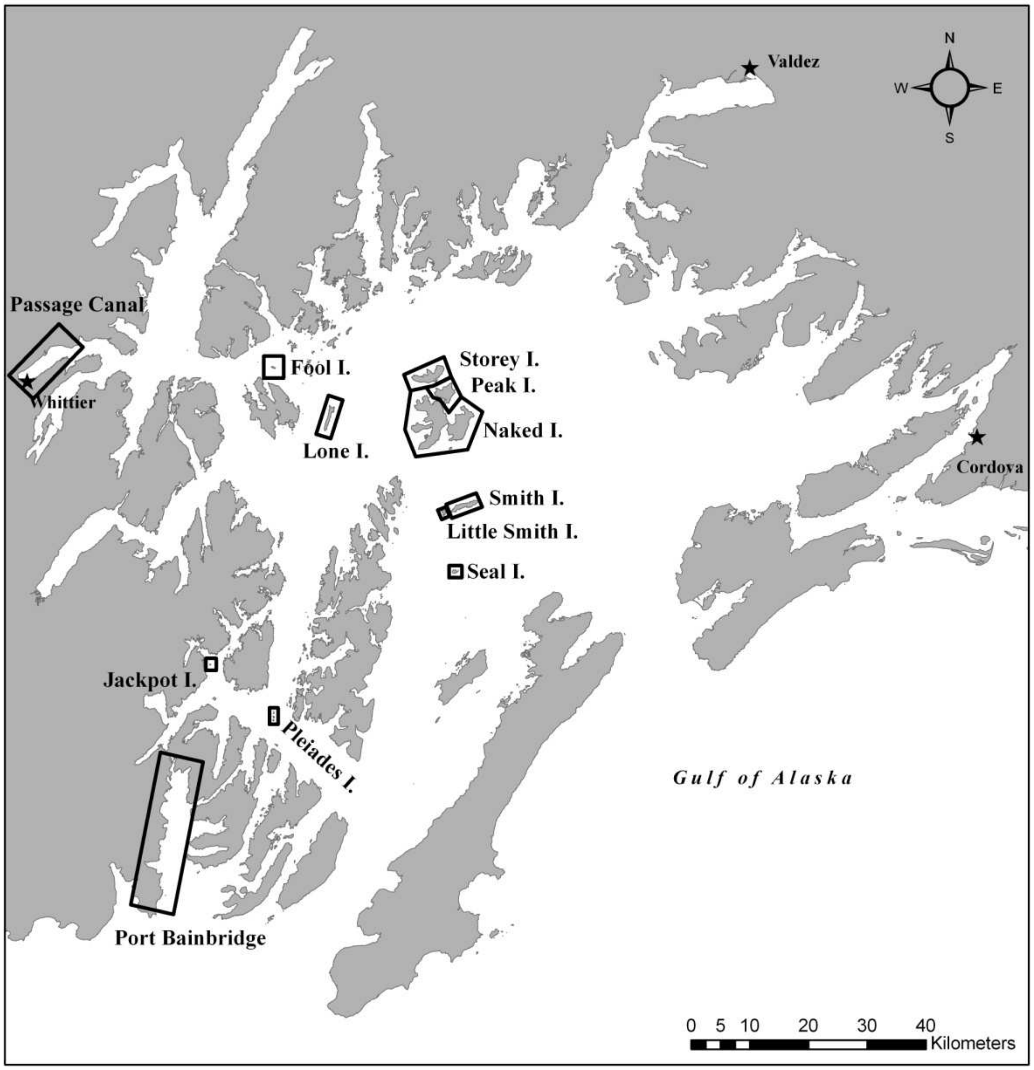


Figure 3.2. Locations with high densities of Pigeon Guillemots (boxed areas) in central and western Prince William Sound, Alaska identified in 1993 by Sanger and Cody (1994). We re-surveyed the shoreline guillemot population in these areas in 2008.

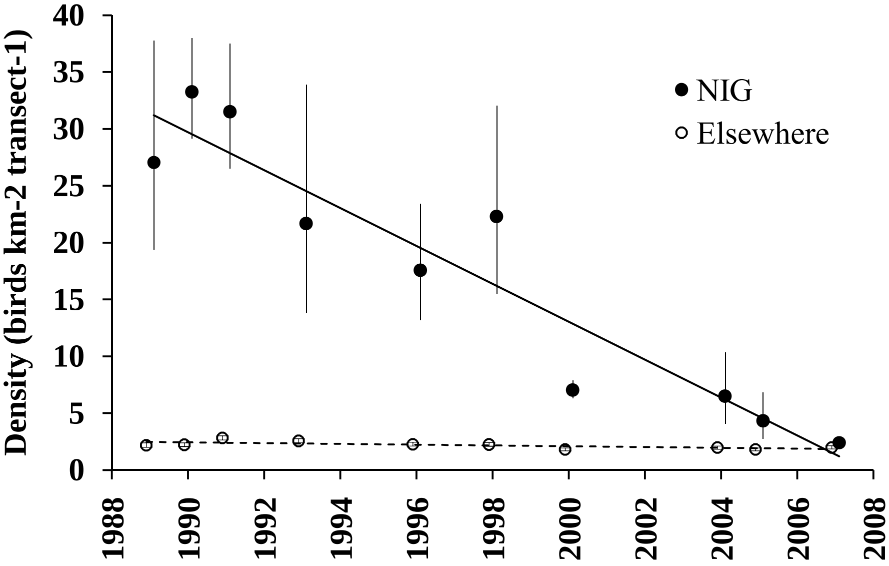


Figure 3.3. Median (± 95% CI) and trend in Pigeon Guillemot densities along transects surveyed at the Naked Island group (solid line) and along oiled transects in the remainder of Prince William Sound, Alaska (dashed line). Data are from McKnight et al. (2008).

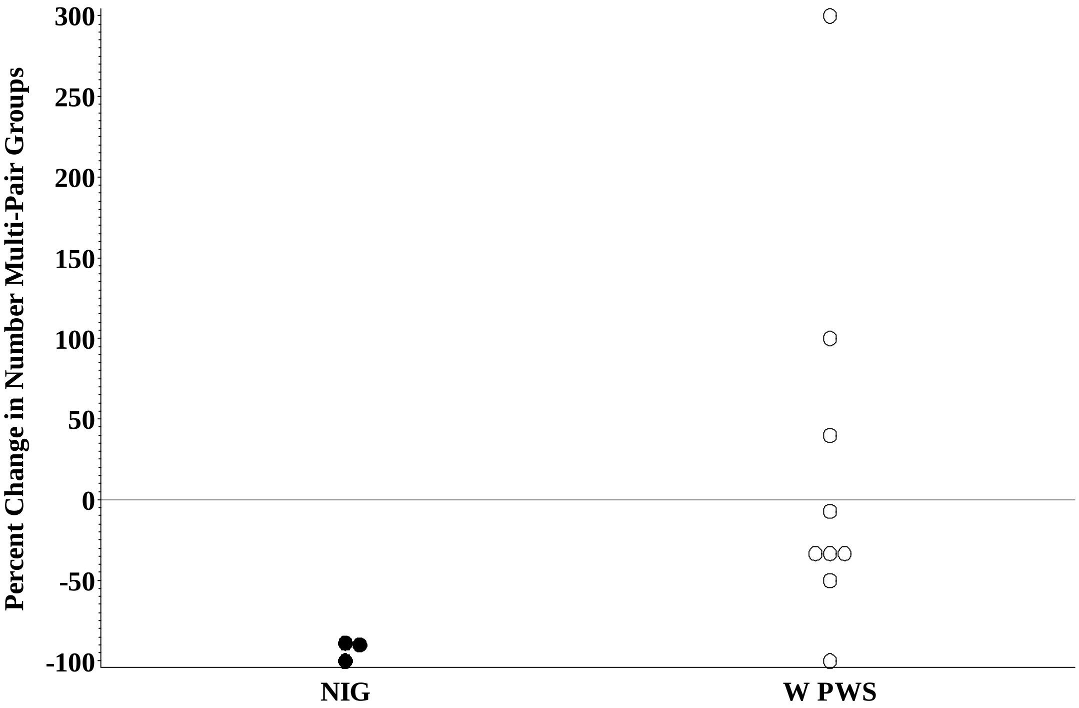
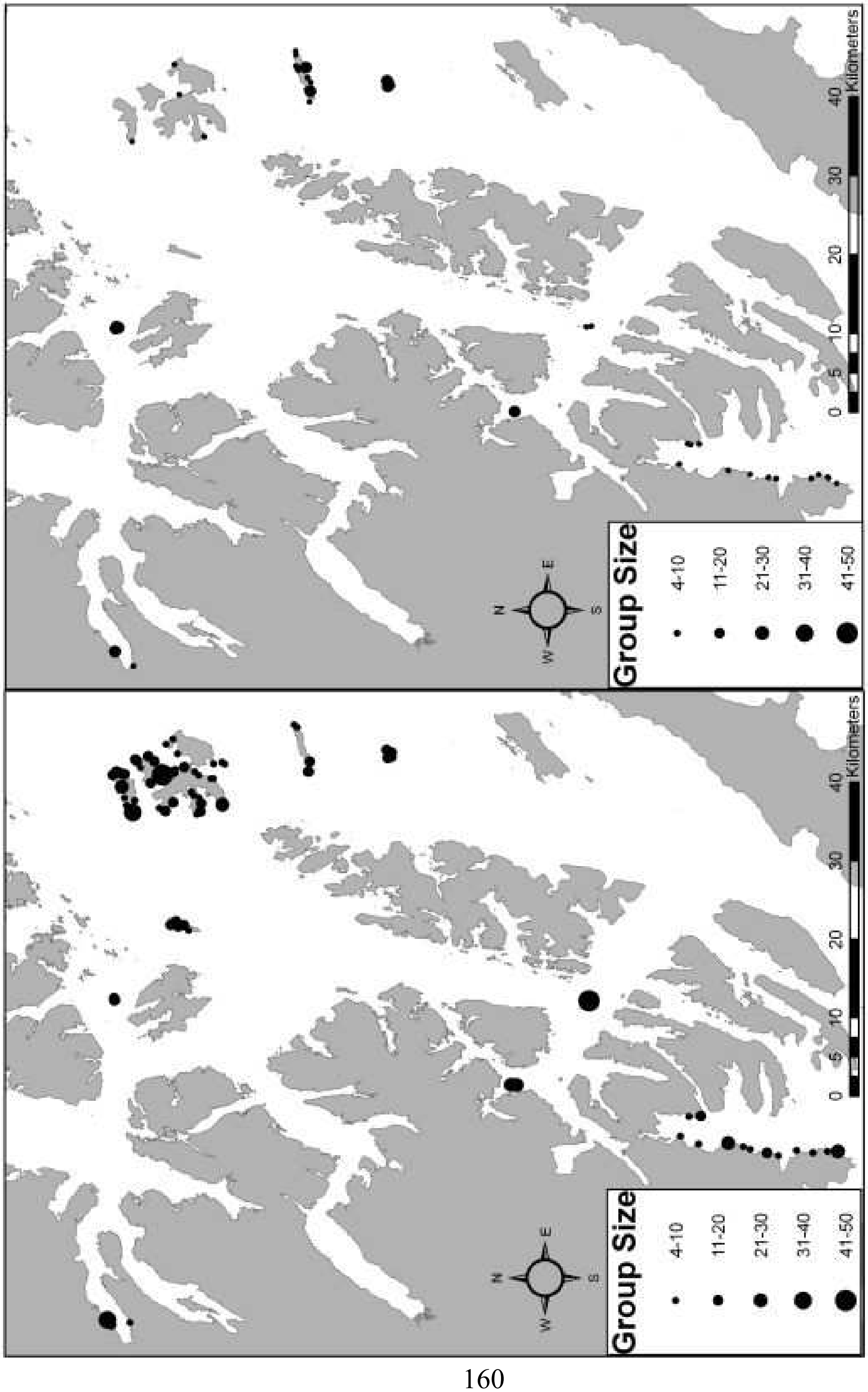


Figure 3.4. The percent change from 1993 to 2008 in the number of multi-pair groups (≥ 4 individuals) of Pigeon Guillemots counted at three islands in the Naked Island group and nine islands or coastal fjords in central and western Prince William Sound, Alaska. Data from 1993 are from Sanger and Cody (1994).

Figure 3.5. Location and size of all multi-pair groups (≥ 4 individuals) of Pigeon Guillemots at 12 islands/coastal fjords in central and western Prince William Sound, Alaska counted in 1993 (left panel) and again in 2008 (right panel). Data from 1993 are from Sanger and Cody (1994).


Group Size
4-10
11-20
21-30
31-40
41-50
N
E
S
W
0
5
10
20
30
40
Kilometers
Group Size
4-10
11-20
21-30
31-40
41-50
N
E
S
W
0
5
10
20
30
40
Kilometers

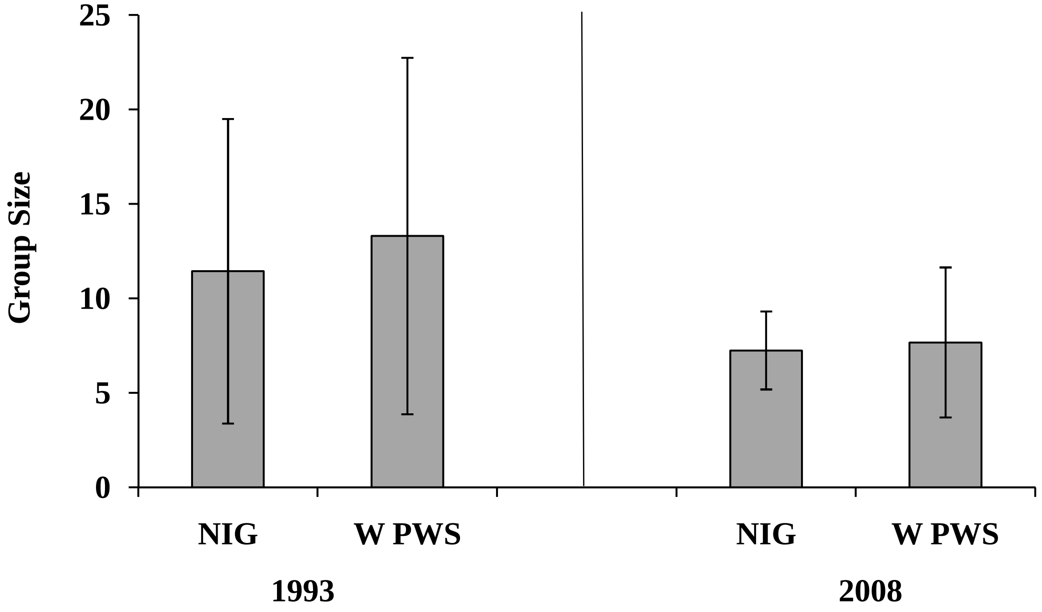


Figure 3.6. Mean (± SE) number of Pigeon Guillemots in multi-pair groups (≥ 4 individuals) at the Naked Island group (NIG) and other high-density guillemot areas in central and western Prince William Sound (W PWS), Alaska in 1993 and 2008. Data from 1993 are from Sanger and Cody (1994).

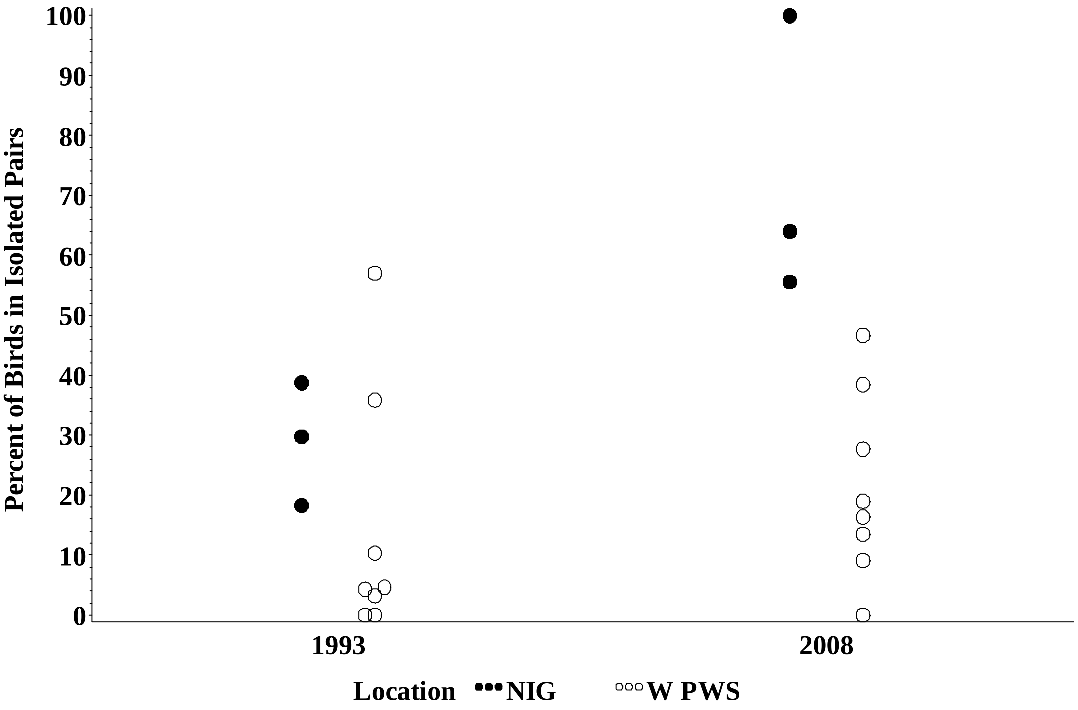


Figure 3.7. Percentage of Pigeon Guillemots located in isolated pairs (< 4 birds) during a census of high-density areas in 1993 and 2008 at three islands in the Naked Island group (NIG) and 8 islands/coastal fjords in central and western Prince William Sound (W PWS), Alaska. Solid circles represent the Naked Island group; open circles represent all other areas surveyed in central and western Prince William Sound. Data from 1993 are from Sanger and Cody (1994).

CHAPTER 4

SYNOPSIS AND CONCLUSIONS

Kirsten S. Bixler

The Pigeon Guillemot (*Cepphus columba*) is currently one of only two species listed as "not recovering" since the *Exxon Valdez* oil spill in 1989 on the *Exxon Valdez* Oil Spill Trustee Council's Injured Resources List (*Exxon Valdez* Oil Spill Trustee Council 2009). The guillemot population declined by more than 85% in Prince William Sound from about 15,500 individuals in 1972 (Agler et al. 1999) to about 2,100 individuals in 2007 (McKnight et al. 2008). A portion of this decline can be directly attributed to the oil spill, which immediately killed from 500 to 1,500 guillemots in Prince William Sound (Litzow et al. 2002). In addition, hepatic cytochrome P4501A, the most reliable known indicator of exposure to residual oil in Pigeon Guillemots (Hovey 2002), remained at elevated levels in the Prince William Sound population for up to 15 years after the spill (B. Ballachey, U.S. Geological Survey, pers. comm., Golet et al. 2002). Although there was no longer evidence from Pigeon Guillemots of direct exposure to residual oil by 2004, the Sound-wide Pigeon Guillemot population continued to decline (McKnight et al. 2008). Other factors appear to now be preventing the recovery of Pigeon Guillemots in Prince William Sound.

I assessed the relative importance of two mechanisms that have been identified in prior studies as probable limiting factors for guillemot population recovery: reduced availability of schooling forage fish and predation, especially by mink (Oakley and Kuletz 1996, Golet et al. 2002). I compared data that I collected on guillemot demography, diet, and prey during 2007 and 2008 with similar data collected during 13 years of previous research on guillemots at the Naked Island group, which at one time was the most important breeding area for guillemots in the Sound.

The lack of recovery of guillemots at the Naked Island group during the 1990s was attributed, in addition to exposure to residual oil (Golet et al. 2002), to a reduction in availability of schooling prey, specifically sand lance (*Ammodytes hexapterus*; Oakley and Kuletz 1996, Agler et al. 1999, Golet et al. 2002) and, to a lesser extent, an increase in local nest predation rates (Hayes 1996, Oakley and Kuletz 1996, Golet et al. 2002). Changes in forage fish availability may be a long-term legacy of the *Exxon Valdez* oil spill (Golet et al. 2002, Marty 2008) and/or the result of a shift in the Pacific Decadal Oscillation during 1976 to a warmer regime of ocean conditions (Agler et al. 1999, Golet et al. 2002). This regime shift has been associated with reductions in schooling fish species in the Gulf of Alaska that have yet to recover (Anderson and Piatt 1999). Changes in species composition within the guillemot prey base can have population level effects on guillemots. The percent of high-lipid schooling fish (sand lance, herring, and smelt spp.) in the diet of guillemot chicks has been correlated with higher nestling survival, higher productivity, and higher chick growth rates (Golet et al. 2000, Litzow et al. 2002).

The level of nest predation has also had a direct effect on the productivity of Pigeon Guillemots in Prince William Sound. Significant spatial and temporal variation in nest predation rates have been documented for guillemots in the Sound (Golet et al. 2002). In some areas of the Sound, there was evidence of an increase in the rate of predation on guillemot nests after the *Exxon Valdez* oil spill (Oakley and Kuletz 1996, Golet et al. 2002).

I demonstrated, using multiple measures of population size and distribution, that the decline in the guillemot breeding population at the Naked Island group was more severe than at other locations in Prince William Sound. Between 1989 and 2007, the median density of guillemots along transects at the Naked Island group declined by 12.5% per year, compared to an average decline of only 1.5% per year throughout the remainder of Prince William Sound. The relative contribution of the guillemot population at the Naked Island group to the total numbers of guillemots nesting in Prince William Sound shifted from more than 20% in 1989 to about 1% in 2007. Between 1993 and 2007, there was also a greater percentage decline in the number of guillemots at the Naked Island group compared to other areas in western Prince William Sound that supported high-densities of nesting guillemots. The percentage of all guillemots in high-density areas throughout Prince William Sound that were found at the Naked Island group declined from 51.4% in 1993 to 15.8% in 2008.

Changes in the size of guillemot aggregations also differed markedly between the Naked Island group and other high-density guillemot areas in the Sound. The number of multi-pair groups declined at the Naked Island group, but not in other high-density guillemot areas in the Sound. The percentage of all guillemots that were found in isolated pairs increased at the Naked Island group, but not at other high-density guillemot areas, indicating that the incidence of coloniality decreased disproportionately at the Naked Island group. These results suggest that population limiting factors for guillemots at the Naked Island group are more severe than, if not different from, those in other areas of Prince William Sound. However, the size of multi-pair groups of guillemots, an indicator of the size of breeding colonies, declined consistently across Prince William Sound by about 1/3, from an average of 12 to 8 individuals per group, suggesting that a region-wide factor, such as food availability, may also limit population recovery.

I demonstrated that the proportion of schooling fish (sand lance, herring, and smelt spp.) in the diet of guillemots at the Naked Island group in 2008 had not returned to pre-spill levels, and this was reflected in lower chick condition indices and possibly lower chick growth rates compared to pre-spill conditions. However, I found evidence that the abundance of schooling forage fish at the Naked Island group is recovering since the 1990s. Beach seine catches at Naked Island suggested an increase (though not significant) in overall forage fish abundance, while aerial surveys for schooling forage fishes indicated a strong increase in abundance at the Naked Island group since the 1990s. In 2008, the percentage of schooling forage fish in chick diets, as well as chick growth rates, were higher than those recorded in several studies at locations outside Alaska (Drent 1965, Ainley et al. 1990, Emms and Verbeek 1991, Vermeer et al. 1993b, Golet et al. 2000).

I found that mink predation appeared to be the primary factor limiting recovery of the population of guillemots at the Naked Island group in 2008. The Pigeon Guillemot population crashed at islands with mink (Naked Island group), but remained stable at nearby mink-free islands (Smith Island group) between 1990 and 2008. Records of shoreline oiling in the aftermath of the spill and aerial surveys of schooling forage fish in 1998-1999 and 2008 suggest that this difference in guillemot population trends was not a function of differences between the two island groups in either oiling or food availability. Mink apparently first arrived at the Naked Island group between 1981 and 1994 (K. Kuletz, unpubl. data; Hayes 1995). Although depredated guillemot nests usually did not contain sufficient evidence to conclusively identify the type of predator, records of mink predation on guillemot nests increased at the Naked Island group through the 1990s. The highest recorded rate of mink predation occurred in 1998, when 60% of monitored guillemot nests were depredated by mink and 4.5% of adults associated with those nests were killed by mink. I confirmed that mink predation was as a cause of guillemot chick mortality at the Naked Island group in

2008, even though there were only 17 - 22 active guillemot nests at the entire Naked Island group in that year. In 2008, the majority of guillemot chick mortality was again attributable to predation.

I found evidence of a dramatic shift in the type of nest sites used by guillemots at the Naked Island group between 1978 and 2008. The prevalence of guillemot nests in sites that were apparently inaccessible to mink (crevices in cliff faces) increased, while the prevalence of nest sites likely to be accessible to mink (crevices in talus and burrows at the top edge of cliffs and steep banks) decreased. In 2008, not a single active nest site was found in talus, although previously 25% of all nests had been located in talus. The percentage of all eggs and chicks that were depredated increased during the 1990s compared to earlier years. The majority (57%) of chick and egg mortality was caused by predation during the 1990s and overall productivity of guillemots was correlated to the rate of nest predation.

My study was able to demonstrate through aerial surveys and beach seines that both schooling and demersal forage fish abundance was higher in 2008 than during the 1990s. The prevalence of schooling forage fish in the diet of Pigeon Guillemots had not recovered to pre-EVOS levels, however, and was potentially a contributing factor in limiting the recovery of guillemots at the Naked Island group. The consistent decline in the average size of guillemot groups across PWS suggested that food availability may affect recovery Sound-wide. However, the weight of evidence indicated that predation by mink was the *primary* limiting factor for nest success and guillemot population recovery at the Naked Island group. The marked dissimilarity in population trends indicated that the population limiting factors at the Naked Island group were different from and more severe than at other breeding locations in Prince William Sound, consistent with my expectations given a local primary limiting factor, mink predation, at the Naked Island group. Continued study of these island populations of guillemots and their predators and prey is certainly warranted given the extraordinary population crash at what was once the most important nesting location for the species in Prince William Sound, along with the difficulty of devising any feasible and cost-effective means for restoration of Pigeon Guillemots at the Naked Island group or elsewhere in the Sound.

CONSERVATION IMPLICATIONS

Restoration of the Pigeon Guillemot population in the aftermath of the *Exxon Valdez* oil spill requires identification of both feasible restoration sites and cost-effective restoration options. This study provided current information on factors that limit guillemot recovery in Prince William Sound and it was conducted at a logical area for future restoration action. This area, the Naked Island group, was at one time the single most important breeding location for Pigeon Guillemots in Prince William Sound. In

1972, one-third of the Sound-wide population of guillemots was counted there, though these islands include just 2% of the total shoreline in the Sound (Isleib and Kessel 1972). Recovery of the guillemot population at the Naked Island group to its estimated size in 1972 would triple the current population of guillemots in all of Prince William Sound.

My study suggested that nest predation, particularly by mink, is currently the primary limiting factor for nest success and population recovery of guillemots at the Naked Island group. The mink on the Naked Island group are descended in part from fur farm mink (Fleming and Cook 2010), and all available data suggest that mink arrived on the islands about 15-30 years ago and were introduced there by humans. Similar range expansions of fur farm mink have been documented in other locations, with devastating results for seabirds, shorebirds, passerines, waterfowl, amphibians, and potentially, the intertidal community (Cairns 1985, Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, Delibes et al. 2004, Banks et al. 2008). This type of predation can be addressed successfully for guillemots through restoration actions that include the control or eradication of mink, or the provision of safe nesting habitat that is inaccessible to mink (Nordström et al. 2003). However, because I was not able to quantify the impact of mink on guillemot population trends, I cannot predict the guillemot population response should mink be eradicated at the Naked Island group. Complete recovery of the Pigeon Guillemot population in Prince William Sound to numbers recorded in the early 1970s may not occur until availability of schooling forage fish has returned to levels pre-EVOS and to pre-1976 regime shift conditions in the Pacific Decadal Oscillation. But removal of the population of mink on the Naked Island group, which appears to have been introduced, would likely result in a pronounced increase in the local breeding population of Pigeon Guillemots, as well as increased guillemot productivity at the Naked Island group. This would constitute the first step in recovery of the Pigeon Guillemot population from damages caused by EVOS, as well as help restore breeding populations of other seabirds and ground-nesting birds at the Naked Island group.

LITERATURE CITED

Agler, B. A., S. J. Kendall, D. B. Irons, and S. P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. Waterbirds 22:98-103.

Ainley, D. G., R. J. Boekelheide, S. H. Morrell, and C. S. Strong. 1990. Pigeon Guillemot. Pages 276-305 *in* D. G. Ainley, and R. J. Boekelheide, editors. Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Stanford University Press, Stanford, CA.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117-123.

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

Cairns, D. K. 1985. Ermine visitation to Black Guillemot colonies in northeastern Hudson Bay. Condor 87:144-145.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Delibes, M., M. Clavero, J. Prenda, M. D. C. Blázquez, and P. Ferreras. 2004. Potential impact of an exotic mammal on rocky intertidal communities of northwestern Spain. Biological Invasions 6:213-219.

Drent, R. H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba*. Ardea 53:3-4.

Emms, S. K., and N. A. M. Verbeek. 1991. Brood size food provisioning and chick growth in the pigeon guillemot *Cepphus columba*. Condor 93:943-951.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Fleming, M. A., and J. A. Cook. 2010. MtDNA and microsatellite DNA provide evidence of fur farm ancestry for mink populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project 070853. Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on Pigeon Guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Hayes, D. L. 1995. Recovery monitoring of Pigeon Guillemot populations in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Unpubl. Report, Anchorage, AK.

_____. 1996. A comparison of the breeding and feeding ecology of Pigeon Guillemots at Naked and Jackpot islands in Prince William Sound, APEX: 95163 F. U.S. Fish and Wildlife Service, Anchorage, AK.

Hovey, A. K. 2002. Effects of diet and crude oil ingestion on growth and biochemistry of captive-reared pigeon guillemots (*Cepphus columba*). Unpubl. M.S. Thesis, Oregon State University, Corvallis, OR.

Litzow, M. A., J. F. Piatt, A. K. Prichard, and D. D. Roby. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286-295.

Marty, G. D. 2008. Effects of the *Exxon Valdez* oil spill on Pacific herring in Prince William Sound, Alaska. Pages 925-932 *in* R. T. D. Giulio, and D. E. Hinton, editors. Toxicology of fishes. CRC Press, Boca Raton, FL.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Oakley, K. L., and K. J. Kuletz. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:759-769.

Vermeer, K., K. H. Morgan, and G. E. J. Smith. 1993. Nesting biology and predation of pigeon guillemots in the Queen Charlotte Islands, British Columbia. Colonial Waterbirds 16:119-127.

BIBLIOGRAPHY

Agler, B. A., S. J. Kendall, D. B. Irons, and S. P. Klosiewski. 1999. Declines in marine bird populations in Prince William Sound, Alaska coincident with a climatic regime shift. Waterbirds 22:98-103.

Ainley, D. G., G. Ballard, and K. M. Dugger. 2006. Competition among penguins and cetaceans reveals trophic cascades in the Western Ross Sea, Antarctica. Ecology 87:2080-2093.

Ainley, D. G., R. J. Boekelheide, S. H. Morrell, and C. S. Strong. 1990. Pigeon Guillemot. Pages 276-305 *in* D. G. Ainley, and R. J. Boekelheide, editors. Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community. Stanford University Press, Stanford, CA.

Ainley, D. G., R. G. Ford, E. D. Brown, R. M. Suryan, and D. B. Irons. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. Ecology 84:709-723.

Ainley, D. G., and T. J. Lewis. 1974. The history of Farallon Island marine bird populations, 1854-1972. Condor 76:432-446.

Ainley, D. G., C. A. Ribic, G. Ballard, S. Heath, I. Gaffney, B. J. Karl, K. J. Barton, P. R. Wilson, and S. Webb. 2004. Geographic structure of Adélie Penguin populations: overlap in colony-specific foraging areas. Ecological Monographs 74:159-178.

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transaction on Automatic Control 19:716-723.

Anderson, P. J., J. E. Blackburn, and B. A. Johnson. 1997. Declines of forage species in the Gulf of Alaska, 1972-1995, as an indicator of regime shift. Pages 531-543 *in* Forage Fishes in Marine Ecosystems. Proceedings of an International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Report No.97-01. Fairbanks, AK.

Anderson, P. J., and J. F. Piatt. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. Marine Ecology Progress Series 189:117-123.

Anthony, J. A., D. D. Roby, and K. R. Turco. 2000. Lipid content and energy density of forage fishes from the northern Gulf of Alaska. Journal of Experimental Marine Biology and Ecology 248:53-78.

Ballance, L. T., D. G. Ainley, G. Ballard, and K. Barton. 2009. An energetic correlate between colony size and foraging effort in seabirds, an example of the Adélie penguin *Pygoscelis adeliae*. Journal of Avian Biology 40:279-288.

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

Benson, J., R. M. Suryan, and J. F. Piatt. 2003. Assessing chick growth from a single visit to a seabird colony. Marine Ornithology 31:181-184.

BirdLife International. 2009. Species factsheet: *Cepphus columba*. Downloaded from http://birdlife.org on 5/1/2010.

Brown, C. R., and M. B. Brown. 1996. Coloniality in the Cliff Swallow: the effect of group size on social behavior. University of Chicago Press, Chicago, IL.

Brown, E. D. 2003. Stock structure and environmental effects on year class formation and population trends of Pacific herring, *Clupea pallasi*, in Prince William Sound, Alaska. Ph.D. dissertation, University of Alaska Fairbanks, Fairbanks, AK.

Brown, E. D., and M. G. Carls. 1998. Pacific herring. Restoration Notebook. *Exxon Valdez* Oil Spill Trustee Council. Anchorage, AK.

Brown, E. D., and S. M. Moreland. 2000. Ecological factors affecting the distribution and abundance of forage fish in Prince William Sound, Alaska; an APEX synthesis product, Restoration Project 00163T. Anchorage, AK.

Brown, E. D., J. Wang, S. L. Vaughan, and B. L. Norcross. 1999. Identifying seasonal spatial scale for the ecological analysis of herring and other forage fish in Prince William Sound, Alaska. *in* Proceedings of Lowell Wakefield Fisheries Symposium: Ecosystem approaches in fisheries management AK-SG-99-01, Fairbanks, AK.

Brunton, D. 1999. "Optimal" colony size for Least Terns: an inter-colony study of opposing selective pressures by predators. Condor 101:607-615.

Burger, J. 1984. Colony stability in Least Terns. Condor 86:61-67.

Cailliet, G. M., M. S. Love, and A. W. Ebeling. 1986. Fishes: A field and laboratory manual on their structure, identification, and natural history. Wadsworth Publishing, Belmont, CA.

Cairns, D. K. 1985. Ermine visitation to Black Guillemot colonies in northeastern Hudson Bay. Condor 87:144-145.

Carlson, H. R. 1980. Seasonal distribution and environment of Pacific herring near Auke Bay, Lynn Canal, Southeastern Alaska. Transactions of the American Fisheries Society 109:71-78.

Churnside, J. H., D. A. Demer, and B. Mahmoudi. 2003. A comparison of lidar and echosounder measurements of fish schools in the Gulf of Mexico. ICES Journal of Marine Science 60:147-154.

Clarke, K. R. 1993. Nonparametric multivariate analysis of changes in community structure. Australian Journal of Ecology 18:117-143.

Clarke, K. R., and R. H. Green. 1988. Statistical design and analysis for a 'biological effects' study. Marine Ecology Progress Series 46:213-226.

Clarke, K. R., and R. M. Warwick. 2001. Change in marine communities: an approach to statistical analysis and interpretation, 2nd edition, PRIMER-E, Plymouth, UK.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Cooper, W. S. 1942. Vegetation of the Prince William Sound region, Alaska; with a brief excursion into post-Pleistocene climatic history. Ecological Monographs 12:2-22.

Day, R. H., S. M. Murphy, J. A. Wiens, G. D. Hayward, E. J. Harner, and L. N. Smith. 1997. Effects of the *Exxon Valdez* Oil Spill on habitat use by birds in Prince William Sound, Alaska. Ecological Applications 7:593-613.

Delibes, M., M. Clavero, J. Prenda, M. D. C. Blázquez, and P. Ferreras. 2004. Potential impact of an exotic mammal on rocky intertidal communities of northwestern Spain. Biological Invasions 6:213-219.

Drent, R. H. 1965. Breeding biology of the Pigeon Guillemot, *Cepphus columba*. Ardea 53:3-4.

Eggers, S., M. Griesser, M. Nystrand, and J. Ekman. 2006. Predation risk induces changes in nest-site selection and clutch size in Siberian jay. Proceedings of the Royal Society B: Biological Sciences 273:701-706.

Emms, S. K., and N. A. M. Verbeek. 1989. Significance of the pattern of nest distribution in the pigeon guillemot (*Cepphus columba*). Auk 106:193-202.

_____. 1991. Brood size food provisioning and chick growth in the pigeon guillemot *Cepphus columba*. Condor 93:943-951.

Eslinger, D. L., R. T. Cooney, C. P. McRoy, A. Ward, T. C. Kline, E. P. Simpson, J. Wang, and J. R. Allen. 2001. Plankton dynamics: observed and modeled responses to physical conditions in Prince William Sound, Alaska. Fisheries Oceanography 10:81-96.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). *in* A. Poole, and F. Gill, editors. Birds of North America. Academy of Natural Sciences, Philadelphia and American Ornithologists' Union, Washington, D.C.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

_____. 2010. *Exxon Valdez* oil spill restoration plan. Update on injured resources & services. May 2010. Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Fleming, M. A., and J. A. Cook. 2010. MtDNA and microsatellite DNA provide evidence of fur farm ancestry for mink populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project 070853. Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM.

Forero, M. G., J. L. Tella, K. A. Hobson, M. Bertellotti, and G. Blanco. 2002. Conspecific food competition explains variability in colony size: a test in Magellanic penguins. Ecology 83:3466-3475.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 1998. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7:1-21.

Fréon, P., F. Gerletto, and O. A. Misund. 1993. Consequences of fish behaviour for stock assessment. ICES Journal of Marine Science 196:190-195.

Frostmeier, W., and I. Weiss. 2004. Adaptive plasticity in nest-site selection in response to changing predation risk. Oikos 104:487-499.

Gaston, A. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. Ibis 139:673-678.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on Pigeon Guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Groom, M. J., G. K. Meffe, and C. R. Carroll. 2006. Principles of conservation biology. 3rd edition. Sinauer, Sunderland, MA.

Hare, S. R., and N. J. Mantua. 2000. Empirical evidence for North Pacific regime shifts in 1977 and 1989. Progress in Oceanography 47:103-145.

Hayes, D. L. 1995. Recovery monitoring of Pigeon Guillemot populations in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Unpubl. Report, Anchorage, AK.

_____. 1996. A comparison of the breeding and feeding ecology of Pigeon Guillemots at Naked and Jackpot islands in Prince William Sound, APEX: 95163 F. U.S. Fish and Wildlife Service, Anchorage, AK.

Hensler, G. L., and J. D. Nichols. 1981. The Mayfield method of estimating nesting success: a model, estimators and simulation results. Wilson Bulletin 93:42-53.

Hovey, A. K. 2002. Effects of diet and crude oil ingestion on growth and biochemistry of captive-reared pigeon guillemots (*Cepphus columba*). Unpubl. M.S. Thesis, Oregon State University, Corvallis, OR.

Hunt, G. L., Z. A. Eppley, and D. C. Schneider. 1986. Reproductive performance of seabirds: the importance of population and colony size. Auk 103:306-317.

Irons, D. B., S. J. Kendall, W. P. Erickson, L. L. McDonald, and B. K. Lance. 2000. Nine years after the *Exxon Valdez* oil spill: Effects on marine bird populations in Prince William Sound, Alaska. Condor 102:723-737.

Irons, D. B., D. R. Nysewander, and J. L. Trapp. 1988. Prince William Sound waterbird distribution in relation to habitat type. U.S. Fish and Wildlife Service, Anchorage, AK.

Isleib, M. E. P., and B. Kessel. 1973. Birds of the north Gulf Coast - Prince William Sound region, Alaska. Biological Papers of the University of Alaska 14:1-149.

Jennrich, R. I., and M. D. Schluchter. 1986. Unbalanced repeated-measures models with structured covariance matrices. Biometrics 42:805-820.

Jewett, S. G., W. P. Taylor, W. T. Shaw, and J. W. Aldrich. 1953. Birds of Washington State. University of Washington Press, Seattle, WA.

Jones, H. P., B. R. Tershy, E. S. Zavaleta, D. A. Croll, B. S. Keitt, M. E. Finkelstein, and G. R. Howald. 2008. Severity of the effects of invasive rats on seabirds: a global review. Conservation Biology 22:16-26.

Kitaysky, A. S., J. F. Piatt, J. C. Wingfield, and M. Romano. 1999. The adrenocortical stress-response of Black-legged Kittiwake chicks in relation to dietary restrictions. Journal of Comparative Physiology B 169:303-310.

Kline, T. C., Jr. 1999. Temporal and spatial variability of $^{13}C/^{12}C$ and $^{15}N/^{14}N$ in pelagic biota of Prince William Sound, Alaska. Canadian Journal of Fisheries and Aquatic Sciences 56:94-117.

Klosiewski, S. P., and K. K. Laing. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. U.S. Fish and Wildlife Service, Anchorage, AK.

Kuletz, K. J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. Unpubl. M.Sc. thesis in Biological Sciences, University of California, Irvine, CA.

Lack, D. 1968. Ecological adaptations for breeding birds. Methuen, London.

Lethcoe, J., and N. Lethcoe. 2001. A history of Prince William Sound, Alaska. 2nd edition. Prince William Sound Books, Valdez, AK.

Lewis, S., T. N. Sherratt, K. C. Hamer, and S. Wanless. 2001. Evidence of intra-specific competition for food in a pelagic seabird. Nature 412:816-819.

Litzow, M. A., and J. F. Piatt. 2003. Variance in prey abundance influences time budgets of breeding seabirds: Evidence from pigeon guillemots *Cepphus columba*. Journal of Avian Biology 34:54-64.

Litzow, M. A., J. F. Piatt, A. A. Abookire, A. K. Prichard, and M. D. Robards. 2000. Monitoring temporal and spatial variability in sandeel (*Ammodytes hexapterus*) abundance with pigeon guillemot (*Cepphus columba*) diets. ICES Journal of Marine Science 57:976-986.

Litzow, M. A., J. F. Piatt, A. A. Abookire, and M. D. Robards. 2004. Energy density and variability in abundance of pigeon guillemot prey: support for the quality-variability trade-off hypothesis. Journal of Animal Ecology 73:1149-1156.

Litzow, M. A., J. F. Piatt, A. K. Prichard, and D. D. Roby. 2002. Response of Pigeon Guillemots to variable abundance of high-lipid and low-lipid prey. Oecologia 132:286-295.

Logerwell, E. A., and N. B. Hargreaves. 1997. Seabird impacts on forage fish: populations and behavioral interactions. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. University of Alaska Sea Grant Program Report 97-01, Fairbanks, AK.

Mantua, N. J., S. R. Hare, Y. Zhang, J. M. Wallace, and R. C. Francis. 1977. A Pacific interdecadal climate oscillation with impacts on salmon production. Bulletin of the American Meteorological Society 78:1069-1079.

Marty, G. D. 2008. Effects of the *Exxon Valdez* oil spill on Pacific herring in Prince William Sound, Alaska. Pages 925-932 *in* R. T. D. Giulio, and D. E. Hinton, editors. Toxicology of fishes. CRC Press, Boca Raton, FL.

Marty, G. D., M. S. Okihiro, E. D. Brown, D. Hanes, and D. Hinton. 1999. Histopathology of adult Pacific herring in Prince William Sound, Alaska, after the *Exxon Valdez* oil spill. Canadian Journal of Fisheries and Aquatic Sciences 56:419-426.

McKinney, M. L. 1997. Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495-516.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Misund, O. A., and A. Aglen. 1992. Swimming behaviour of fish schools in the North Sea during acoustic surveying and pelagic trawl sampling. ICES Journal of Marine Science 49:325-334.

Misund, O. A., J. T. Ovredal, and M. T. Hafsteinsson. 1996. Reactions of herring schools to the sound field of a survey vessel. Aquatic Living Resources 9:5-11.

Munro, J., and J. Bédard. 1977. Gull predation and creching behaviour in the Common Eider. Journal of Animal Ecology 46:799-810.

Murphy, S. M., R. H. Day, J. A. Wiens, and K. R. Parker. 1997. Effects of the *Exxon Valdez* oil spill on birds: Comparisons of pre- and post-spill surveys in Prince William Sound, Alaska. Condor 99:299-313.

Neff, J. M., E. H. Owens, S. W. Stoker, and D. M. McCormick. 1995. Shoreline oiling conditions in Prince William Sound following the *Exxon Valdez* oil spill. *in* P. G. Wells, J. N. Butler, and J. S. Hughes, editors. *Exxon Valdez* oil spill: fate and effects in Alaskan waters. ASTM Special Technical Publication no. 1219, American Society of Testing Materials, Philadelphia, PA.

Niebauer, H. J., T. C. Royer, and T. J. Weingartner. 1994. Circulation of Prince William Sound, Alaska. Journal of Geophysical Research 99:14113-14126.

Norcross, B. L., E. D. Brown, R. J. Foy, M. Frandsen, S. M. Gay, T. C. Kline, D. M. Mason, E. V. Patrick, A. J. Paul, and K. D. E. Stokesbury. 2001. A synthesis of the life history and ecology of juvenile Pacific herring in Prince William Sound, Alaska. Fisheries Oceanography 10:42-57.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Oakley, K. L., and K. J. Kuletz. 1979. Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot. U.S. Fish and Wildlife Service, Office of Special Studies, Anchorage, AK.

_____. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:759-769.

Paul, T. 2009. Game transplants in Alaska. Technical bulletin No. 4, second edition. Alaska Department of Fish and Game, Juneau, AK.

Piatt, J. F., and R. G. Ford. 1996. How many seabirds were killed by the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:712-719.

Piatt, J. F., D. W. Macdonald, C. J. Lensink, W. Butler, M. Kendziorek, and D. R. Nysewander. 1990. Immediate impact of the *Exxon Valdez* oil spill on marine birds. Auk 107:387-397.

Pitcher, T. J., and C. J. Wyche. 1983. Predator-avoidance behaviors of sand-eel schools: why schools seldom split. Dr. W. Junk Publishers, Boston, MA.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis. Duxbury Press, Belmont, CA.

Robards, M. D., and J. F. Piatt. 1999. Biology of the genus Ammodytes, the sand lances. U. S. Department of Agriculture Forest Service Pacific Northwest Research Station Research Paper:1-16.

Romano, M. D., J. F. Piatt, and D. D. Roby. 2006. Testing the junk-food hypothesis on marine birds: effects of prey type on growth and development. Waterbirds 29:407-414.

Rosen, D. A. S., and A. W. Trites. 2000. Pollock and the decline of Steller sea lions: testing the junk food hypothesis. Canadian Journal of Zoology 78:1243-1250.

Sagar, P. M., and D. S. Horning. 1998. Mass-related survival of fledgling Sooty Shearwaters *Puffinus griseus* at The Snares, New Zealand. Ibis 140:329-339.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Sargeant, A. B., G. A. Swanson, and H. A. Doty. 1973. Selective predation by mink, *Mustela vison*, on waterfowl. American Midland Naturalist 89:208-214.

Seiser, P. E., L. K. Duffy, A. D. McGuire, D. D. Roby, G. H. Golet, and M. A. Litzow. 2000. Comparison of pigeon guillemot, *Cepphus columba*, blood parameters from oiled and unoiled areas of Alaska eight years after the *Exxon Valdez* oil spill. Marine Pollution Bulletin 40:152-164.

Stienen, E. W. M., and A. Brenninkmeijer. 2002. Variation in growth in Sandwich Tern chicks *Sterna sandvicensis* and the consequences for pre- and post-fledging mortality. Ibis 144:567-576.

Suryan, R. M., D. B. Irons, and J. Benson. 2000. Prey switching and variable foraging strategies of Black-legged Kittiwakes and the effect on reproductive success. Condor 102:374-384.

Suryan, R. M., D. B. Irons, E. D. Brown, P. G. R. Jodice, and D. D. Roby. 2006. Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. Progress in Oceanography 68:303-328.

Terborgh, J. 1974. Preservation of natural diversity: the problem of extinction prone species. Bioscience 24:715-722.

Vaughan, S. L., C. N. K. Mooers, and S. M. Gay. 2001. Physical variability in Prince William Sound during the SEA study (1994-98). Fisheries Oceanography 10:58-80.

Vermeer, K., K. H. Morgan, and G. E. J. Smith. 1993a. Colony attendance of pigeon guillemots as related to tide height and time of day. Colonial Waterbirds 16:1-8.

_____. 1993b. Nesting biology and predation of pigeon guillemots in the Queen Charlotte Islands, British Columbia. Colonial Waterbirds 16:119-127.

Wiens, J. A., T. O. Crist, R. H. Day, S. M. Murphy, and G. D. Hayward. 1996. Effects of the *Exxon Valdez* oil spill on marine bird communities in Prince William Sound, Alaska. Ecological Applications 6:828-841.

Wittenberger, J. F., and G. L. Hunt. 1985. The adaptive significance of coloniality in birds. Volume 8. Academic Press, San Diego, CA.

MtDNA and Microsatellite DNA Provide Evidence of Fur Farm Ancestry for Mink Populations in Prince William Sound, Alaska

By
Melissa A. Fleming and Joseph A. Cook
Museum of Southwestern Biology
University of New Mexico,
Albuquerque, NM 87131

Final Report to David B. Irons and Daniel D. Roby for
"Pigeon Guillemot Restoration Research in Prince William Sound,"
Exxon Valdez Oil Spill Trustee Council Project 070853.

Corresponding Author:
Melissa A. Fleming
7860 NE Seawind Ave
Poulsbo, WA 98370
(360) 779-5382
maflemin@myuw.net

EXECUTIVE SUMMARY

Prince William Sound (PWS) supports native mink (*Neovison vison*) on its nearshore islands and mainland, but non-native mink were also introduced on several islands in the Sound during the 20th Century for fur trapping and fur farming. Currently, mink predation appears to be a major factor limiting pigeon guillemot (*Cepphus columba*) population recovery on the Naked Island Archipelago (NIA) following the *Exxon Valdez* oil spill. Prior to the 1990s, however, researchers and trappers did not report mink on the NIA, suggesting that the current large population of mink has resulted from a recent natural colonization or human introduction. This report confirms that these mink are not endemic to the NIA (i.e., not an evolutionarily significant unit unique to Naked, Storey, and Peak islands) and their removal should be considered a prudent management strategy to aid the recovery of the pigeon guillemot breeding population on the NIA.

Fur farm mink were developed over the last century by crossing mink from across North America, with mink from Alaska and eastern Canadian predominating. Genetic studies using mitochondrial (mtDNA) cytochrome b gene sequencing have identified at least three distinct forms of mink in North America: one on the coast of British Columbia and Alaska, another in interior BC and Alaska, and the last occurring east of Alberta, Canada. Contemporary fur farm mink have ancestors from all three regions. We used both mtDNA sequencing (n = 135 individual mink) and nuclear microsatellite genotyping (n = 211 individual mink) to determine whether the mink on the NIA are endemic, similar to other native populations in PWS, or have fur farm ancestry. We analyzed samples from seven PWS localities (including Montague I., a remote island without native mink, where there was a documented fur farm mink introduction in 1951), two fur farm color phases, and 8-24 localities across North America.

Both the NIA and Montague I. (including nearby Green I.) populations carry genetic signatures consistent with admixture of fur farm and native mink. An “eastern” mtDNA haplotype was found in mink from the NIA (n = 9 of 9), Montague I. (n = 1 of 9), and the Knight Island Archipelago (n = 3 of 7), reflecting fur farm ancestry. Nuclear analyses further confirmed fur farm ancestry for mink from Montague I. (e.g., high numbers of microsatellite alleles, 24% of which were found nowhere else in PWS but were common outside the region), but suggested native ancestry for NIA mink (e.g., low numbers of alleles typical of a small island population, and 95% of alleles shared with the nearby Knight Island Archipelago). The Montague I. population also included a haplotype characteristic of PWS and alleles unique to the PWS

region, suggesting that the admixture of native and fur farm mink occurred *in situ*. These results clearly indicate that the mink population on the NIA is not endemic and the strong fur farm genetic signature in mtDNA, but not in nuclear microsatellites, further implies that the NIA was colonized by an already admixed population of native and fur farm mink.

These genetic studies, in combination with data on mink behavior and their distributional history in PWS, can help reconstruct when and how the current NIA mink population became established, and its likelihood of becoming re-established if removal of all mink from the NIA were to occur. Statistical simulations confirmed that the Knight Island Archipelago (6 km distant) was the most likely source of the mink population currently on the NIA. Mink were not noted on the NIA prior to the 1990s and 6 km of open water is further than they would be expected to swim with any regularity. The genetic diversity observed on the NIA is not consistent with the current population resulting from either the natural migration of a few individuals over many years or a pre-existing introduced population expanding after experiencing a very low population size for much of the past century. Model simulations further suggested that the number of founder mink was equivalent to approximately five breeding pairs, the duration of the associated population bottleneck was only a few years, and a founding population of five pairs could have expanded to reach carrying capacity within 10-20 years. Taken together, the genetic data and other sources of information are most consistent with an anthropogenic introduction of mink from the Knight Island Archipelago to the Naked Island Archipelago in the 1970s or 1980s. That there must have also been an anthropogenic introduction of native PWS mink to Montague I. to mix with the introduced population of fur farm mink provides further support for this hypothesis.

Because the current mink population on the NIA has genes from fur farm mink, the population could be removed to aid pigeon guillemot recovery without negatively affecting native mink populations in PWS. The remoteness of the NIA from other mink populations in PWS should make the complete removal of mink possible to achieve and the NIA is likely to remain mink-free for an extended period. Subsequent monitoring would provide sufficient warning of newly arriving mink thereafter. The mink collected for this study have had tissue and skeletal material permanently archived at the University of New Mexico, and these are available for future studies. Additional archiving of mink tissues during mink removal (if managers decide this action is warranted) and monitoring efforts would allow the investigation of the source(s) of new colonists and their method of arrival, which would provide important information for improving mink control on the NIA and on other seabird islands worldwide.

Contents

List of Tables

List of Figures

Introduction

Mink predation appears to be a major factor limiting pigeon guillemot (*Cepphus columba*) population recovery in Prince William Sound (PWS), Alaska following the *Exxon Valdez* oil spill (Hayes 1996, Prichard 1997, Golet 1998). Although mink predation was not a recorded cause of pigeon guillemot nesting failure on the Naked Island Archipelago (NIA) in central PWS during studies in the late 1970s and early 1980s, mink predation on guillemot nests was frequently recorded by the mid-1990s (Hayes 1995, Golet *et al.* 2002). This apparent dramatic increase in mink predation on guillemot nests in the NIA may be the result of an intentional introduction of mink from fur farms or from wild populations on nearby islands, or a natural, but rare, long-distance movement, perhaps prompted by the impact of the 1989 *Exxon Valdez* oil spill (EVOS) on the intertidal zone of neighboring islands (i.e., Eleanor and other islands in the Knight Island Archipelago in western PWS). Alternatively, mink may have been on the NIA for a longer time and their foraging behavior has changed, perhaps due to EVOS or other factors affecting food availability in the nearshore or intertidal, resulting in greater predation on nesting seabirds, including pigeon guillemots. However, prior to the 1990s, researchers and trappers did not report mink on the NIA, suggesting that the large population found there currently is unusual and may well be the result of, or have been greatly enhanced by, a recent introduction. To identify the most likely source of the mink population on the NIA, we used both mitochondrial DNA (mtDNA) control region (CR) sequences and nuclear microsatellite genotypes to compare mink from the NIA to mink from other localities in PWS, from fur farms, from other regions in Alaska, and from across North America to determine their ancestry.

The American mink (*Neovison vison* AKA *Mustela vison*) is native to North America, but has been widely introduced across Eurasia and to Argentina and Chile via fur farms.
The species has been farmed in North America for at least 100 years (Adams 1935). Initially, mink farmers obtained their stocks locally, but by the 1930s breeders recognized that superior mink were coming from eastern Canada and Alaska and became interested in supplementing their herds with mink from these regions. Eastern Canada mink were prized for their relatively uniform dark, almost black color. Alaska mink (e.g., "Yukon" and "Kenai") were initially prized for their large size, and later for their contribution to the production of mutation coat colors, such as "platinum" (Bock 1942). The development and popularity of these "mutation mink" in the 1940s further contributed to the crossing of mink that originated from populations throughout North America in attempts to obtain more unique coat colors (Shackelford 1950). By 1950, Dr. Richard Shackelford, a University of Wisconsin mink geneticist, claimed that the ranch-bred mink was a mixture of most subspecies and that few, if any, ranch mink were more than 8-10 generations from wild ancestry (Shackelford 1950). Shackelford (1950) reported that the most well represented subspecies were thought to be the Eastern mink (*N. v. vison,* of eastern Canada),

the Kenai mink (*N. v. melampeplis*, ranging across south-central Alaska from the Alaska Peninsula to Prince William Sound) and the Yukon or Alaskan mink (*N. v. ingens*, from interior Alaska and the Yukon Territory). The legacy of Alaskan mink in modern fur farm mink is still apparent in the larger size, slightly later breeding season, and greater genetic susceptibility to the Aleutian disease retrovirus of certain lighter color phases (sometimes referred to collectively as “Aleutian” mink).

It is unlikely that fur farm mink have been domesticated long enough for unique genetic markers to have evolved that could distinguish them reliably from wild mink. However, to the extent that there are genetic differences among mink from different regions across North America (geographic structuring), the fact that geographically distant populations of mink in northwestern (Alaska and the Yukon) and northeastern (Quebec, New Brunswick) North America made large contributions to fur farm mink genetics increases the likelihood that fur farm mink differ genetically from native populations in having a mixture of both eastern and western genomes. Thus, the fur farm contamination of wild populations may be detected by finding “eastern” genetic types in “western” populations or *vice versa*.

By 1917, many islands in PWS, including Naked, Storey, and Peak in the Naked Island Archipelago, had fur farms raising primarily blue fox (Bower 1917; Janson 1985; Lethcoe & Lethcoe 1994). But by the 1930s, many fox farms began to raise mink which had become more popular (particularly Kenai crosses; Gothier 1941) and were cheaper to feed, thus more profitable (Janson 1985). It is not clear whether the fox farms on the NIA, which closed in the 1950s (Lethcoe & Lethcoe 1994), ever had mink as many of their counterparts did. Nonetheless, the genetic legacy of mink farm escapees and introductions, documented (like on Montague Island; Burris & McKnight 1973) and undocumented, may be widespread in PWS.

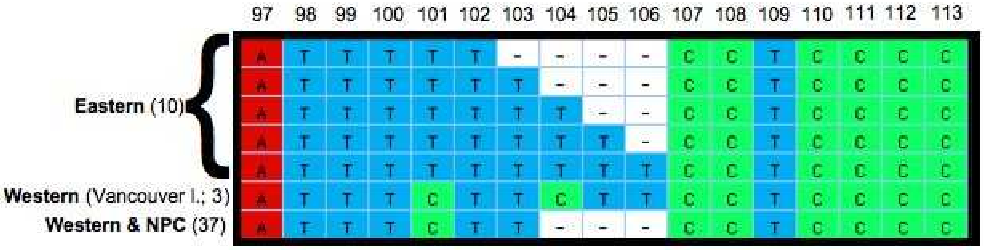
We used a multi-gene approach to investigate the origin of mink on the Naked Island Archipelago. MtDNA is maternally inherited and evolves via mutation only (without recombination), providing a record of female population history (e.g., population isolation, demographic expansions) spanning thousands of years. As such, mtDNA is particularly susceptible to differentiation due to genetic drift in small, isolated populations (e.g., on islands). Also, historical differences between adjacent populations can be maintained longer after barriers to gene flow are removed if gene flow is predominantly male-biased, as it is in mink. Microsatellites are highly polymorphic nuclear markers that are biparentally inherited and evolve rapidly via mutation and recombination. They are markers of choice for determining relationships between individuals within populations and among recently diverged populations, and for addressing questions related to contemporary gene flow, hybridization, and more recent demographic history (e.g., population bottlenecks).

I. Genetic evidence for fur farm mink introductions in PWS from mtDNA control region.

Our previous work on the phylogeography of mink on the North Pacific coast and across North America revealed low levels of both mtDNA cytochrome b (cyt b) and control region (CR) sequence variation (Fleming *et al.*, unpublished manuscript). For cyt b, only ~1% of nucleotides differ between the most divergent taxa (west coast of Vancouver Island versus Arkansas) and about ~2% for the control region. Nonetheless, there are two distinct clades of mink native to western North America. One is found primarily on the North Pacific coast (NPC) from the east coast of Vancouver Island to southwestern Alaska, and the other (Western) is found primarily inland in British Columbia and Alaska, but is abundant in some coastal areas as well. Both of these clades are distinguishable from mink east of Alberta, Canada by single nucleotide substitutions in both cyt b and in the control region.

In this study, we used 309 bp of the mtDNA control region alone to 1) distinguish mink from different parts of North America, 2) confirm that fur farm mink have ancestors from both eastern and western North America, 3) determine whether there are unusual fur farm haplotypes on Montague Island (where fur farm mink are known to have been introduced; Burris & McKnight 1973) and other sites of possible mink introductions or fur farm escapes, which may be used to differentiate introduced and native ancestry in mink, and 4) determine whether mink samples from the NIA also include unusual haplotypes suggesting fur farm ancestry. We focused on the control region because it is more variable than cyt b (~9% versus 3.5% of sites variable in mink) and the variable site distinguishing mink from eastern and western North America is in a segment with multiple nucleotide insertions and deletions (indels) also consistent with geographic structure (Fig. 1). Eastern samples are characterized by a thymine repeat of various lengths. Samples from west of Alberta in both the Western and NPC clades all have a cytosine substitution at site 101 followed by two thymine bases. Three Vancouver Island samples shared this cytosine substitution, but also had a second CTT sequence at sites 104-106.

PWS samples were collected from 29 localities and grouped into seven putative populations (Fig. 2): five presumed to support predominantly native mink and two from islands where fur farm mink are known or suspected to have been introduced. Presumed



	97	98	99	100	101	102	103	104	105	106	107	108	109	110	111	112	113
Eastern (10)	A	T	T	T	T	T	-	-	-	-	C	C	T	C	C	C	C
	A	T	T	T	T	T	T	-	-	-	C	C	T	C	C	C	C
	A	T	T	T	T	T	T	T	-	-	C	C	T	C	C	C	C
	A	T	T	T	T	T	T	T	T	-	C	C	T	C	C	C	C
	A	T	T	T	T	T	T	T	T	T	C	C	T	C	C	C	C
Western (Vancouver I.; 3)	A	T	T	T	C	T	T	C	T	T	C	C	T	C	C	C	C
Western & NPC (37)	A	T	T	T	C	T	T	-	-	-	C	C	T	C	C	C	C

Figure 1: A 13-17 bp segment of mink mtDNA control region (aligned using MacClade; Maddison & Maddison 1992) that has a pattern of indels consistent with geographic structure identified from variable sites. MtDNA cyt b/CR clade membership is indicated in bold on the left, along with sample size in parentheses.

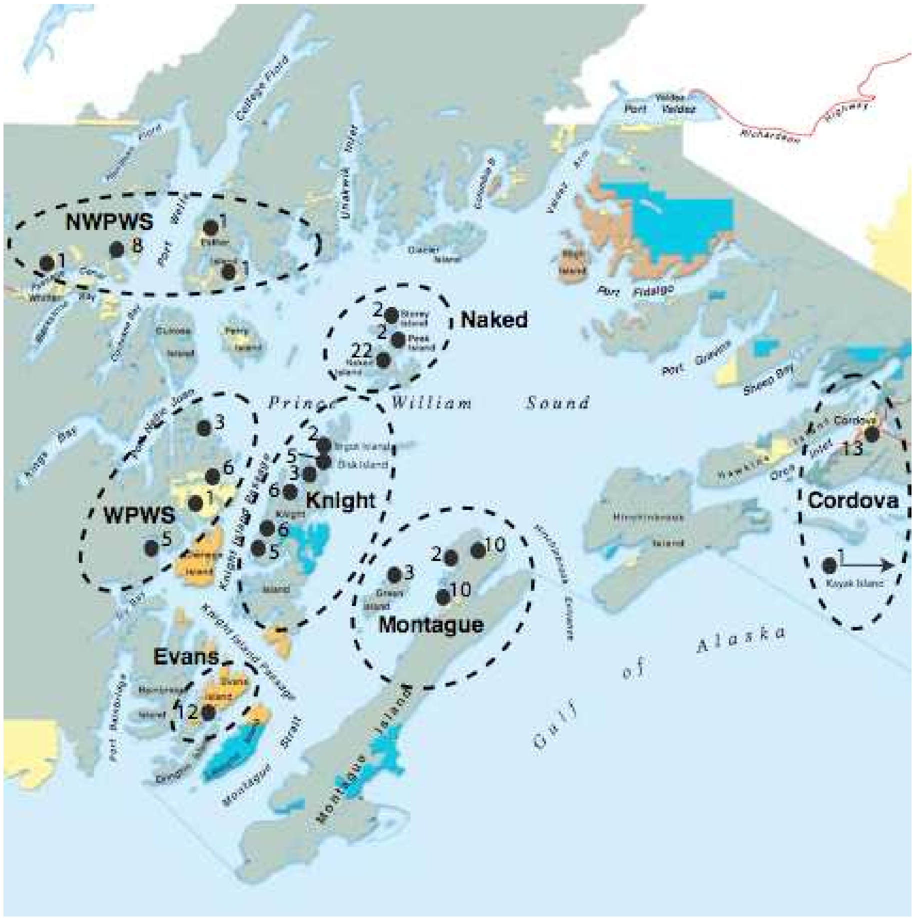


Figure 2: Mink from 24 capture localities (black dots with sample sizes) that were sequenced and/or genotyped in this study. Samples were grouped geographically (dashed lines) and seven putative PWS populations were designated: Cordova, NWPWS, WPWS, Evans I., Knight I., Montague I., and Naked I.

native populations include Cordova (including Kayak I.); Northwestern Mainland (Passage Canal, Pigot Bay and Esther I.; NWPWS); Western Mainland (WPWS); Evans Island; and Knight Island (including Disk I. and Ingot I.). Thirty-two mink from the Petersburg Experimental Fur Farm (16 females and 8 males) were introduced to Montague I. in 1951 (Burris & McKnight 1973), so samples from Montague I. and the adjacent Green I. (Montague Island) were presumed to be of fur farm ancestry. The seventh population, Naked Island, included samples from the NIA (Naked I., Peak I. and Storey I.) where mink (native or fur farm) are suspected to have been introduced for trapping or fur farming.

In addition to sequences from our phylogeographic study (60) and from new samples collected in PWS (44), we sequenced another 31 mink from fur farms, eastern North America, and western localities, particular those with a history of fur farms, including SE Alaska and Vancouver Island. Non-PWS Alaska localities included interior Alaska (IAK; north of the Alaska Range, near Fairbanks), southwestern Alaska (SWAK; Naknek, at the base of the Alaskan Peninsula), Copper River (Copper R.; from the vicinities of Glenallen and the Tonsina River, south of the Alaska Range) and southeast Alaska (SEAK; mainland as well as seven of the largest islands). Outside of Alaska, sampling localities included interior British Columbia (IBC), Vancouver Island (VI), Washington state (WA), and Montana (MT). Samples of two common color phases of fur farm mink, standard Dark (FFD) and Blue Iris (FFI; an "Aleutian" type), from the same farm in Washington state were included to provide examples of contemporary fur farm genomes. Finally, we included samples from six "eastern" localities (collectively, "East"; individually - Arkansas, ARK; Texas, TX; New York, NY; Ontario, ONT; New Brunswick, NB; and Alberta, AB) that could be source populations for haplotypes in fur farm mink that were not found in "western" populations.

Sequencing methods generally followed Fleming & Cook (2002), except that primers CTRL-L (Bidlack & Cook 2001) and TKDK (Kocher *et al.* 1993), PTC-0200 Thermocyclers (MJ Research), and an ABI 3110 sequencer were used. Analyses were based on control region sequences from 135 mink: 46 from PWS, 23 from SE Alaska, 12 from interior AK (including SWAK and Copper R.), 13 from Vancouver Island, 12 from interior BC/WA/MT, 17 from the East, and 12 from fur farms (Table 1), including three feral mink from Ireland (from Genbank #AJ585350-2).

Table 1: Distribution of 35 control region haplotypes in PWS (in color) compared to other localities (black). MtDNA clades were determined from cyt b and control region sequences from Fleming *et al.* (unpubl. manuscript) and are included to show evolutionary relationships. The "?" indicates the uncertainty about the relationship of three new CR haplotypes to those in the previous study.

Haplotypes	**?**			**Western clade**										**North Pacific Coast clade**									**Eastern clade**					
Localities	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8**	**9**	**10**	**11**	**12**	**13**	**14**	**15**	**16**	**17**	**18**	**19**	**20**	**21**	**22**	**23**	**24**	**25**	**26**	***27**	**n**
Int					**1**	**2**	**3**		**4**							**1**			**1**									**12**
Interior AK												**4**				**1**		**1**										**6**
SWAK														**1**	**1**			**1**										**3**
Copper R.							**1**									**1**		**1**										**3**
Cordova							**4**	**1**																				**5**
NWPWS																		**1**	**4**									**5**
WPWS			**2**															**5**										**7**
Evans I																	**1**	**3**										**4**
Knight I			**3**						**1**															**3**				**7**
Naked I																								**9**				**9**
Montague I																		**8**						**1**				**9**
East**																			**1**					**3**	**2**	**1**	**10**	**17**
Fur Farm													**2**			**3**			**2**			**1**		**1**				**9**
Feral Ireland																			**1**						**1**	**1**		**3**
SE AK	**2**	**1**			**1**				**5**	**2**	**1**						**1**		**6**	**1**	**2**		**1**					**23**
Vancouver I				**6**															**7**									**13**

*27 includes nine different eastern haplotypes from 10 mink.

** East includes AB, ONT, NB, NY, ARK, and TX

Phylogeography of American mink and evidence of mixed ancestry in fur farm mink

We found 35 different haplotypes among the 135 CR sequences: 10 belonged to the Western clade, nine to the NPC clade, 13 were "Eastern," and three were unlike any we had sequenced in the previous study and could not be assigned to a clade (Table 1). The data include 29 sites with base changes (variable sites) and seven indels (Fig. 1). Indels were coded as presence-absence characters using the method of Simmons & Ochoterena (2000). We used the median joining method and maximum parsimony option in Network 4.5 (Fluxus Technology; http://www.fluxus-engineering.com/sharenet.htm) to determine the relationships among the haplotypes (Fig. 3).

Mink showed geographic variation in CR across North America (Fig. 3) similar to that found using mtDNA cyt b and CR together. Most haplotypes from western mink (non-PWS) identifiable to either the Western or NPC clades grouped on the left side of Figure 3 (59 of 60; green), while those of most eastern mink (16 of 17; red) grouped loosely on the right. New haplotypes 1-3, which could not be assigned to mtDNA/CR clades, are in the middle along with a highly divergent Western clade haplotype from Vancouver Island (#4; Fig. 3). The only exceptions to this pattern are a single Ontario sample with the most common western haplotype (#19) and a sample from Farragut Bay on mainland SE Alaska that has eastern haplotype #23, both of which may be due to fur farm ancestry. Ontario had some of the first fur farms in Canada and has the second largest number of fur farms in the country after Nova Scotia (Statistics Canada 2006). Western haplotype #19 is widespread on the coast and in the interior and is also found in fur farm mink of both color phases (below), consistent with its possible arrival in Ontario via fur farms. Similarly, Farragut Bay once had the highest concentration of fur farms in SE Alaska involving 60 small islands in and near the bay (Smythe 1988). The eastern haplotype (#23) observed there is unique in our sample, but combined cyt b and CR sequences place it among other eastern haplotypes (Fleming *et al.*, unpubl. manuscript).

As expected, fur farm and feral mink samples include both eastern and western haplotypes, reflecting their mixed ancestry: three have three different eastern haplotypes, and nine share four western haplotypes (Fig. 3; Table 1). One of the Iris mink has a widespread 'Eastern' haplotype (#24) shared with wild mink in Alberta and Ontario. One feral mink shares a haplotype with two samples from Arkansas (#26) and another shares a haplotype with a mink from coastal Texas (#25). The remaining feral mink, another Iris, and a Dark mink share a widespread western, apparently NPC, haplotype (#19), from which another Dark (#22) differs by a single nucleotide change. The remaining two Dark mink and an Iris share another NPC haplotype (#16) with mink from interior Alaska, the Copper River drainage, and western WA. The last two Iris sequences (#13) share a Western haplotype that differs from an interior BC, Copper River, and Cordova haplotype (#7) by only one nucleotide change.

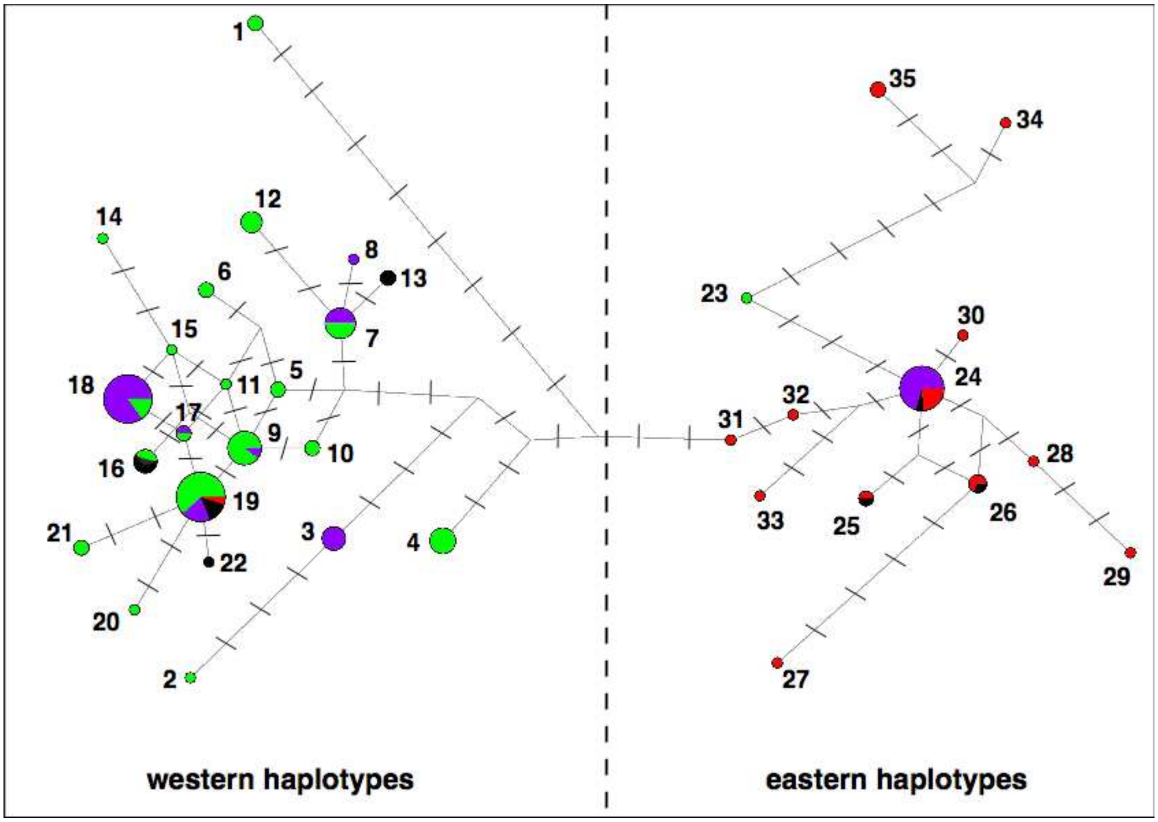


Figure 3: Haplotype network of 135 mink with 35 numbered haplotypes. Circle size is proportional to the number of mink that share a haplotype. Colors indicate the proportion of mink with a haplotype from different sampling localities: red for mink from eastern localities, green for western, black for fur farm, and purple for PWS. Hatch marks on the lines between haplotypes indicate the number of genetic changes (nucleotide substitutions or indels) between them. Specific geographic localities for each haplotype are listed below with the numbers of samples (greater than 1) in parentheses from each locality with the haplotype.

1. SEAK (2)
2. SEAK
3. WPWS (2), Knight (3)
4. WCVI (6)
5. SEAK, IBC
6. IBC (2)
7. Cordova (4), IBC (3), Copper R
8. Cordova
9. SEAK (5), IBC (2), MT (2), Knight
10. SEAK (2)
11. SEAK
12. IAK (4)
13. FFI (2)

14-15. SWAK; SWAK
16. Copper R, IAK, WA, FFD (2), FFI
17. SEAK, Evans I
18. SWAK, IAK, Copper R, NWPWS, WPWS (5), Evans (3), Montague (8)
19, SEAK (6), ECVI (7), NWPWS (4), WA, ONT, FFI, FFD, Feral Ireland
20-21. SEAK; SEAK (2)
22. FFD
23. SEAK
24. ONT (2), AB, FFI, Knight (3), Montague (1), Naked (9)
25. TX, Feral Ireland
26. ARK (2), Feral Ireland
27-35. ARK; NY; NY; NB; ONT; ONT; ONT; NY; ONT, NB.

Phylogeography of PWS mink and evidence for Fur Farm mink in PWS

The 46 mink in the PWS sample had eight diverse haplotypes: one unique (#3), three Western, three NPC, and one eastern (#24). It is notable that all nine mink in the Naked I. sample shared a single haplotype – eastern haplotype #24 (Table 1; Fig. 4a). Haplotype #24 was also found in fur farm, Ontario, and Alberta mink (Fig. 3; Table 1). Although the number of samples sequenced from each PWS locality is small, the differences among control region haplotypes from different localities suggest considerable phylogeographic structure in PWS (Fig. 4a). Cordova mink are distinct from other PWS populations, with one unique haplotype (yellow, Fig. 4a) and another shared with Copper River and Interior BC/WA/MT (brown; Fig. 4a), perhaps due to gene flow from interior Alaska along the Copper River drainage. Samples from Pigot Bay and Esther Island in northwestern PWS are also distinctive from other PWS localities in sharing one haplotype #19 (green; Fig. 4a) with mink from the SE Alaska mainland and eastern coast of Vancouver Island, as well as from fur farms.

The rest of the presumed wild populations in PWS – western mainland (WPWS), Evans I. and Knight I. – shared haplotypes (Fig. 4a). Mink from WPWS had one of two haplotypes. Haplotype #3 (light blue, Fig. 4a) was found in samples from Main Bay, appears unique to PWS, and was also found on Knight I. Haplotype #18 was widespread in Alaska (outside of SE), including interior AK, SW Alaska, and Copper R. (Fig. 4b), and was also found on Evans I. (3 of 4 mink) and Montague I. (8 of 9 mink; Fig. 4a). One mink from the north side of Passage Canal, initially considered a NWPWS locality, also had this haplotype (Fig. 4a), despite being captured closer to Pigot Bay than any of the localities designated WPWS (Fig. 2). Thus, although our preliminary designation of NWPWS and WPWS as putative populations appears to have some biological basis based on haplotype differences (Fig. 4a), the biogeographic basis for this distinction is unclear.

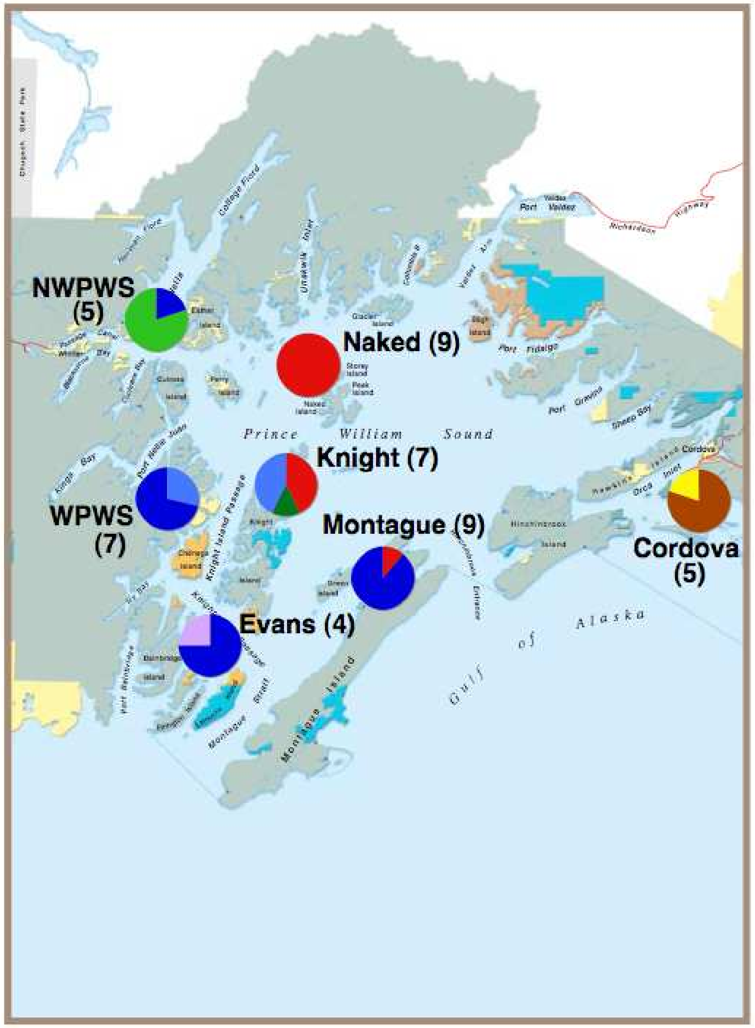
Like NWPWS mink, mink on Evans I. and Knight I. share some haplotypes with SE Alaska. Haplotype #17 (lavender; Fig. 4) was shared by mink on Evans I. in PWS and Revillagigedo I. in SE Alaska. Haplotype #9 (dark green; Fig. 4) on Knight I. was also widespread on the Alexander Archipelago of SE Alaska, in interior BC, and on the Copper River. Any of these haplotypes shared between PWS and SE Alaska could be due to shared ancestry from postglacial recolonization of the coast or from more recent introductions associated with fur farming.

Clear evidence for fur farm ancestry in PWS comes from a single, apparently Eastern, haplotype found in Knight I., Montague I., and Naked I. populations (#24; red; Fig. 4a). This haplotype is also found in samples from Alberta and Ontario (Fig. 4b), as well as in fur farm mink and feral mink from Ireland. All nine mink sequenced from the NIA share this haplotype, which is rare on Montague I. (one of nine), but more common on Knight I. (three of seven). This eastern haplotype is not found anywhere else in our western sample (n=93 mink), nor is any similar haplotype (the eastern haplotype found in Farragut Bay differs by three nucleotide changes), indicating that it was introduced to PWS from outside the region. Its occurrence in PWS could be due to independent introductions of mink from eastern fur farms to each island group, or the translocation and/or natural migration of crosses between eastern and native mink bred on local fur farms and in the wild. The Knight I. sample has the highest haplotype diversity of the samples from PWS and is quite distinctive from other western PWS samples and from Montague I. (Fig. 4a), consistent with the influence of fur farms on free-ranging mink in the vicinity. Eleanor Island, the northern-most island associated with the Knight Island Archipelago, is the closest land to the NIA at only 6 km distant, making it a more likely source for the eastern haplotype on the NIA than Montague I. at 30 km distant.

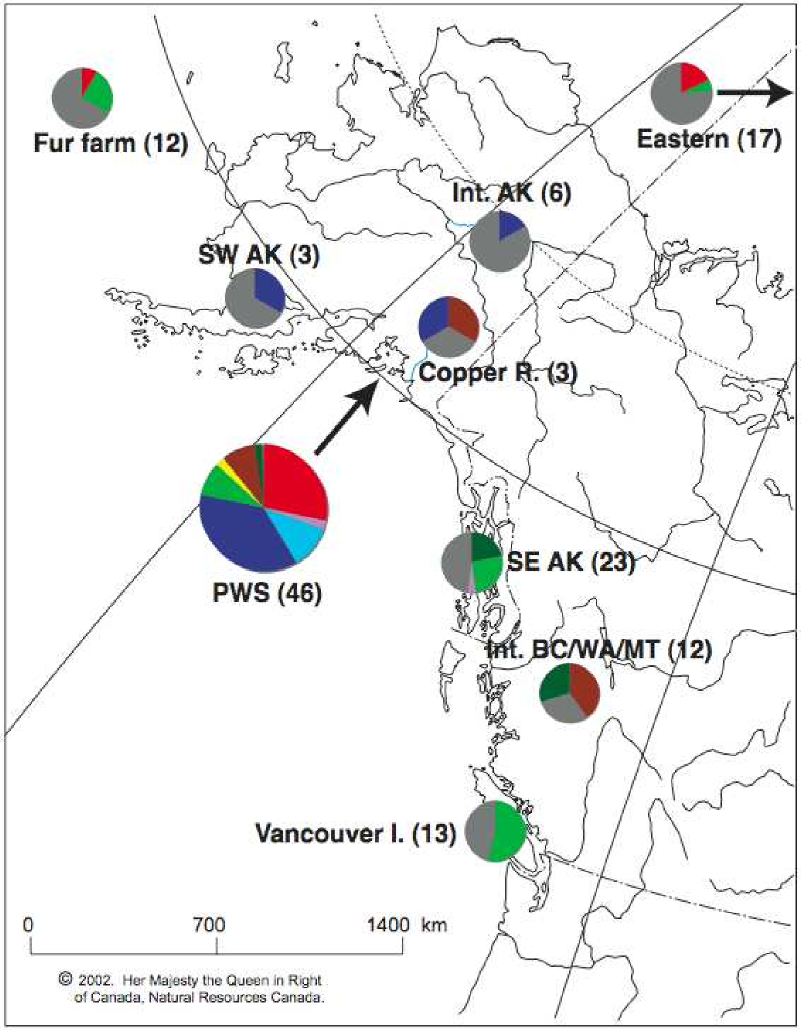
This same eastern haplotype (#24), in one of nine mink from Montague I., was the only unambiguous mtDNA signal in the Montague I. sample of the documented introduction of mink from the Petersburg (AK) fur farm in 1951. The most common haplotype on Montague I. is common in western PWS (Fig. 4a) and was also found in interior Alaska, southwestern Alaska and on the Copper River (Fig. 4b). The high frequency of this PWS haplotype in the Montague I. sample suggests that either (1) there were native mink on Montague I. when the fur farm animals were introduced, (2) native mink have migrated or been moved to Montague I. since the introduction of fur farm mink, or (3) western PWS was a source of mink for the Petersburg fur farm. The first hypothesis seems unlikely, because the absence of mink on Montague Island was well-known by trappers and wildlife managers prior to the introduction of fur farm stock. The subspecies of mink in PWS (*N. v. melampeplus*, known as the Kenai mink in the early fur farming literature) was one of three identified as most prominent in the development of fur farm mink, providing some support for the third hypothesis. On the other hand, this haplotype (#18, dark blue) was not found in our contemporary fur farm sample. The second hypothesis may be the most plausible because soon after the introduction of fur farm stock to Montague I. in 1951, local fur trappers complained to managers that fur quality was poor there (Burris & McKnight 1973). These three hypotheses are not mutually exclusive, however, and the microsatellite data can help determine the likely contributions of these different scenarios.

Figure 4: Maps showing the frequencies of different haplotypes in PWS (a.), indicated by different colors, and their frequencies in non-PWS populations (b.). Putative population designations are followed by sample sizes. Grey (b.) indicates the proportion of samples with haplotypes not found in PWS; colors (b.) correspond to colors of haplotypes in PWS (a.).

a.



b.



© 2002. Her Majesty the Queen in Right of Canada, Natural Resources Canada.

II. Genetic evidence for fur farm mink introductions in PWS using microsatellite markers.

MtDNA genetic diversity is lost more rapidly in small populations than is nuclear diversity. Thus, all but the most recent fur farm introductions may be more reliably detected by looking at nuclear DNA diversity instead of mtDNA diversity in small and/or isolated populations, like those on the NIA and Montague I. Therefore, we also used microsatellite markers to estimate genetic diversity in PWS populations, identify possible introductions and/or founder effects, and determine how PWS populations are related. By including fur farm mink, mink from elsewhere in Alaska, and mink from outside of Alaska (particularly from eastern populations) in our analyses, we are more likely to identify unusual alleles and multilocus genotypes in free-ranging mink populations that may indicate fur farm ancestry. Additional demographic analyses were performed to address questions about founding population size and origin and to evaluate the efficacy of mink removal from the NIA as a potential aid to seabird population recovery.

Table 2: Microsatellite primer sets used in the three multiplex PCRs, their annealing temperatures, and sources.

	Annealing Temp.	**Source**
Multiplex set 1	55° C	
Mer022		Fleming *et al.* 1999
Mvis027		Fleming *et al.* 1999
Mvis075		Fleming *et al.* 1999
Multiplex set 2	55° C	
Mer041		Fleming *et al.* 1999
Mer009		Fleming *et al.* 1999
Mvis072		Wisely *et al.* 2003 (redesign of primers from Fleming *et al.* 1999)
Mvis082		*this study* F GAT CTA AGT GGT TTC CGG GG R TCA GCT GAT GGG GGT TAG AC
Multiplex set 3	53° C	
Mvis002		Fleming *et al.* 1999
Mvis022		Fleming *et al.* 1999
Mvis065		*this study* F TCT GAA GAG GGC AAC TGA GC R GCT CTC CCA TAG CAA ACA GC

We used 10 microsatellite loci, eight of which were previously published (Table 2; Fleming *et al.* 1999, Wisely *et al*. 2003) and two of which were newly designed despite having been developed at the same time. Methods followed Fleming *et al.* (1999) except for the use of multiplex PCR reactions (Table 2), PTC-0200 Thermocyclers (MJ Research; necessitating lower annealing temperatures; Table 2), and genotyping using an ABI 3110 automated sequencer.

A total of 211 samples were grouped into 14 putative populations, including the seven populations previously described for Prince William Sound (Fig 2; PWS): five populations of native mink, and two populations, Montague I. and Naked I., known or hypothesized to have been introduced, respectively. The seven "Non-PWS" populations included the four other Alaskan populations described for mtDNA analyses (IAK, SWAK, Copper R, and SEAK). The last three putative populations were the two fur farm color phases (standard Dark, FFD, and Blue Iris, FFI) and one "Eastern" population sampled from three localities (Arkansas, New York, and Ontario). These were included as potential source populations for unusual allele and genotype variations that would not be expected in PWS or 'western' populations in the absence of fur farm ancestry.

Genetic diversity

Twelve of 14 putative populations were at Hardy-Weinberg equilibrium for all loci (Genepop on the Web; http://genepop.curtin.edu.au/; Raymond & Rousset 1995; Rousset 2008) after Bonferroni correction for multiple tests. Eastern and SEAK samples showed significant homozygous excess (expected heterozygosities, He, greater than observed, Ho; Table 3). This was not surprising as these two "populations" consisted of samples from multiple distinct localities; the Eastern sample included animals from Ontario, New York, and Arkansas and the SEAK sample included animals from all major islands and the mainland of SE Alaska, a region larger than PWS. Combining samples from distinct populations produces a "Wahlund effect" in which there are more different alleles in the combined "population" than in any of the actual populations sampled, inflating expected heterozygosities. So, while this broad locality sampling served its purpose in providing a diverse sample of alleles from eastern parts of North America and from SE Alaska, "Eastern" and "SEAK" samples are not populations in the same sense as the others.

Numbers of alleles in a population tend to be greater for larger, out-bred groups than for smaller, relatively isolated ones. Populations with the highest allelic richness (numbers of alleles observed in a population adjusted for variation in sample size; FSTAT 2.9, Goudet 1995) included the Eastern and SEAK samples, which encompass multiple populations, and also the interior Alaska sample, from a core area of the species range in Alaska (Table 3). Fur farm mink, both color phases, had the next highest allelic richness, reflecting considerable out-breeding as expected from their mixed mtDNA ancestry, despite artificial selection for coat colors. Western PWS populations had low allelic richness, highlighting their relative isolation as populations (particularly the island samples) and the low level of gene flow both within the region and between western PWS and other regions. Montague I. had the highest allelic richness in PWS, despite being the most isolated island population sampled. This anomaly may be a reflection of the non-PWS alleles introduced with fur farm mink in 1951. The Naked I. sample had the lowest allelic richness, similar to levels observed for WPWS and Evans I. However, Naked I. also had considerably higher levels of heterozygosity than WPWS or Evans I., suggesting that the low number of alleles in the Naked I. sample may be attributable to a recent founding event.

Table 3: Descriptive statistics for mink populations. Values for predominantly native PWS populations are shaded.. Values for the two other PWS populations, Naked I. and Montague I., are in bold. Allelic Richness (FSTAT 2.9, Goudet 1995), and observed (Ho) and expected (He) heterozygosity calculations (Genepop) do not include monomorphic loci. SWAK had only 4 samples and was excluded here to improve allelic richness estimates.

	Sample Size	**# of monomorphic loci**	**Allelic Richness**	**Ho**	**He**	**Total # alleles**
FFD	10	1	3.80	0.573	0.543	41
FFI	14		3.94	0.664	0.608	43
Eastern	14		4.86	0.596	0.717	55
IAK	15		4.19	0.619	0.631	49
Copper R.	12		3.70	0.505	0.581	40
Cordova	14		2.68	0.451	0.518	28
NWPWS	11		2.88	0.446	0.487	30
WPWS	15	2	2.01	0.290	0.288	23
Evans I.	11		2.03	0.276	0.294	21
Knight I.	26	1	2.58	0.456	0.458	31
Naked I.	**24**	**2**	**1.99**	**0.461**	**0.430**	**22**
Montague I.	**25**		**3.24**	**0.601**	**0.569**	**37**
SEAK	16		4.16	0.499	0.640	49
Overall	207		4.71		0.670	82

Genetic differentiation

Genetic differences among mink populations based on Fst (Table 4) were all statistically significant, indicating low levels of gene flow among them. Over 60% of all pairwise comparisons had Fsts greater than 0.25 ("very great" genetic differentiation; Wright 1978;

highlighted in Table 4). Only 11% showed “moderate” differentiation (*italics*, Table 4) and the remainder showed “great” differentiation. Most of the very great genetic differentiation occurred between PWS and non-PWS localities or populations. One exception was the Cordova sample, which was less differentiated than other PWS populations from non-PWS populations. Another exception was the SEAK sample, which was more differentiated from other non-PWS populations (and from PWS populations for that matter). The Montague I. population was notable in being less differentiated from non-PWS than PWS populations, except for Knight I. The Naked I. population showed very great differentiation from both PWS and non-PWS populations with the exception of Knight I., Montague I., and fur farm Dark.

Table 4: Pairwise Fst values for 14 putative populations (all statistically significant). Values > 0.25, indicating “very great” differentiation, are highlighted. Values < 0.15, indicating “moderate” differentiation, are in italics. Heavy borders are drawn around pairwise values among non-PWS populations and among presumed native PWS populations (i.e., not including Naked I. and Montague I. populations, which have values in bold).

	FFD	**FFI**	**East**	**IntAK**	**SWAK**	**CopR**	**Cord**	**NWPWS**	**WPWS**	**Evans**	**Knight**	**Naked**	**Mont.**	**SEAK**
FFD	0.000													
FFI	*0.072*	0.000												
East	*0.150*	*0.093*	0.000											
IntAK	0.253	0.163	*0.100*	0.000										
SWAK	0.283	0.232	0.182	0.151	0.000									
CopR	0.180	*0.117*	*0.107*	*0.118*	*0.088*	0.000								
Cord	0.346	0.229	0.170	0.205	0.239	0.192	0.000							
NWPWS	0.314	0.246	0.203	0.267	0.367	0.274	0.322	0.000						
WPWS	0.458	0.379	0.357	0.402	0.541	0.421	0.493	0.337	0.000					
Evans I.	0.443	0.361	0.347	0.362	0.511	0.390	0.440	0.268	0.217	0.000				
Knight I.	0.327	0.280	0.262	0.295	0.314	0.274	0.350	0.203	*0.111*	*0.131*	0.000			
Naked I.	**0.243**	**0.273**	**0.297**	**0.364**	**0.378**	**0.258**	**0.394**	**0.331**	**0.318**	**0.298**	**0.191**	**0.000**		
Mont. I.	**0.221**	**0.181**	**0.151**	**0.239**	**0.278**	**0.179**	**0.298**	**0.263**	**0.310**	**0.305**	**0.241**	**0.245**	**0.000**	
SEAK	0.286	0.238	0.152	0.255	0.344	0.268	0.324	0.283	0.479	0.427	0.382	0.409	0.237	0.000

Population structure and relationships

Cluster analysis is another way to assess the number of and relationships among populations in a sample. We used the Bayesian clustering program, STRUCTURE 2.2 (Pritchard *et al.* 2000, Falush *et al.* 2003), which uses multilocus microsatellite genotypes to identify population structure and relationships, and to detect migrants and population admixture. A total of 211 mink were assigned to clusters based on the log likelihood probability [LnP(D)] of the data fitting 1 through 10 clusters (K), assuming Hardy-Weinberg equilibrium and linkage equilibrium within clusters. Run parameters included 1,000,000 MCMC replicates after the first 100,000 were discarded as burn-in to minimize the effects of starting conditions. Multiple runs (3-5) were performed for each K to assess consistency.

STRUCTURE performed well on simulated data that assumed an island model of migration with complex hierarchical migration schemes (Evanno *et al.* 2005), similar to the assumed situation in PWS. However, the appropriate criterion for identifying the true number of clusters varied and was often not the K at which the LnP(D) "more-or-less" plateaus, as suggested by Pritchard *et al.* (2000). Rather, Evanno *et al.* (2005) found the true number of clusters was most often associated with highest value of ΔK, an *ad hoc* criterion related to the second order rate of change of LnP(D) with respect to K. Because ΔK detects the upper most level of hierarchical structure (or relationships) in a data set, separate analyses of each identified subset are necessary to reveal further within-group substructure. The current data set is a case in point (Table 5). ΔK clearly identifies two clusters in the complete dataset of 211 individual mink, but it is not clear that LnP(D) plateaus at this or some other value of K, as it continues to decrease as K increases.

Table 5: The mean probability over three runs of each K [LnP(D], its standard deviation, and ΔK = $(m(|L(K+1) - 2L(K) + L(K-1)|)/s[L(K)])$. ΔK cannot be calculated for K = 1 or K = 10 (NA). While it is difficult to determine a K-value at which LnP(D) plateaus, the peak in ΔK predicts that K = 2 is the uppermost level of structure in the dataset of 211 mink.

K	m[LnP(D)]	s[LnP(D)]	ΔK
1	-5890.2	5.9	NA
2	-5216.4	10.6	32.4
3	-4886.0	13.4	11.9
4	-4715.4	15.5	3.5
5	-4598.3	48.2	1.4
6	-4416.1	17.0	4.2
7	-4304.5	17.9	2.5
8	-4238.2	19.7	0.7
9	-4186.2	19.9	1.1
10	-4155.7	22.6	NA

Additional substructure was thus detected by running analyses separately on these two clusters. Subsequent clusters were identified using the ΔK criterion until the remaining populations could no longer be differentiated. Nine population groupings were ultimately identified via 10 separate STRUCTURE analyses on hierarchical subsets of the data. The clustering for K = 2, 3, 6, and 9 for the complete data set (Fig. 5) correspond to those identified via subset analyses.

At the highest level of population structure (K = 2), analysis of the complete data set identified mink from three western PWS localities (WPWS, Evans I., and Knight I.; Western PWS), together with Naked I., as a population cluster distinct from all others with mean assignment probabilities of ≥ 97% (Table 6a). Eastern, IAK, and SEAK mink had mean assignment probabilities of ≥ 97% to the 'Other' cluster, along with fur farm mink (≥ 95%), Copper R. mink, and SWAK mink (≥ 90%). Mink from Cordova in eastern PWS also clustered with 'Other,' with a mean membership of > 90%.

Other putative populations from PWS – mink from the northwestern mainland and Esther I. (NWPWS) and from Montague I. – appeared admixed between Western PWS and "Other" (the non-PWS group plus Cordova), with mean assignment probabilities to Western PWS of 61% and 26%, respectively (Fig. 5a; Table 6a). When the two apparently admixed populations were included in an analysis with the Western PWS subgroup, K again equaled two, with NWPWS mink remaining admixed, while Montague I. mink formed a distinct cluster. When these two admixed populations were analyzed with the "Other" subgroup, however, Montague I. and SEAK grouped together in a third cluster (Fig. 5b).

Subsequent analyses on "Western PWS + Naked I.", "Montague I.+ SEAK" and the "Other" subsets also predicted K = 2, distinguishing Naked I. from Western PWS, Montague I. from SEAK, and both types of fur farm mink from "Other," producing the pattern observed under K = 6 in the complete analysis (Fig. 5c). Analyses of the remaining subsets confirmed the clustering in Fig. 5d with K = 9. Eastern mink were weakly distinguishable from mink in IAK, SWAK, and Copper R., which formed a single cluster (Inland AK). Mink in Cordova and NWPWS each formed a population cluster distinct from the other four populations identified in PWS.

The hierarchical clustering of Montague I. mink is consistent with the documented introduction of fur farm mink to the island in 1951 (Burris & McKnight 1973). First, the admixture of Western PWS and "Other" in mink from Montague I. at K = 2 supports either the recent introduction of "Other" mink to a native population, or the introduction of both "Other" and Western PWS to Montague Island. Second, the clustering of Montague I. with SEAK mink at K = 3 could be attributed to the introduced mink being from the Petersburg experimental fur farm in SE Alaska (Fig. 5b). The Petersburg fur farm was established under the auspices of the

Alaska Game Commission in 1938 with stock from a local fur farm owned by the commissioner (Smythe 1988). Throughout the 1930s, mink from SE Alaska were popular breeding stock, with more sold to the rest of North America as breeders than as fur (Smythe 1988). Thus, the Petersburg fur farm stock in 1951 may well have been derived in part from native SE Alaska mink. Similarities between Montague I. and SEAK genotypes may also reflect fur farm influence in both populations. SE Alaska has also had a long history of potential "contamination" from numerous fur farms in the region, which may still be evident in wild populations. In either case, the distinctiveness of Montague I. mink from the other populations sampled in PWS is consistent with a history that includes a fur farm introduction.

Similar patterns of admixture and relationships with mink from outside of PWS were not apparent in the mink samples from the NIA, suggesting a different history for the population there. Their initial grouping with other Western PWS populations supports a predominantly western PWS ancestry. Although subsequent hierarchical analyses support the hypothesis of a distinct genetic identity for mink from the NIA compared to mink from Knight I., Evans I., and the mainland to the west, this distinction is consistent with the greater distances between the NIA and the other localities. Twenty-one of 22 alleles found in the Naked I. sample are shared with its nearest neighbor, Knight I., suggesting common ancestry, and the differences in allelic frequencies between the two populations can be attributed to genetic drift. In contrast, Montague I. mink differ from those in other western PWS localities in allele identity as well as allelic frequencies. Nine of 37 alleles in the Montague I. sample are found nowhere else in PWS, and gene flow from outside of PWS is necessary to account for both the greater allelic richness and the large number of atypical alleles in the population.

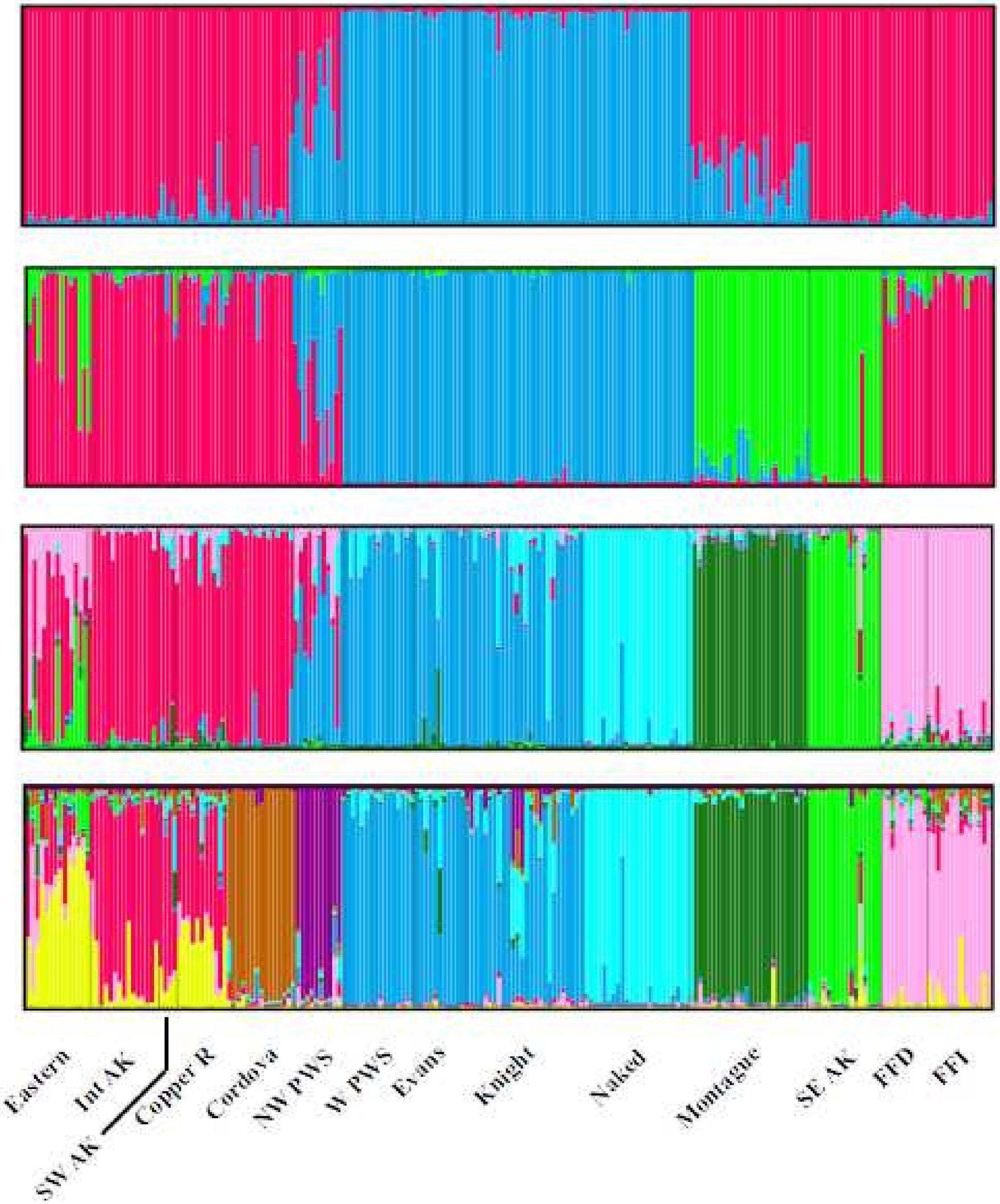


Figure 5: Proportion of ancestry in each cluster (y-axis) estimated for each of 211 mink in 14 putative populations (x-axis) in four different runs (a. - d.) of the clustering program STRUCTURE. Each cluster is represented by a different color (standardized using DISTRUCT; Rosenberg 2004); multiple colors for an individual imply mixed or uncertain ancestry. Different numbers of clusters are assumed in each STRUCTURE run: K = 2 (a.), K = 3 (b.), K = 6 (c.), and K = 9 (d.). Assignment proportions/probabilities for K = 2 and K = 9 are listed in Table 6a. and 6b.

Table 6: Proportions of samples from different putative populations assigned to different clusters (AKA assignment probabilities). a.) K = 2. Clusters and colors correspond to Fig. 5a and probabilities ≥ 90% are in bold. b.) K = 9. Clusters and colors correspond to Fig. 5d and the highest assignment probability for each population is in bold.

a.

Pop.\Cluster	**Western PWS + Naked**	**Other**	**n**
Eastern	0.02	**0.98**	14
IAK	0.03	**0.97**	15
SWAK	0.10	**0.90**	4
Copper R.	0.09	**0.91**	12
Cordova	0.09	**0.91**	14
NWPWS	0.61	0.39	11
WPWS	**0.99**	0.01	15
Evans I.	**0.98**	0.02	11
Knight I.	**0.97**	0.03	26
Naked I.	**0.98**	0.02	24
Montague I.	0.26	0.74	25
SEAK	0.01	**0.99**	16
FFD	0.05	**0.95**	10
FFI	0.03	**0.97**	14

b.

Pop.\ Cluster	**East**	**Inland AK**	**Cordova**	**NWPWS**	**Western PWS**	**Naked**	**Montague**	**SEAK**	**Fur Farm**	**n**
EAST	**0.53**	0.17	0.04	0.02	0.01	0.02	0.03	0.08	0.12	14
IAK	0.34	**0.55**	0.03	0.02	0.01	0.01	0.01	0.02	0.03	15
SWAK	0.21	**0.53**	0.05	0.02	0.03	0.09	0.05	0.01	0.02	4
Copper R.	0.06	**0.69**	0.08	0.02	0.02	0.07	0.02	0.01	0.04	12
Cordova	0.01	0.01	**0.91**	0.02	0.02	0.01	0.01	0.00	0.01	14
NWPWS	0.01	0.01	0.01	**0.77**	0.12	0.03	0.01	0.01	0.03	11
WPWS	0.01	0.01	0.01	0.01	**0.91**	0.04	0.01	0.00	0.01	15
Evans I.	0.00	0.01	0.00	0.01	**0.85**	0.06	0.05	0.01	0.01	11
Knight I.	0.01	0.01	0.03	0.06	**0.71**	0.14	0.01	0.01	0.02	26
Naked I.	0.00	0.00	0.01	0.01	0.06	**0.91**	0.01	0.00	0.01	24
Montague I.	0.01	0.01	0.01	0.01	0.02	0.02	**0.91**	0.01	0.01	25
SEAK	0.03	0.03	0.01	0.01	0.01	0.01	0.01	**0.87**	0.03	16
FFD	0.03	0.02	0.01	0.01	0.01	0.02	0.01	0.02	**0.87**	10
FFI	0.04	0.08	0.05	0.01	0.01	0.01	0.02	0.01	**0.76**	14

Private and "characteristic" alleles

To identify specific alleles from mink on Montague I. and in other PWS localities that were more likely to be introduced than native to PWS, we compared allele frequency distributions of PWS (n = 77) and Non-PWS (n = 85) samples (Table 7). Only "common" alleles that occurred with a frequency of > 0.05 in one or both groups were included in the comparison (55 of 82 alleles). Seventeen "private" alleles were identified: 15 occurred in the Non-PWS sample but not in the PWS sample, and two were found in the PWS sample but not in the Non-PWS sample. Because fur farm mink ancestry is mixed and fur farms have been ubiquitous in parts of Alaska in the past, many of the wild mink populations sampled today may show some genetic evidence of fur farm ancestry in the form of rare alleles (frequency ≤ 0.05). Similarly, wild populations elsewhere may have rare "Alaskan" alleles acquired via escaped fur farm mink. Thus, we considered not only private alleles, but "characteristic" alleles, as well. "Characteristic" alleles were defined as those that were common in (i.e., characteristic of) one group (> 0.05), but rare in the other (≤ 0.05). By this definition, there were also three alleles characteristic of PWS that were rare elsewhere and seven alleles that were characteristic of the Non-PWS sample that were rare in PWS. These characteristic alleles allow us to track rare alleles in PWS attributable to low levels of gene flow from Non-PWS populations, including past introductions.

The occurrence of private and characteristic alleles for PWS in the Naked I. and Montague I. samples indicate their degree of connectivity with other PWS localities (Table 8a). The first private allele for PWS (Mvis002; 175) was common (43% of all alleles at the locus) and widespread (in all PWS samples except Cordova) and was also found on Naked I. (18%), but not on Montague I. The second (Mvis072; 232), occurring at a frequency of only 10% and restricted to Cordova (where its frequency was 58%), was not found on either Naked I. or Montague I. Nor was one characteristic allele (Mer022, 262), which was also restricted to Cordova (frequency 29%). The remaining two alleles characteristic of PWS were found on both Naked I. and Montague I. at high frequencies (Table 8b), including Mvis075 114, which was only found once outside PWS, in SEAK. Over all loci, the frequency of private alleles and alleles characteristic of PWS was similar on Naked I. and in PWS overall (0.10 and 0.14, respectively), but lower on Montague I. (0.03), consistent with its greater isolation (Table 8a).

Several characteristic alleles from the Non-PWS sample turned up rarely in PWS overall, but at moderate (Evans I. and Knight I.) to high (Cordova and NWPWS) frequencies in individual populations (except for WPWS; Table 8b), consistent with past fur farm influence in these distinct populations. The Montague I. sample in particular stood out in this regard. Not only did Montague I. have five Non-PWS alleles (two private and three characteristic), but it had five "Other" alleles at high frequencies that were otherwise rare (≤ 0.05) or non-existent in both Non-PWS and PWS samples. All together, 24% of Montague I. alleles were unlikely to be from PWS (only one of the 10 was found elsewhere in PWS, on Evans I.). These may represent alleles retained directly from the 1951 fur farm introduction. In contrast, only 2% of Naked I. alleles overall were likely to have been introduced. This one Naked I. allele was characteristic of the Non-PWS sample, occurred at a frequency of 23%, and was shared with Montague I., WPWS, Evans I., and Knight I. samples (all ≤ 0.05). It seems unlikely that the Naked I. sample would have so little evidence of fur farm ancestry in its nuclear DNA if a direct introduction of fur farm stock had occurred as recently as on Montague I. Rather, sharing a rare allele and an eastern haplotype with other PWS localities may indicate that the NIA shares a more diffuse fur farm ancestry with western PWS as a whole.

Table 7: Frequencies of private and characteristic microsatellite alleles for PWS and Non-PWS localities. Private alleles occur in either the PWS or Non-PWS group only. Alleles were defined as "characteristic" of a group if they occurred commonly in that group and at frequencies of ≤ 0.05 in the other.

Locus	Allele	Freq in non-PWS	Freq in PWS	Category
M2	175	0.000	**0.434**	private PWS
M72	232	0.000	**0.100**	private PWS
M75	114	0.006	**0.506**	Characteristic PWS
E9	208	0.048	**0.068**	Characteristic PWS
E22	262	0.043	**0.052**	Characteristic PWS
M72	236	**0.208**	0.000	private Non-PWS
M82	167	**0.159**	0.000	private Non-PWS
E22	258	**0.146**	0.000	private Non-PWS
M27	184	**0.125**	0.000	private Non-PWS
M2	189	**0.125**	0.000	private Non-PWS
M75	116	**0.119**	0.000	private Non-PWS
M65	239	**0.116**	0.000	private Non-PWS
M72	238	**0.113**	0.000	private Non-PWS
E9	210	**0.096**	0.000	private Non-PWS
M82	165	**0.094**	0.000	private Non-PWS
M75	112	**0.077**	0.000	private Non-PWS
M82	169	**0.076**	0.000	private Non-PWS
M65	241	**0.061**	0.000	private Non-PWS
M2	183	**0.060**	0.000	private Non-PWS
M75	128	**0.054**	0.000	private Non-PWS
M22	287	**0.144**	0.007	Characteristic Non-PWS
E41	152	**0.107**	0.021	Characteristic Non-PWS
M75	124	**0.095**	0.026	Characteristic Non-PWS
E22	266	**0.085**	0.013	Characteristic Non-PWS
M65	237	**0.073**	0.029	Characteristic Non-PWS
M65	235	**0.067**	0.029	Characteristic Non-PWS
M72	240	**0.054**	0.007	Characteristic Non-PWS

Table 8: Frequencies and numbers of private or characteristic (Char.) alleles in samples from localities presumed native to PWS (PWS), hypothesized to have fur farm ancestry (Introduced?), and outside of PWS (Non-PWS), including Eastern, IAK, SWAK, Copper R., SEAK and two fur farm color phases. Alleles with frequencies of ≤ 0.05 in both groups, but also found on Naked I. or Montague I., were termed "Other". a.) Frequencies of private and characteristic alleles for PWS compared between PWS and "Introduced?" b) Frequencies of private and characteristic alleles for Non-PWS and "Other" alleles compared among PWS, "Introduced?" and Non-PWS.

a.

Population	n	Freq. at locus of each		# of Private + Char. PWS alleles	Overall freq. of Private + Char. PWS alleles
		Private PWS Allele	Char. PWS Allele		
PWS	77	0.43 0.10	0.51 0.07 0.05	5	0.14
Introduced?					
Naked I.	24	0.18	0.50 0.25	3	0.10
Montague I.	25		0.16 0.18	2	0.03

b.

Population	N	Freq at locus of each Non-PWS allele		Freq at locus of Other Private & Char. alleles	Total # of Private & Char. alleles	Overall Freq of Private & Char. alleles
		ABSENT in PWS	Char. in PWS			
PWS:	77					
Cordova	14		0.15 0.08		2	0.02
NWPWS	11		0.18 0.20 0.05		3	0.04
WPWS	15					
Evans I.	11		0.09 0.06	0.22	3	0.03
Knight I.	26		0.09		1	<0.01
Introduced?:						
Naked I.	24		0.23		1	0.02
Montague I.	25	0.23 0.16	0.36 0.08 0.08	0.14 0.12 0.54 0.16 0.36	10	0.24
		Ave. Freq (n)	**Ave. Freq (n)**	**Ave. Freq. (n)**		
Non-PWS:	**85**	0.11 (15)	0.10 (7)	0.03 (7)	29	0.24

Identification and characterization of population bottlenecks

If mink populations on Montague I. and the Naked Island Archipelago are attributable to fur farm introductions, translocations, or recent founder events, the effects of a population bottleneck may still be evident in the relationship between microsatellite allele numbers and heterozygosities. We used several methods that have been developed to 1) recognize a population that has experienced a bottleneck, 2) identify the likely source population, bottleneck size, and duration, and 3) determine how many generations have elapsed since a population bottleneck.

BOTTLENECK

Recently bottlenecked populations show a greater loss of allele numbers relative to heterozygosity (i.e., greater observed than expected heterozygosity) compared to large populations in mutation-drift equilibrium (Hardy-Weinberg Equilibrium, HWE). Although significant deviations from HWE were not observed, both the Naked I. and Montague I. samples showed this tendency (Table 2), as did fur farm mink. To determine whether a small founding population of mink could have colonized and/or was introduced to the NIA and Montague I., we used the program BOTTLENECK (Cornuet & Luikart 1997). BOTTLENECK utilizes several simple statistics to evaluate whether sampled microsatellite loci show significant deviations from HWE under different models of microsatellite evolution. The two statistics used here are the Sign test and Wilcoxon signed rank test, both valid for tests of 10 or more loci. The former is valid only for larger sample sizes of 20-30, while the later is valid for samples as small as 4.

BOTTLENECK results support the occurrence of population bottlenecks in mink on Montague I. ($n = 25$ mink in sample), and possibly the NIA ($n = 24$ mink in sample) as well. The Montague I. sample had reduced gene diversity relative to heterozygosity as indicated by both the significant Sign test ($p < 0.017$ under the infinite allele model, IAM) and the Wilcoxon test ($p < 0.003$ under the IAM). The same effect was observed in the Naked I. sample, with the Sign test ($p < 0.026$ under the IAM), but not the Wilcoxon test ($p = 0.098$ under the IAM). The lack of significance for the latter, reputedly more sensitive, test may be due to the Naked I. sample having two monomorphic loci. With no heterozygosity, there could be no change in heterozygosity for these two loci; thus, the sample size for the Wilcoxon test was effectively reduced by two, reducing the test's power.

A population bottleneck due to a mink founding event on the NIA is consistent with the allele numbers (relatively low), heterozygosities (relatively high), allelic identities (a subset of those in the Knight I. sample), and population relationships (with Western PWS) observed in the Naked I. sample. It is less clear that a population bottleneck on Montague I. is consistent with the relatively large number of alleles in that sample and the likelihood of mixed (PWS/Other) ancestry detected by STRUCTURE. Possibly, another post-introduction bottleneck occurred in the Montague I. population, but a bottleneck is not the only demographic event that could produce high heterozygosity relative to allele numbers. Heterozygote excess can also result when males and females have different allele frequencies in a population (Rousset & Raymond 1995, Luikart & Cornuet 1999). Under natural conditions this can occur by chance in small populations (bottlenecks). However, the artificial condition of introducing animals to Montague I. from a more diverse population (fur farm) and a less diverse one (Western PWS) could also have the same effect: numbers of heterozygotes greater than that expected from the increased numbers of alleles after population admixture.

The effects of a recent population bottleneck were not detected in any other sample, including fur farm mink. Despite the WPWS sample (n = 15) having the lowest allelic diversity, its proportionally low heterozygosity suggests that the population has had sufficient time to recover from a earlier bottleneck and/or a long history of isolation resulting in a gradual loss of alleles via genetic drift.

GENELOSS

Because allele numbers and heterozygosities decrease in a predictable manner as the result of a bottleneck, bottleneck size and duration can be estimated from pre-bottleneck data. In the case of founding events, these estimates can also be used to distinguish between potential source populations. We used the program GENELOSS (England & Osler 2001) to test different scenarios for the origin of the mink population on the NIA. The program uses Monte Carlo sampling to simulate the effects of a population bottleneck on allelic diversity over multiple generations using allele frequency information from potential source populations, putative bottleneck sizes (in numbers of breeding pairs), and bottleneck durations (in generations). However, it ignores the potential effects of demographic processes after the bottleneck, such as population growth rate, on genetic diversity. Instead, it provides idealized estimates that may be most accurate for populations that rapidly regain sufficient size to avoid additional loss of diversity due to genetic drift. Under favorable conditions, as appear to be the case on Naked I. and Montague I., mink populations probably grow fast enough and get large enough to initially avoid post-bottleneck allele loss due to genetic drift.

Naked Island Archipelago

At the outset, we predicted that the number of founders was likely to be rather small in the case of a natural colonization, given that NIA is 6 km from the next nearest island or mainland. An intentional introduction from elsewhere in PWS or from a non-PWS fur farm would probably involve more than one or two founders (16 females and 8 males were introduced to Montague in 1951). Thus our simulations included founding (bottleneck) population sizes of 1, 5, or 10 breeding pairs.

Assuming that the habitat for mink on the NIA is similar to that on other mink inhabited islands in PWS, we also expect that the bottleneck duration would be brief once mink colonized the island. Mink populations invading new habitats in Eurasia and South America can expand rapidly (Dunstone 1992), and the island environments of the North Pacific coast support the highest densities of mink reported (2 or more per km of shoreline; Hatler *et al.* 2009). Thus, we simulated bottleneck sizes of 1, 3, and 5 generations without population growth, which correspond to durations of 1, 3, and 5 years because mink breed at one year of age.

We used the above parameters and allele frequencies from three different potential founder populations: Knight Island (n = 26 mink samples), Montague Island (n = 25), and a typical west coast fur farm (n = 24). Knight I. was chosen due to its proximity to Naked I. and to the results of the STRUCTURE analysis that initially placed the two samples in the same cluster. Montague I. was chosen because of its history as an introduced population that may have inspired similar introductions of fur farm mink to other mink-free islands in PWS. The fur farm sample was chosen to test the hypothesis that an introduction of fur farm mink from stock other than that used to introduce mink on Montague I. could have been responsible for the mink population on the NIA. Simulations for other PWS samples, namely NWPWS, Cordova, and WPWS, were also run assuming 1-5 founders and a one-generation bottleneck to determine whether there were other potential sources of immigrants/introductions to the NIA. One thousand iterations of each scenario were run.

GENELOSS provides mean expected heterozygosity (H_e) and mean number of alleles retained (N_A) over iterations, as well as the proportion of simulations in which each allele in the source population is retained (allelic retention rate) during the simulated bottleneck. Hanson & Taylor (2008) and Taylor & Cooper (1999), in their studies of known and suspected introduced populations of possums and wallabies, used the allelic retention rate to estimate a probability that the allele loss patterns simulated for various putative source populations (e.g., in the present study, Knight I., Montague I., fur farm) would deviate in the manner observed in the population of interest (in our case, the NIA). We followed their method, multiplying together the proportions of simulation replicates in which an allele was retained if it was common in the putative source population (frequency > 5%) but absent on Naked I., to quantify the probability of deviation in allele loss patterns. Higher allele loss probabilities indicate greater correspondence between observed allele loss on Naked I. and that expected from the various source populations under different bottleneck scenarios. Because of the non-independence of alleles in a genotype (particularly relevant in the case of small founder populations over short bottleneck durations), this method is not strictly correct, but it provides a way to rank the probabilities of different source and bottleneck scenarios.

The simulation that best fit the Naked I. data involved five founding pairs from Knight I. that experienced a three-generation bottleneck (Fig. 6a & b). The greatest overlap between the number of alleles (N_A) and heterozygosity (H_e) per locus for the Naked I. data versus the simulated data was observed when Knight I. was the source population over the entire range of scenarios (Fig. 6a & b). By themselves, simulated N_A and H_e estimates cannot distinguish source populations because similar N_A and H_e estimates can be generated with entirely different alleles. However, allele loss patterns also suggested Knight as the source population with relatively high probability (Fig. 6a and b; $P = 9 \times 10^{-4}$). Other simulations with allele loss patterns more similar to that observed on Naked I. (e.g., fur farm, Fig. 6e and f,; one founding pair and a five generation bottleneck, $P = 2 \times 10^{-3}$) did not fit the Naked Island Archipelago data as well overall because their corresponding N_A and H_e values were too low (fewer alleles found on Naked I. were retained in the simulation).

In some simulations, single founder scenarios using allele frequencies from Montague I. (Fig. 6c & d) and fur farm samples generated allele loss probabilities higher or nearly as high as those from Knight, but scenarios with five (or more) founding pairs from these populations inevitably resulted in the fixation of an allele that was absent on Naked I. (and allele loss probabilities equaling zero). To make sure that there wasn't a founder number between one and five pairs that was more likely to generate an allele loss pattern similar to that observed for Naked I. than that found using five pairs from Knight I., additional scenarios with two founding pairs were run. In most subsequent scenarios, simulations based on Montague I. and fur farm mink included one or more alleles which became fixed that were lost on Naked I. The one exception was the simulation with fur farm mink bottlenecked for five generations, but fur farm mink were still less likely than mink from Knight I. to produce the allele loss pattern observed for Naked I. ($P = 1.5 \times 10^{-5}$, $N_A = 1.94 \pm 0.1237$, $H_e = 0.3091 \pm 0.393$).

The allele distribution of the Naked I. sample is not simply a subset of any one source population, however, and alleles found on Naked I. that are missing in various source populations must also be considered (Table 9). The Naked I. sample shares the great majority of its alleles (21 of 22) with the Knight I. sample and the one additional allele from the Naked I. sample was found in only a single individual. It is not unusual to find additional alleles relative to the source population in populations that have experienced known bottlenecks. There are three possible explanations: 1) microsatellites mutate very rapidly and a new allele may have arisen post-bottleneck, 2) sample sizes of close to 30 are preferred in microsatellite studies because they are likely to include all alleles present in the population at frequencies greater than 5%, but it is possible that a rarer allele not sampled in the source population could have been sampled in the smaller bottlenecked population, and 3) post-bottleneck immigration could introduce additional alleles. The "extra" allele in the Naked I. sample was present at low frequencies on Montague I. and in eastern mink. Migration directly from Montague seems unlikely, given the distance, but human agencies could have moved Montague I. mink to Naked I. or introduced similar fur farm mink there. Knight I. and Montague I. mink share other alleles and one CR haplotype (with Naked I. mink as well) that are unusual in PWS, but found in eastern or fur farm mink, suggestive of mink movement between Knight and Montague islands and/or fur farm ancestry on both. Thus, it is also possible that the "extra" allele in the Naked I. sample may be present at low frequency on Knight I. as well, and may have arrived on Naked I. as part of a natural colonization or human introduction.

Table 9: Sample size (n), total number of alleles (N_A) at all 10 loci for seven PWS sampling localities, number of alleles shared with the Naked I. sample (n = 24 mink, 22 alleles), and the proportion shared between Naked Island and other populations.

	n	Total N_A	N_A shared w/Naked	Proportion of Naked N_A shared
Knight	26	31	21	0.95
Montague	25	37	19	0.86
Fur farm	24	52	18	0.82
NW PWS	11	30	17	0.77
Cordova	14	28	16	0.73
W PWS	15	22	18	0.82
Evans	11	22	15	0.68

Montague Island

To confirm the efficacy of GENELOSS in identifying bottleneck parameters for the Naked I. population, we conducted similar tests on Montague I. samples. Montague I. mink are assumed to be descendents of 16 female mink and 8 males introduced from the Petersburg Experimental Fur Farm by ADF&G in 1951 (Burris & McKnight 1973). The introduction was carried out because there were reportedly no native mink on Montague Island (Heller 1910, Sheldon 1912). Simulations using samples from a current Washington state fur farm as a proxy for the Petersburg fur farm (closed in the 1970s) do not recover allele loss patterns, allele numbers, or heterozygosities consistent with those of the current Montague I. sample.

As in the Naked I. simulations, a small enough number of fur farm founders, bottlenecked for long enough, did show alleles loss patterns similar to those observed on Montague I., but the resulting allele numbers and heterozygosities were far too low (data not shown). Fur farm mink have high allelic diversity and thus possess most of the alleles found on Montague I., or in almost any other mink population, in low frequencies. But only a bottleneck more severe than is likely given the high level of allelic diversity remaining on Montague I. could result in the apparent loss of so many alleles common in the fur farm sample. Because the Petersburg farm was established using a variety of mink with an ancestry in southeast Alaska, we also ran simulations using the SEAK sample (contemporary wild mink) to check the possibility that the Petersburg farm was established with more local stock than a modern WA fur farm. These simulation results were similar to those with fur farm mink: the severity of the bottleneck that produced results consistent with allele loss patterns in Montague I. mink did not produce the high allele numbers and level of heterozygosity also observed on Montague I.

Previous results (e.g., Fig. 1, Fig. 5a, Table 4b) suggesting that both native PWS and non-PWS mink have contributed to the genetics of the Montague I. mink population may explain GENELOSS's inability to confirm a founder effect as a result of the known introduction of fur farm mink to Montague Island in 1951. The Montague I. sample is not only missing alleles that are common in both the fur farm and the SEAK samples, but it has several alleles that are common in (and in some cases unique to) PWS and missing in the fur farm and SEAK samples, consistent with multiple source populations. If native PWS mink were not present on Montague I. at the time of the introductions, it is presumably because the island is too isolated for mink to have established a population there naturally. Thus, it seems likely that humans must have introduced native mink to Montague I. as well, perhaps to enhance fur quality which was reported to be poor after the fur farm introduction there (Burris & McKnight 1973). It is also possible that PWS mink made more of a contribution to the genetics of Petersburg farm mink in 1951 than is retained in present day fur farm animals, but that would not account for the high allelic diversity and heterozygosity evident in Montague I. mink today (Table 2).

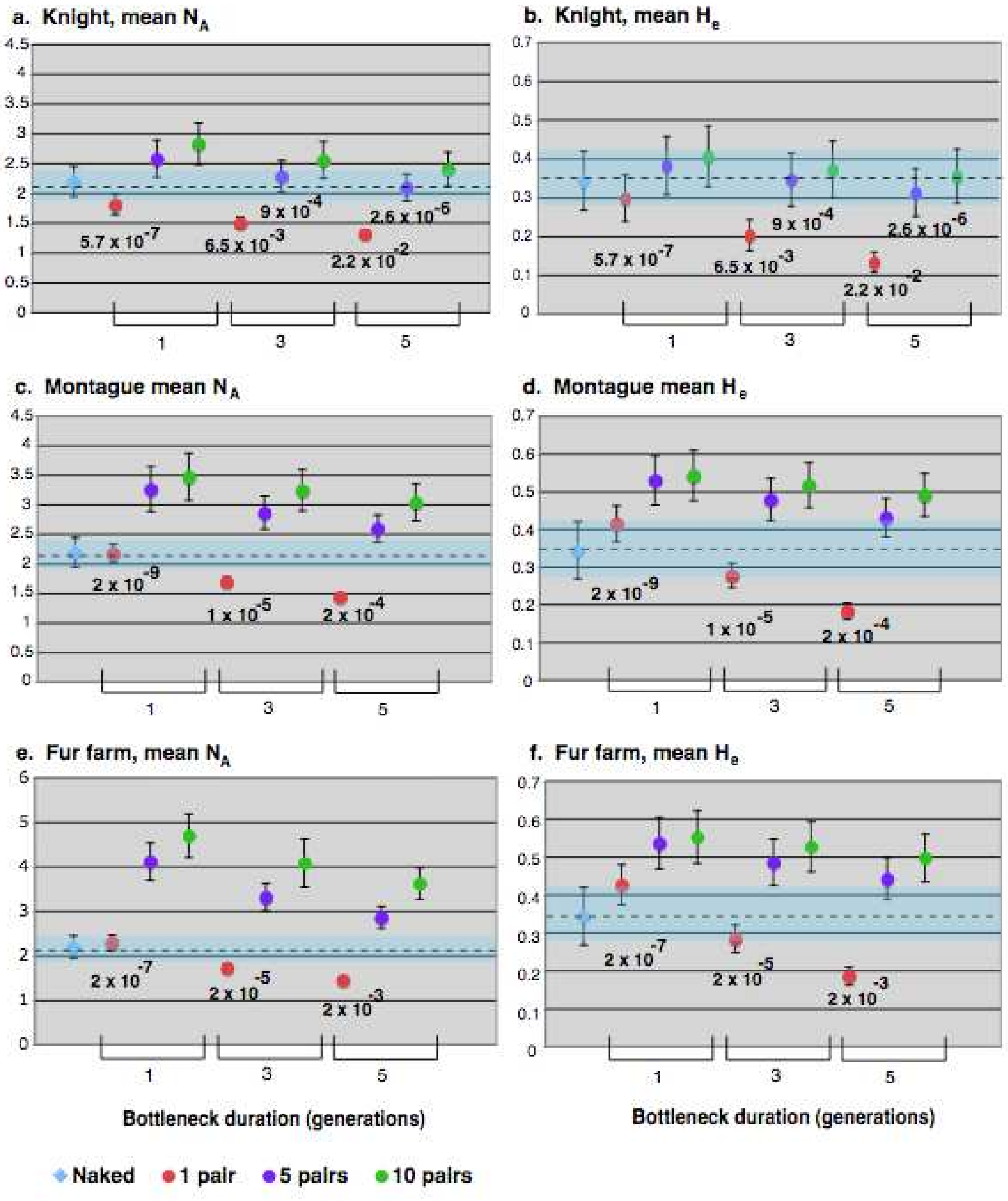


Figure 6: Results of GENELOSS bottleneck simulations using Knight I. (a. & b.), Montague I. (c. & d.), and fur farm (e. & f.) as putative source populations. The Y-axis shows mean (± standard error) of the simulation averages for allelic diversity (N_A; left hand column) and expected heterozygosity (H_e; right hand column). The X-axis groups results by bottleneck durations of 1, 3, and 5 generations. Different bottleneck sizes (numbers of founding pairs) are labeled according to the legend. The mean N_A and H_e for the Naked Island Archipelago sample is indicated by a dotted line in each graph with the standard error shaded in light blue. Note the change in scale for e. Non-zero allele loss probabilities for each scenario are shown below the relevant symbol.

BOTTLESIM

The predictability of gene loss and decreases in heterozygosity via genetic drift allow the estimation of the number of generations that have passed since a population bottleneck. BOTTLESIM (Kuo & Janzen 2003) assumes the source of migrants (or pre-bottleneck population) is known, and then takes into account the subsequent effects of demographic variables to estimate when a bottleneck occurred. This requires specifying not only founding population size and bottleneck duration, but also how post-bottleneck population size has varied over time. Assuming that a newly founded population in a favorable environment is going to grow rapidly, a logistic growth curve was adopted to describe mink population growth on Naked Island. We used 1.17 as the population growth rate, r, calculated for mink by Hennemann (1983). We estimated the carrying capacity of the environment, K, using two estimates of coastal mink population density – one from feral mink on islands in Europe (0.66 per km of coastline; Craik 1997) and the other from coastal mink on islands off Vancouver Island (2.0 per km of coastline; Hatler 1976) – and an estimate of the length of coastline in the Naked Island Archipelago (104 km; http://www.uas.alaska.edu/spatialdata/download/). This provided K values of 70 mink and 208 mink for the archipelago. Under the logistic growth model, a founding population bottlenecked at the demographic equivalent of five pairs of mink for three years still reached carrying capacity within 9 to 11 years (for K=70 and 208, respectively) when r = 1.17.

We used the bottleneck population size and duration from the most likely scenario in GENELOSS (Knight I., ~5 founding pairs, bottlenecked for 3 generations) and looked at simulated allelic diversity measures for three time frames: 20 years (since the EVOS), 57 years (when mink were introduced to Montague I.) and 85 years (an estimate of the earliest date that fur farm mink from elsewhere were likely to have been brought to PWS to supplement local populations in farming efforts). The model also included overlapping generations, reproductive maturity at 1 year, a life expectancy of 3 years (Hatler 1976), and 100 iterations.

The simulations did not greatly narrow the time frame in which the Naked I. mink population could have been founded by migrants or introductions from Knight I. (Table 10). When K = 208 mink, simulated populations founded 20, 57, and 85 years ago all could have produced the observed values for N_A and H_O on the NIA. At K = 70, the simulated population founded 85 years ago lost too many alleles (barely), and could not have produced Naked I. values for N_A. Decreasing bottleneck length, decreasing the number of migrants to two pairs, and even halving the estimate of r (at which carrying capacity would be reached in 11 to 14 years), did not change these results. Unless the carrying capacity of the NIA is 70 or fewer, BOTTLESIM estimated that the population could have been founded at any time during the last ~80-100 years.

Table 10: The mean and SEM of N_A and H_O over 10 microsatellite loci observed for the Naked Island Archipelago, and estimated from BOTTLESIM at two different carrying capacities (K) and after 20, 57 and 85 years from founding. Shading indicates a simulation result that is not consistent with observed values.

	N_A (mean)	SEM	H_O	SEM
Observed values	**2.2**	**0.249**	**0.3684**	**0.0826**
K = 70				
Years from founding				
20	2.215	0.251	0.3231	0.0648
57	1.911	0.186	0.2659	0.0517
85	1.785	0.161	0.2468	0.0484
K = 204				
Years from founding				
20	2.330	0.261	0.3475	0.0647
57	2.212	0.244	0.3245	0.0643
85	2.126	0.229	0.3080	0.0606

Conclusions

Two independent sets of genetic markers were analyzed and results indicate that mink on the Naked Island Archipelago (NIA) have both fur farm (introduced) and local (native) ancestry. The predominant mtDNA haplotype on the NIA is found in both eastern and fur farm mink (Fig. 4a., b.), on Montague I. where fur farm mink are known to have been introduced, and on Knight I., which had nearby mink farms (e.g., Latouche Island; Andy McLaughlin, pers. comm.). We have not identified this haplotype elsewhere in western North America (n = 93 mink samples). The only other eastern haplotype found in a western sample differed considerably and was found in a part of Southeast Alaska (SEAK) known for a high concentration of mink farms during the 1930s (Smythe 1988). Altogether, the distribution of this haplotype suggests that it arrived in Prince William Sound (PWS) via fur farms.

In contrast, the microsatellite data show the affinity of the NIA mink with native populations on nearby islands and the mainland of western PWS, including shared private alleles. The NIA mink population was one of five distinct genetic clusters in PWS, but was closely related to the western PWS cluster (including western mainland, Evans I., and Knight I.; Fig. 5). The NIA mink are distinctive only because of allele frequency differences that are consistent with losses via genetic drift (including a founder effect): 21 of 22 alleles from Naked I. mink are also found in mink from the Knight I. population.

For both sets of genetic markers, the population structure is consistent with Knight I. mink being involved in either a small recent founder event on the NIA or a larger past founding event on the NIA followed by genetic drift. The former scenario seems more likely as the existing literature and eyewitness reports related to mink presence on islands in PWS does not support the occurrence of mink on the NIA until the 1990s (see ‘Other considerations’ below).

Both sets of genetic markers also confirmed the known fur farm ancestry of mink on Montague I. The population genetic structure of Montague I. mink, however, is consistent with admixture between fur farm and native western PWS mink *in situ*, rather than with a founding event from an already admixed population. Montague I. mink have both the eastern haplotype found in NIA mink and a native haplotype characteristic of western PWS. The microsatellite data also support admixture. The Montague I. population has a large number of alleles for such a secluded island, including alleles not otherwise found in PWS, and cluster analysis revealed admixture from PWS and non-PWS sources (Fig. 5a; K = 2). Taken together, the clustering of Montague I. mink with SEAK (Fig. 5b; K = 3) rather than other PWS populations, the high frequencies of several non-PWS alleles, and the presence of an eastern haplotype in the population are consistent with Montague I. mink having a mixed ancestry involving both fur farm and native mink. The reported absence of native mink on Montague I. (Heller 1910, Sheldon 1912) and the distances between Montague I. and abundant native mink populations described on the Knight Island Archipelago to the west (8 km; Heller 1910) and Hinchinbrook I. to the east (10 km; Sheldon 1912) argue against native western PWS mink colonizing Montague I. on their own. It is more likely that trappers or fur farmers associated with a fox farm on Green I. (Janson 1985) transported native western PWS mink to Montague I. (or Green I.) independent of the 1951 introduction of fur farm mink by federal and state wildlife managers.

We did not find evidence of genetic differences among mink populations within PWS that support long-term isolation and divergence for any island population of mink, including those on the NIA. Microsatellites revealed considerable differences among islands (Table 4), but this is as likely to be due to differences in amount of fur farm influence (i.e., the distribution of alleles characteristic of non-PWS samples) as it is to restricted gene flow. Other mammals are endemic to PWS islands (e.g., Montague marmot, Montague vole; MacDonald & Cook 2009), but unlike the mink, they are not semi-aquatic, nor are they furbearers likely to have been translocated from island to island by trappers or fur farmers. Clearly, the mink found on the NIA are not endemic and do not represent a genetically distinct population segment that would argue against their removal.

Other considerations

Determining when and how the current mink population on the NIA became established, and thus its likelihood of being re-established if removed, is not possible based on the current genetic data alone. Statistical simulations of the microsatellite data support the hypothesis that Knight I. was the most likely source of the NIA mink, that the number of founders was small (the equivalent of approximately five breeding pairs), that the duration of the related bottleneck was brief, and that the current mink population on the NIA was founded within the last 100 years and could have reached carrying capacity within 10-20 years. Determining whether the founding event is attributable to natural, long-distance migration or human intervention, and further narrowing the timeframe in which it may have occurred, requires ancillary data on both mink behavior and their distributional history in PWS.

Evidence from a number of sources support the conclusion that mink have not always been present on the NIA in the high numbers currently observed. In 1908, a collecting expedition from the Museum of Vertebrate Zoology at the University of California, Berkeley reported mink on the Knight Island Archipelago and Hinchinbrook Island, but not on Naked, Storey, or Peak islands (or on Montague or Green Island; Heller 1910). In the 1970s and 1980s, seabird biologists studying pigeon guillemots on Naked Island did not report mink among the predators of guillemot nests and did not note the presence of mink or their sign on the island (Kuletz 1983). Ed Bilderback of Cordova (pers. comm.) reported that he trapped mink and otter throughout PWS between 1946 and 2002, but never saw or caught mink on Naked, Storey, or Peak islands until the mid-1990s. By the mid-1990s, mink were considered a major predator of guillemots nesting on the NIA (Hayes 1996, Prichard 1997, Golet 1998) and, in May 2008, five people trapped 27 mink in five days on Naked, Storey, and Peak islands (147 traps, 413 trap/nights), indicating a large mink population.

Although mink are always found in close association with water, they are not strong swimmers or divers like river otters (Dunstone 1992), so the 6 km of open water between the NIA and the nearest island or mainland locality (the northern tip of Eleanor I. in the Knight Island Archipelago) may be sufficient to preclude mink from successfully colonizing the NIA naturally. Studies of introduced mink colonizing islands in Europe suggest that they will traverse no more than 2 km of open water (e.g., Craik 1997, Clode & MacDonald 2002), although a study in Tierra del Fuego reported that mink swam 4 km to reach an island (Anderson 2006). Whether mink populations that evolved in a marine environment, such as those in PWS, are more inclined to swim distances of 6 km is not known, but *N. v. melampeplis* is one of the larger subspecies, so long-distance dispersal over open water may be more likely for them than for a smaller, freshwater-adapted subspecies (or their fur farm descendents). On the other hand, the documented absence of mink on Montague I. prior to the 1951 introduction suggests that 8-10 km of open water exceeds the upper limit for over water dispersal by mink in PWS and, thus, 6 km is further than mink would be expected to swim on a regular basis.

Even if mink had been a natural part of the fauna of the NIA in the past or were introduced via an early fur farm, a number of factors could have contributed to their absence for much of the last century. The first fox farm in PWS was established on Storey I. in 1895 (Janson 1985) and by 1908 free-ranging foxes had extirpated all small mammals (shrews and rodents) from both Storey and Peak islands (Heller 1910) and there were foxes on Naked I. as well. Because these foxes foraged in the intertidal, they would have been competitors (and possible predators) of mink, if mink were present during this time. Coastal mink are readily accessible to trappers and periodic overharvest is thought to have limited their numbers in PWS between 1931 and 1955 (Crowley 2001). The March 1964 Alaska earthquake resulted in tsunamis and Naked I. was uplifted almost five feet, permanently exposing nearly half of the intertidal (Johanson 1971) and eliminating important foraging areas for mink for several years. The ability of any mink population on the NIA to rebound from losses due to these and other random ecological and demographic disturbances to which small island populations are particularly vulnerable would no doubt be impeded by the relative seclusion of the archipelago.

In the absence of evidence for mink on the NIA prior to the 1990s, we conclude that the current mink population was most likely established during the mid-1970s to early 1990s, which is consistent with the genetic evidence. A mink population small enough to go unnoticed prior to that time and persisting to the present day could not support the level of genetic diversity currently observed on the NIA. However, in a favorable environment for mink, as the NIA appears to be, a small founding population of mink could easily expand to carrying capacity within 10 to 20 years. Several factors may have increased the favorability for mink of the habitat on the NIA by the 1970s and 1980s: (1) the last fox farm on the NIA closed in the 1950s (Lethcoe & Lethcoe 1994), (2) most prey species in the intertidal zone had recovered within 10 years of the 1964 uplift (Haven 1971, Paul 1976), and (3) declining fur prices during the 1980s resulted in decreased trapping pressure, which was thought to have resulted in increased mink populations throughout the Sound (Crowley 2001).

Given the relative isolation of the NIA, a natural migration seems less likely than an anthropogenic introduction to provide the number of mink necessary to ensure the allele numbers and heterozygosity levels observed in the Naked I. sample (equivalent to five successfully breeding pairs). The introduction and translocation of mink and other furbearers for trapping and fur farming has a long and successful history in coastal Alaska (Janson 1985, Smythe 1988, Bailey 1993, Wooley 2002, Paul 2009), as the occurrence of fur farm haplotypes and non-PWS alleles throughout PWS attests. The apparent admixture of introduced fur farm and PWS mink on Montague and Green islands is also best explained by an undocumented translocation of western PWS mink shortly after the documented fur farm mink introduction there. Undocumented introductions and translocations of more than sufficient size to account for the genetic diversity of mink on the NIA still occurred in the latter half of the last century; e.g., in 1968, a fur farmer introduced more than 200 mink to Sitkalidak Island south of Kodiak (Don Owens, pers. comm.). In contrast, a natural mass-migration of mink to establish the population on the NIA has no precedent.

Management recommendations

Because the current NIA mink population is introgressed – a 'hybrid' of fur farm and PWS genetic types – they are clearly not an evolutionarily significant unit. As such, and because the pigeon guillemot breeding population on the Naked Island Archipelago is sufficiently low that even a single mink could be a significant threat to the guillemot population as a whole, we recommend the removal of the current mink population as an aid to pigeon guillemot recovery.

There is an extensive literature on predation by introduced mink and on removal of mink from seabird islands in Europe that is encouraging regarding the potential success of similar efforts on the NIA. Many of the islands where mink have been removed are not very remote from larger islands and mainland localities with uncontrolled mink populations, making these European efforts long-term and likely never-ending (e.g., Clode & MacDonald 2002, Nordstrom & Korpimaki 2004). The NIA is remote from other mink populations by comparison, making the initial task of mink removal more readily achievable. In Europe, large seabird colonies have been found to coexist more successfully with feral mink predation than small colonies. Thus, a single exhaustive removal effort on the NIA now may allow seabird colonies there to attain sufficient size to continue recovery despite any subsequent rare, long-distance migration or accidental translocation (coastal mink have been known to take up temporary residence on small fishing boats; David Hatler, pers. comm.) in the future. As in Europe, efforts should also be made to educate trappers and others in PWS about the inadvisability of further intentional introductions of mink or other furbearers to the NIA.

To ensure the effectiveness of mink removal during pigeon guillemot recovery, the NIA should be regularly monitored for the subsequent reappearance of mink, as is done on seabird islands in Europe. Here too, mink removal efforts in PWS have an advantage over similar efforts in other parts of the world where mink are not native. The tradition of mink trapping in Alaska (and on-going river otter trapping on the NIA) and the pre-existing market for their wild fur provide additional opportunities to monitor the islands by enlisting trappers to help detect whether mink reappear and control their population numbers if they do.

A total of 169 mink collected from PWS localities for this project (including 42 from the NIA), have tissues and skeletal material permanently archived at the Museum of Southwestern Biology at the University of New Mexico. Additional collecting and archiving of specimens and associated capture information during a mink removal program at the NIA would provide a more comprehensive record of the population's genetic and morphological variation, health, and demography. This would be useful in determining whether any mink trapped on the island post-removal were new colonists or previously undetected survivors of removal efforts. If these later-caught mink appear to be new colonists, the materials archived from throughout PWS during the current project and other museum specimens could aid in identifying the source(s) of the new arrivals. Knowing the source of these 'immigrants' and how soon they arrived after removal would help determine what further steps could be taken; e.g., Cordova as a source population at any time would imply a human translocation, while the arrival of Knight I. mink within a year would suggest that long-distance migration is not uncommon for PWS mink; multiple genetically diverse mink captured in the same season would suggest a large founder event (i.e., intentional translocation), while the same number of genetically similar mink would suggest a smaller founder event with successful subsequent reproduction. These efforts would provide biologists and managers with a great deal of additional information about how native (and introgressed) mink populations on seabird islands grow and disperse among islands, which could aid other seabird recovery efforts in PWS and other parts of North America (e.g., similar mink removal efforts are being considered in the Scott Islands off Vancouver Island, British Columbia; www.islandconservation.org).

Acknowledgments

We would like to thank our lab technician, Brad Truett, and acknowledge the technical help received from Natalie Dawson, Jerry Dragoo, Andrew Hope, Jolene Rearick and others in the Cook Lab, Museum of Southwestern Biology and UNM Department of Biology. Daniel Roby and David Irons' PWS field crews (2007-2008) provided the bulk of the PWS mink samples. Other samples were provided by trappers, in particular members of the Alaska Trappers' Association, BC Trappers' Association, and Washington State Trappers' Association, with the help of the Alaska Department of Fish and Game, the USDA Forest Service in the Tongass National Forest, BC Wildlife, the Canadian Wildlife Service, and the Royal British Columbia Museum. Eastern samples were obtained with the help of Gordon Batcheller, Alison Beal, Paul Jensen, Wayne Kelly, Chris Kyle, Al Lackey, Cade Libby, Frank Phillips, and Rich Stevens. Special thanks to Jeff Bowman and Anne Kidd who shared mink samples from their ongoing study of native and fur farm mink hybridization in Ontario. Harvey and Gincy Beck provided fur farm mink samples. The remaining samples were obtained from the University of Alaska Museum of the North and Museum of Southwestern Biology. Kirsten Bixler provided information about the history of the Oregon State University fur farm and perimeters of islands associated with the Naked Island Archipelago and Montague I. Phillip England kindly provided GENELOSS software.

Literature cited

Adams, L.H. 1935. *Mink Raising*. 3rd Edition. A. R. Harding Pub. Co., Columbus, Ohio. 225 pp.

Anderson, C.G., R. Rozzi, J.C. Torres-Mura, S.M. McGehee, M.F. Sherriffs, E. Schuttler, and A.D. Rosemond. 2006. Exotic vertebrate fauna in the remote and pristine sub-Antarctic Cape Horn Archipelago, Chile. Biodiversity and Conservation 15:3295-3313.

Bailey, E.P. 1993. Introduction of foxes to Alaskan islands – history, effects on avifauna, and eradication. United States Fish and Wildlife Service, Technical Report Series 193. 53 pp.

Bock, H. 1942. The history of platinum mink. Columbia Empire Furs 2:7-14.

Bower, W.T. 1917. Alaska Fisheries and Fur-seal industries in 1917. United States Government Printing Office. 118 pp.

Bidlack, A. and J.A. Cook. 2001. Reduced genetic variation in insular northern flying squirrels (*Glaucomys sabrinus*) along the North Pacific Coast. Animal Conservation 4:283–290.

Burris, O.E. and D.E. McKnight. 1973. Game transplants in Alaska. Alaska Department of Fish and Game, Game Technical Bulletin No. 4.

Clode, D. and D.W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Cornuet, J.M. and G. Luikart. 1997. Description and power analysis of two tests for detecting recent population bottlenecks from allele frequency data. Genetics 144:2001-2014.

Craik, J.C.A. 1997. Long-term effects of North American mink *Mustela vison* on seabirds in western Scotland. Bird Study 44:303-309.

Crowley, D.W. 2001. Unit 6 furbearer management report. Pp. 83-93 *in* C. Healy, editor. Furbearer management report of survey and inventory activities 1 July 1997-30 June 2000. Alaska Department of Fish and Game. Project 7.0. Juneau, Alaska.

Dunstone, N. 1992. The Mink. T & AD Poyser, London. 232 pp.

England, P.R. and G.H.R. Osler. 2001. GENELOSS: a computer program for simulating the effects of population bottlenecks on genetic diversity. Molecular Ecology Notes 1:111–113.

Evanno, G., S. Regnaut, and J. Goudet. 2005. Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14:2611-2620.

Falush, D., M. Stephens, and J.K. Pritchard. 2003. Inference of population structure: using multilocus genotype data: linked loci and correlated allele frequencies. Genetics 164:1567-1587.

Fleming, M.A., E.A. Ostrander, and J.A. Cook. 1999. Microsatellite markers for American mink (*Mustela vison*) and ermine (*Mustela erminea*). Molecular Ecology 8:1352-1354.

Fleming, M.A. and J.A. Cook. 2002. Phylogeography of endemic ermine (*Mustela erminea*) in southeast Alaska. Molecular Ecology 11:795-807.

Fleming, M.A., D.F. Hatler, and J.A. Cook. *In prep.* Genetic differentiation and the evolution of late breeding in coastal mink (*Neovison vison*).

Golet, G.H. 1998. The breeding and feeding ecology of Pigeon Guillemots at Naked Island, Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project Annual Report, (Restoration Project 97163F), U.S. Fish and Wildlife Service, Anchorage, Alaska.

Golet, G.H., P.E. Seiser, A.D. McGuire, D.D. Roby, J.B. Fischer, K.J. Kuletz, D.B. Irons, T.A. Dean, S.C. Jewett, and S.H. Newman. 2002. Long-term direct and indirect effects of the *Exxon Valdez* oil spill on pigeon guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

Gothier, F. 1941. Kenai mink. Columbia Empire Furs 5:6-8.

Goudet, J. 1995. Fstat (version 1.2): a computer program to calculate F-statistics. Journal of Heredity 86:485-486.

Hanson, B.D. and A.C. Taylor. 2008. Isolated remnant of recent introduction? Estimating the provenance of Yellingbo Leadbeater’s possums by genetic analysis and bottleneck simulation. Molecular Ecology 17:4039-4052.

Hatler, D.F. 1976. The coastal mink of Vancouver Island, British Columbia. Ph.D. Thesis. University of British Columbia, Canada.

Hatler, D.F., D.W. Nagorsen, and A.M. Beal. 2009. Carnivores of British Columbia. University of British Columbia Press. 407 pp.

Haven, S.B. 1971. Effects of land-level changes on intertidal invertebrates with discussion of postearthquake ecological succession. *in* The Great Alaska Earthquake of 1964: Biology. NAS Pub. 1604. Washington: National Academy of Sciences. Pp. 82-127.

Hayes, D.L. 1995. Recovery monitoring of pigeon guillemot populations in Prince William Sound, Alaska. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 94173), U.S. Fish and Wildlife Service, Anchorage, Alaska.

Hayes, D.L. 1996. A comparison of the breeding biology and feeding ecology of pigeon guillemots at Naked and Jackpot islands in Prince William Sound, Alaska. Appendix F in D.C. Duffy, compiler. APEX: Alaska Predator Ecosystem Experiment. Exxon Valdez Oil Spill Restoration Project Annual Report, Project 95163. USDI Fish and Wildlife Service, Anchorage, AK.

Heller, E. 1910. Mammals of the 1908 Alexander Alaska Expedition with descriptions of the localities visited and notes on the flora of the Prince William Sound region. Univ. Calif. Publ. Zool. 5:321-360.

Hennemann, W.W. 1983. Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. Oecologia 56:104-108.

Janson, L. 1985. Those Alaska Blues: a fox tail. Alaska Historical Commission Studies in History No 186. Department of Education, State of Alaska, Anchorage.

Johanson, H.W. 1971. The effects of elevation changes on benthic algae in Prince William Sound. *in* The Great Alaska Earthquake of 1964: Biology. NAS Pub. 1604. Washington: National Academy of Sciences. Pp. 35-68.

Kocher T.D., J.A. Conroy, K.R., McKaye, and J.R. Stauffer. 1993. Similar morphologies of cichlid fish in Lakes Tanganyika and Malawi are due to convergence. Molecular Phylogenetics and Evolution 2:158–165.

Kuletz, K.J. 1983. Mechanisms and consequences of foraging behavior in a population of breeding pigeon guillemots. Unpubl. M.Sc. thesis. Univ. California, Irvine. 79 pp.

Kuo, C-H. and F.J. Janzen. 2003. BottleSim: a bottleneck simulation program for long-lived species with overlapping generations. Molecular Ecology Notes 3:669-673.

Lethcoe, J. and N. Lethcoe. 1994. A History of Prince William Sound. Todd Publications, Anchorage. 160 pp.

Luikart, G. and J. Cornuet. 1999. Estimating the effective number of breeders from heterozygote excess in progeny. Genetics 151:1211-1216.

MacDonald, S.O. and J.A. Cook. 2009. Recent Mammals of Alaska. University of Alaska Press. 300 pp.

Maddison, W.P. and D.R. Maddison. 1992. MacClade: analysis of phylogeny and character evolution. Sinauer, Sunderland, Mass.

Nordstrom, M. and E. Korpimaki. 2004. Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. Journal of Animal Ecology 73: 424-433.

Paul, A.J., J. Paul, and H.M. Feder. 1976. Recruitment and growth in the bibalve *Protothaca staminea* at Olsen Bay, Prince William Sound, ten years after the 1964 Earthquake. Veliger 18(4):385-392.

Paul, T. 2009. Game transplants in Alaska. Alaska Department of Fish and Game, Game Technical Bulletin 4.

Prichard, A.K. 1997. Evaluation of Pigeon Guillemots as bioindicators of nearshore ecosystem health. M.S. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Pritchard, J.K., M. Stephens, and P. Donnelly. 2000. Inference of population structure using multilocus genotype data. Genetics 155:945-959.

Raymond, M. and F. Rousset, 1995. GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86:248-249.

Rosenberg, N.A. (2004). Distruct: a program for the graphical display of population structure. Molecular Ecology Notes 4:137-138.

Rousset, F. 2008. Genepop'007: a complete reimplementation of the Genepop software for Windows and Linux. Molecular Ecology Resources 8:103-106.

Rousset, F. and M. Raymond. 1995. Testing heterozygote excess and deficiency. Genetics 140:1413-1419.

Shackelford, R.M. 1950. Genetics of Ranch Mink. Pilsbury Publishers, New York. 91pp.

Sheldon, C. 1912. The Wilderness of the North Pacific Coast Islands: a hunter's experiences while searching for wapiti, bears, and caribou on the larger coast islands of British Columbia and Alaska. Charles Scribner's Sons, New York. 246 pp.

Simmons, M.P. and H. Ochoterena. 2000. Gaps as characters in sequence-based phylogenetic analyses. Systematic Biology 49:369-381.

Smythe, C.W. 1988. Harvest and use of fish and wildlife resources by residents of Petersburg, Alaska. Technical Paper Number 164. Division of Subsistence, Alaska Department of Fish and Game. Juneau: State of Alaska.

Statistics Canada. 2006. Fur Statistics. Catalogue #23-013-NIA, Statistics Canada, Ottawa.

Taylor, A.C. and D.W. Cooper. 1999. Microsatellites identify introduced New Zealand tammar wallabies (*Macropus eugenii*) as an 'extinct' taxon. Animal Conservation 2:41–49.

Wisely, S.M., S.W. Buskirk, M.A. Fleming, D.B. McDonald, and E.A. Ostrander. 2002. Genetic diversity and fitness in black-footed ferrets before and during a bottleneck. Journal of Heredity 93(4):231–237.

Wooley, D. 2002. The myth of the "pristine environment": past human impacts in Prince William Sound and the northern Gulf of Alaska. Spill Science and Technology Bulletin 5(1):89-104.

Wright, S. 1978. Evolution and the Genetics of Populations, Vol. 4, Variability Within and Among Natural Populations. University of Chicago Press, Chicago, Illinois. 439pp.

APPENDIX C
Methods for Lethal Trapping of Mink at the Naked Island Group in Prince William Sound, Alaska

By Kirsten S. Bixler and David B. Irons

This document includes detailed methods for the lethal collection of American mink (*Neovison vison*) at the Naked Island group in Prince William Sound, Alaska. These methods balance efficacy, humane euthanasia, and human safety and include techniques that lessen or eliminate the capture of non-target species. These methods have been successfully tested at the Naked Island group.

TRAP PREPARATION

Mink would be captured using lethal body grip traps such as Oneida-Victor Conibear® 110 and 220 traps. These traps are strong enough to capture a mink but will allow a river otter (*Lontra canadensis*) to escape. A piece of 16-guage wire, approximately 2 feet in length, should be attached to the chain. Prior to use, the traps should be coated in trap dip such as N/B Formula One Instant Trap Kote. Artificial tunnels, created with black motor route tubes, would minimize or prevent the capture of non-target species by making the trap less visible. The tubes must be altered with a 4 to 6 inch horizontal cut down the center of one side of the tube for a Conibear®110 and both sides for a Conibear® 220 traps (Fig. 1).

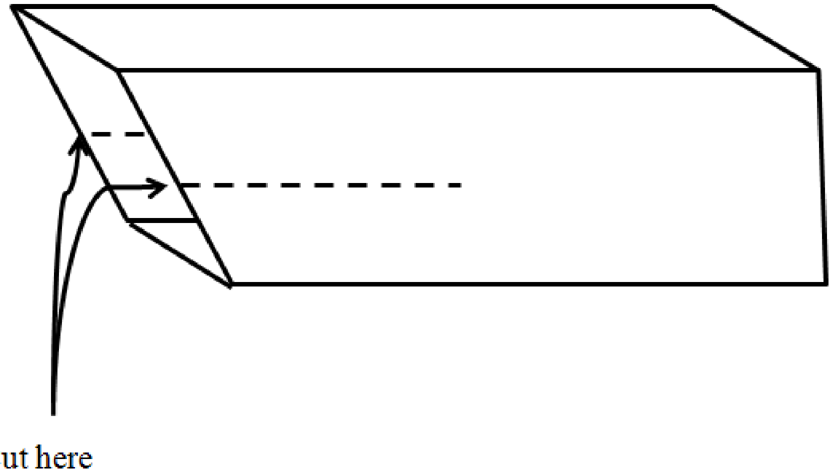


Figure 1. A diagram of a motor route tube used to create artificial tunnels in trapping mink. The dotted lines refer to the locations that must be cut to fit set traps.

PLACEMENT OF TRAPS

Appropriate placement of traps is exceptionally important. The object is to position the traps along a path used frequently by mink. All traps should be set above the high tide line.

Traps should be set primarily along beaches, preferably below a shallow vegetated hillside, with a large rocky intertidal area. Within a beach, traps should be set along creek outflow(s) and/or at the lowest point. In addition, traps should be placed about every 200 m along and at each end of the beach. Traps should be placed under cover of vegetation and along the easiest path of travel, such as along game trail or line of driftwood. Also, set traps beside a path where mink would be forced to travel, such as at the base of a cliff or point of land connecting adjacent beaches.

TRAP SETTING

Prior to setting traps, a bait fish (e.g., 4-inch trolling herring) is placed into the back of the motor route tube. Attach the trap to a tree or rock using the 16-guage wire. The trap should then be set. Instructions for setting Conibear® 110 and 120 traps are available online at http://www.oneidavictor.com/trapsettinginstructions.html. Once set, slide the trap into the motor route tube with the spring(s) extended out of the side(s) of the tube. Place a small rock on top of the tube. It should weigh down the tube but not cause it to bend. If the tube bows, the trap will not close properly. Lightly spray the trap with mink lure (e.g., Big Sky Co. Ambra musk or Grawes Co. mink #1). Mark the location with a long strip of brightly colored flagging tape tied to a tree branch. Record the latitude and longitude of the trap using a handheld global positioning system (GPS) device.

Trappers will be set ashore by boat. The boat captain records the latitude and longitude of the beach and the number of traps set per beach. About 25 traps can be set per trapper in a day.

TRAP CHECKING

A .22 rifle should be available as a back-up euthanasia technique if the trap does not instantly kill the trapped mink. Traps should be checked once per day. If nothing is captured, add bait and lure as necessary. The boat captain ensures that all traps are checked. Record the location (i.e., latitude and longitude) and sex of each mink captured. Mink carcasses should be frozen and either donated to a museum or otherwise made available for research.

APPENDIX D

Compliance of Preferred Alternative with Standards Used to Judge Importance of Restoration Under the 1994 *Exxon Valdez* Oil Spill Restoration Plan

This document lists the seven standards used to assess the importance of restoration by the *Exxon Valdez* Oil Spill (EVOS) Trustee Council (*Exxon Valdez* Oil Spill Trustee Council 1994). Following each quoted policy, we provide details on compliance of the preferred alternative for restoration of Pigeon Guillemots (*Cepphus columba*) in Prince William Sound (i.e., eradication of mink at the Naked Island group; Restoration Project 10070853) with that standard.

1. "NATURAL RECOVERY"

There is no evidence that the population of Pigeon Guillemots in Prince William Sound (PWS) is recovering from the EVOS (McKnight et al. 2008, Appendix A). Given the persistent long-term population declines, even in the absence of exposure to residual oil (B. Ballachey, U.S. Geological Survey, pers. comm.), the population is unlikely to recover in the foreseeable future without restoration. Following action under the preferred alternative, we estimate that guillemot population at the Naked Island group would show significant signs of recovery within a decade and the Sound-wide guillemot population would show signs of increase within 15 years (Figure 3). This project provides a unique opportunity for recovery of an injured resource. There are no other restoration options currently available that are likely to be effective in addressing factors limiting recovery of the guillemot population in PWS.

2. "THE VALUE OF AN INJURED RESOURCE TO THE ECOSYSTEM AND TO THE PUBLIC"

The Pigeon Guillemot is neither federally endangered nor threatened, but it now the only marine bird species injured by EVOS that is listed as "not recovering" on the Exxon Valdez Oil Spill Trustee Council's Injured Resources List and has shown no sign of population recovery (*Exxon Valdez* Oil Spill Trustee Council 2009).

The Pigeon Guillemot is an apex predator in PWS, consuming a variety of nearshore demersal and schooling forage fishes. As such, the guillemot has been a sensitive indicator of both residual oil and changes in availability of marine forage fish in PWS (Golet et al. 2002). With its charisma and striking appearance the species contributes to the success of ecotourism, vital to the economy of the Sound.

3. "DURATION OF BENEFITS"

The benefits of the preferred alternative will be recognized indefinitely. The eradication of mink and subsequent monitoring will benefit the survival of both Pigeon Guillemot chicks and adults at the Naked Island group, increasing the viability of the species in the Sound in the face of large-scale environmental change.

4. “TECHNICAL FEASIBILITY”

Success in eradication of mink at the Naked Island group is expected. Due to geographic isolation, immigration by mink to the islands and natural recolonization is unlikely (Nordström and Korpimäki 2004). Methods of mink removal have been developed through several successful eradication campaigns in Europe, where feral American mink have had disastrous effects on native fauna (Bonesi and Palazon 2007). Methods for the lethal capture of mink have been successfully tested at the Naked Island group (see Appendix C)

5. "LIKELIHOOD OF SUCCESS"

The best available science indicates that mink predation on guillemot nests and adults is the primary limiting factor for Pigeon Guillemots nesting at the Naked Island group (Appendix A). Further, there are striking declines in the guillemot population at the Naked Island group, where mink are present, and stable guillemot populations at nearby mink-free islands (Smith Island group). This suggests that mink eradication will result in a significant increase in guillemot adult survival, reproductive success, and population size. The effect of the proposed restoration action on the population size of guillemots at the Naked Island group would be readily measurable through periodic shoreline censuses using established protocols.

6. "HARMFUL SIDE EFFECTS"

The methods proposed in the preferred alternative include actions to minimize capture of non-target species (see Appendix C). There is no evidence to suggest that restoration of guillemots at the Naked Island group would have a significant negative effect on herring (*Clupea pallasi*) because this fish has never been a large part of the diet of guillemots at this location (Golet et al. 2000). The unintended negative consequence of abrupt and destructive increases in the population of small exotic herbivores or omnivores following invasive carnivore removal (Bergstrom et al. 2009) is not a concern at the Naked Island group because no such exotic species (e.g., rabbits, rats) are present. Because mink at the Naked Island group are descendants in part from fur farm stock, their eradication would not have a negative impact on the Sound-wide population of native mink. Removal of mink from the Naked Island group would not pose a hardship to trappers in PWS because these islands are rarely used for mink harvest (R. Ellis, U. S. Department of Agriculture – Wildlife Services, pers. comm.).

7. "OPERATION AND MAINTENANCE SUPPORT REQUIRED"

Independent operational and maintenance funding will be identified during the competitive bid process.

8. "BENEFIT TO A SINGLE RESOURCE OR MULTIPLE RESOURCES"

The preferred alternative would be implemented specifically to address impacts on Pigeon Guillemots, but may also benefit a suite of seabird species whose breeding populations have declined or been locally extirpated at the Naked Island group including Arctic Terns (*Sterna paradisaea*), Parakeet Auklets (*Aethia psittacula*), Tufted Puffins (*Fratercula cirrhata*), and

Horned Puffins (*Fratercula corniculata*) (Oakley and Kuletz 1979, KSB, pers. obs). Mink eradication may also benefit other populations of ground-nesting birds (Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, Banks et al. 2008), small mammals, amphibians (Banks et al. 2008), and crustacea (Bonesi and Palazon 2007).

9. "EFFECTS ON HEALTH AND HUMAN SAFETY"

The lethal mink removal methods proposed as part of the preferred alternative are specific to mink and would pose no risk to human health and safety.

10. "CONSISTENCY WITH APPLICABLE LAWS AND POLICIES"

The preferred alternative complies with the mission and policies of the EVOS Restoration Plan as well as the state and federal agencies responsible for the involved resources. Prior to implementation, this plan requires permit approval from responsible agencies (U.S. Forest Service, Alaska Department of Fish and Game).

11. "DUPLICATION"

The proposed action is a unique opportunity for the restoration of Pigeon Guillemots in PWS and does not duplicate other projects.

LITERATURE CITED

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

Bergstrom, D. M., A. Lucieer, K. Kiefer, J. Wasley, L. Belbin, T. K. Pedersen, and S. L. Chown. 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46:73-81.

Bonesi, L., and S. Palazon. 2007. The American mink in Europe: status impacts, and control. Biological Conservation 134:470-483.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Exxon Valdez Oil Spill Trustee Council. 1994. *Exxon Valdez* oil spill restoration plan. Anchorage, AK.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Golet, G. H., P. E. Seiser, A. D. McGuire, D. D. Roby, J. B. Fischer, K. J. Kuletz, D. B. Irons, T. A. Dean, S. C. Jewett, and S. H. Newman. 2002. Long-term direct and indirect effects of the 'Exxon Valdez' oil spill on Pigeon Guillemots in Prince William Sound, Alaska. Marine Ecology Progress Series 241:287-304.

McKnight, A., K. M. Sullivan, D. B. Irons, S. W. Stephensen, and S. Howlin. 2008. Prince William Sound marine bird surveys, synthesis and restoration. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 080751). U.S. Fish and Wildlife Service, Anchorage, AK.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Nordström, M., and E. Korpimäki. 2004. Effects of island isolation and feral mink removal on bird communities on small islands in the Baltic Sea. Journal of Animal Ecology 73:424-433.

Oakley, K. L., and K. J. Kuletz. 1979. Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot. U.S. Fish and Wildlife Service, Office of Special Studies, Anchorage, AK.

APPENDIX E
Compliance of Preferred Alternative with Policies of the 1994 *Exxon Valdez* Oil Spill Restoration Plan

This document lists all 21 restoration policies of the *Exxon Valdez* Oil Spill (EVOS) Trustee Council (*Exxon Valdez* Oil Spill Trustee Council 1994). Following each quoted policy, we provide details on compliance of the preferred alternative for restoration of Pigeon Guillemots (*Cepphus columba*) in Prince William Sound (i.e., eradication of mink at the Naked Island group; Restoration Project 10070853) with that policy.

1. "RESTORATION SHOULD CONTRIBUTE TO A HEALTHY, PRODUCTIVE, AND BIOLOGICALLY DIVERSE ECOSYSTEM WITHIN THE SPILL AREA THAT SUPPORTS THE SERVICES NECESSARY FOR THE PEOPLE WHO LIVE IN THE AREA"

The proposed restoration would occur within the EVOS area at the Naked Island group in PWS. This location is the most important historical breeding site for Pigeon Guillemots in Prince William Sound. Guillemots are a conspicuous and particularly stunning resident of nearshore waters, and thus contribute to ecotourism in Prince William Sound. Eradication of mink at this location is likely to benefit not just the population of Pigeon Guillemots but a variety of locally depressed breeding populations of seabirds including Arctic Terns (*Sterna paradisaea*), Parakeet Auklets (*Aethia psittacula*), Tufted Puffins (*Fratercula cirrhata*), and Horned Puffins (*Fratercula corniculata*) (Oakley and Kuletz 1979, KSB, pers. obs). Mink eradication at the Naked Island group may also benefit additional taxa for which population declines due to predation by invasive mink have been documented in other areas. These taxa include ground-nesting birds (e.g., waterfowl; Ferreras and MacDonald 1999, Clode and MacDonald 2002, Nordström et al. 2002, Nordström et al. 2003, e.g., waterfowl; Banks et al. 2008), small mammals, amphibians (Banks et al. 2008), and crustacea (Bonesi and Palazon 2007).

2. "RESTORATION WILL TAKE AN ECOSYSTEM APPROACH TO BETTER UNDERSTAND WHAT FACTORS CONTROL THE POPULATIONS OF INJURED RESOURCES"

There has been intensive research on the nesting ecology and mechanisms regulating the population of Pigeon Guillemots nesting at the Naked Island group during 15 breeding seasons in the last 30 years. This research has identified three main factors constraining guillemot population recovery following EVOS; 1) exposure to residual oil, 2) availability of preferred prey, and 3) nest predation. The most recent study of Pigeon Guillemot nesting ecology at the Naked Island group suggests that mink predation on guillemot nests and adults is now the primary factor limiting their recovery (Appendix A). A study of mink genetic structure at the Naked Island group and other locales in PWS determined that mink at the Naked Island group are in part descendants of fur farm stock and were most likely introduced to the Naked Island group by humans (Appendix B). The restoration alternatives evaluated as part of this plan were based upon the extensive research previously conducted on Pigeon Guillemots at the Naked

Island group and elsewhere in PWS, and the preferred alternative was selected because it most effectively addressed our understanding of the current primary factor limiting recovery of the Pigeon Guillemot population at the Naked Island group.

3. “RESTORATION ACTIVITIES MAY BE CONSIDERED FOR ANY INJURED RESOURCE OR SERVICE”

The Pigeon Guillemot is the only marine bird species known to have been injured by EVOS that is listed as "not recovering" on the Exxon Valdez Oil Spill Trustee Council's Injured Resources List and has shown no sign of population recovery (*Exxon Valdez* Oil Spill Trustee Council 2009).

4. “RESTORATION WILL FOCUS UPON INJURED RESOURCES AND SERVICES AND WILL EMPHASIZE RESOURCES AND SERVICES THAT HAVE NOT RECOVERED”

The population of Pigeon Guillemots in PWS was injured by EVOS and has declined by more than 90% on the Naked Island group since 1990. Although there is no longer evidence that residual oil from EVOS is having a direct negative effect on Pigeon Guillemots in the Sound (B. Ballachey, U.S. Geological Survey, pers. comm.), the population continues to decline.

5. “RESOURCES AND SERVICES NOT PREVIOUSLY IDENTIFIED AS INJURED MAY BE CONSIDERED FOR RESTORATION IF REASONABLE SCIENTIFIC OR LOCAL KNOWLEDGE OBTAINED SINCE THE SPILL INDICATES A SPILL-RELATED INJURY”

The Pigeon Guillemot in PWS is considered a resource injured by EVOS (*Exxon Valdez* Oil Spill Trustee Council 2009).

6. “PRIORITY WILL BE GIVEN TO RESTORING INJURED RESOURCES AND SERVICES WHICH HAVE ECONOMIC, CULTURAL AND SUBSISTENCE VALUE TO PEOPLE LIVING IN THE OIL SPILL AREA, AS LONG AS THIS IS CONSISTENT WITH OTHER POLICIES”

Although Pigeon Guillemots have little subsistence value, they contribute to the local culture as well as the success of ecotourism in PWS. Guillemots are conspicuous, vocal, and charismatic and thus play a role in the auditory and visual experience of all who frequent the shoreline of PWS.

7. “POSSIBLE NEGATIVE EFFECTS ON RESOURCES OR SERVICES MUST BE ASSESSED IN CONSIDERING RESTORATION PROJECTS”

The preferred alternative includes actions to minimize capture of non-target species (i.e., trap type and use of artificial burrows for trap deployment; see Appendix C). There is no evidence to suggest that restoration of guillemots at the Naked Island group would have a significant negative effect on Pacific herring (*Clupea pallasi*). Herring have never been an important part of the diet of guillemots nesting at the Naked Island group (Golet et al. 2000). Mink at the Naked Island group are rarely exploited for their fur (R. Ellis, U.S. Department of Agriculture – Wildlife Services, pers. comm.), and thus a mink eradication project at this location would not pose a hardship to trappers in PWS. Due to fur farm ancestry, the eradication of mink at the Naked Island group would not have a negative impact on the Sound-wide population of native mink. Finally, because there are no small exotic herbivores or omnivores (e.g., rabbits, rats) at the Naked Island group, there is no concern for abrupt and destructive increases in the population of exotic species following invasive carnivore removal (Bergstrom et al. 2009).

8. “RESTORATION ACTIVITIES WILL OCCUR PRIMARILY WITHIN THE SPILL AREA”

The preferred alternative consists of restoration actions at the Naked Island group located in the EVOS area. In fact, the first shoreline to be oiled following EVOS was the Naked Island group in the center of PWS (Oakley and Kuletz 1996).

9. “PROJECTS DESIGNED TO RESTORE OR ENHANCE AN INJURED SERVICE”

The preferred alternative is the most effective alternative available for increasing the reproductive success and population size of Pigeon Guillemots at the Naked Island group and would facilitate the recovery of this injured resource within PWS. However, the Pigeon Guillemot is not considered an injured service.

10. “COMPETITIVE PROPOSALS FOR RESTORATION PROJECTS WILL BE ENCOURAGED”

The restoration would be conducted by a team chosen through a competitive bid process.

11. “RESTORATION WILL TAKE ADVANTAGE OF COST SHARING OPPORTUNITIES WHERE EFFECTIVE”

Opportunities for cost sharing, especially with the U.S. Fish and Wildlife Service, will be identified during the competitive bid process.

12. “RESTORATION SHOULD BE GUIDED AND REEVALUATED AS INFORMATION IS OBTAINED FROM DAMAGE ASSESSMENT STUDIES AND RESTORATION ACTIONS”

The preferred alternative would use an adaptive management approach. Data collected through trapping (e.g., trapping success, sex of trapped animals), as well as shoreline censuses for Pigeon Guillemots would be reviewed regularly. If there is evidence that the project’s objective is not being met, restoration project methods would be modified.

13. "PROPOSED RESTORATION STRATEGIES SHOULD STATE A CLEAR, MEASURABLE AND ACHIEVABLE ENDPOINT"

The restoration action includes eradication of mink at the Naked Island group, which should be achievable within 5 years or less. Continued monitoring, to document the response by the guillemot breeding population and verify the continued absence of mink at the Naked Island group, is recommended.

14. "RESTORATION MUST BE CONDUCTED AS EFFICIENTLY AS POSSIBLE, REFLECTING A REASONABLE BALANCE BETWEEN COSTS AND BENEFITS"

The preferred alternative is the most effective method to elevate the productivity and population size of Pigeon Guillemots nesting at the Naked Island group and facilitate the recovery of the species in PWS. This alternative is less expensive, both economically and in numbers of mink and other guillemot predators sacrificed, compared to culling methods (Courchamp et al. 2003). Other alternatives are either currently unavailable or unlikely to be effective in restoring Pigeon Guillemots.

15. "PRIORITY SHALL BE GIVEN TO STRATEGIES THAT INVOLVE MULTI-DISCIPLINARY, INTERAGENCY, OR COLLABORATIVE PARTNERSHIPS"

The Pigeon Guillemot restoration plan was developed by employees of the U.S. Fish and Wildlife Service, Oregon State University, and U.S. Geological Survey - Oregon Cooperative Fish & Wildlife Research Unit at Oregon State University. In addition, employees of the Museum of Southwestern Biology at the University of New Mexico contributed to the most current research used in the development of this restoration plan.

16. "RESTORATION PROJECTS WILL BE SUBJECT TO OPEN, INDEPENDENT SCIENTIFIC REVIEW BEFORE TRUSTEE COUNCIL APPROVAL"

In addition to the EVOS Trustee Council review, Appendix A and B of this report have or will be subjected to the peer-review process required for M.Sc. thesis defense and/or publication in peer-reviewed scientific journal(s).

17. "PAST PERFORMANCE OF THE PROJECT TEAM SHOULD BE TAKEN INTO CONSIDERATION WHEN MAKING FUNDING DECISIONS ON FUTURE RESTORATION PROJECTS"

The past performance of potential project teams would be reviewed by the Council during the competitive bid process for restoration implementation.

18. "RESTORATION WILL INCLUDE A SYNTHESIS OF FINDINGS AND RESULTS, AND WILL ALSO PROVIDE AN INDICATION OF IMPORTANT REMAINING ISSUES OR GAPS IN KNOWLEDGE"

The preferred alternative would provide new quantitative information on the population response of Pigeon Guillemots within PWS to release from intense predation pressure by mink at the Naked Island group. These results would clarify the importance of predator management for seabirds in PWS and provide important information to seabird managers world-wide. The project team responsible for implementation of the restoration project would adhere to all EVOS Trustee Council reporting requirements.

19. RESTORATION MUST INCLUDE MEANINGFUL PUBLIC PARTICIPATION AT ALL LEVELS - PLANNING, PROJECT DESIGN, IMPLEMENTATION AND REVIEW”

Prior to implementation, the restoration plan would be subject to a public comment period.

20. “RESTORATION MUST REFLECT PUBLIC OWNERSHIP OF THE PROCESS BY TIMELY RELEASE AND REASONABLE ACCESS TO INFORMATION AND DATA”

The project team responsible for implementation would adhere to all EVOS Trustee Council reporting requirements.

21. “GOVERNMENT AGENCIES WILL BE FUNDED ONLY FOR RESTORATION PROJECTS THAT THEY WOULD NOT HAVE CONDUCTED HAD THE SPILL NOT OCCURRED”

There are currently no plans by government agencies to restore the breeding population of Pigeon Guillemots, either on the Naked Island group or within Prince William Sound.

LITERATURE CITED

Banks, P. B., M. Nordström, M. Ahola, P. Salo, K. Fey, and E. Korpimäki. 2008. Impacts of alien mink predation on island vertebrate communities of the Baltic Sea Archipelago: review of a long-term experimental study. Boreal Environment Research 13:3-16.

Bergstrom, D. M., A. Lucieer, K. Kiefer, J. Wasley, L. Belbin, T. K. Pedersen, and S. L. Chown. 2009. Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology 46:73-81.

Bonesi, L., and S. Palazon. 2007. The American mink in Europe: status impacts, and control. Biological Conservation 134:470-483.

Clode, D., and D. W. MacDonald. 2002. Invasive predators and the conservation of island birds: the case of American mink *Mustela vison* and terns *Sterna* spp. in the Western Isles, Scotland. Bird Study 49:118-123.

Courchamp, F., J.-L. Chapuis, and M. Pascal. 2003. Mammal invaders on islands: impact, control and control impact. Biological Review 78:347-383.

Exxon Valdez Oil Spill Trustee Council. 1994. *Exxon Valdez* oil spill restoration plan. Anchorage, AK.

Exxon Valdez Oil Spill Trustee Council. 2009. Legacy of an oil spill: 20 years after the *Exxon Valdez*. 2009 Status Report. Northern Printing, Anchorage, AK.

Ferreras, P., and D. W. MacDonald. 1999. The impact of American mink *Mustela vison* on water birds in the Upper Thames. Journal of Applied Ecology 36:701-708.

Golet, G. H., K. J. Kuletz, D. D. Roby, and D. B. Irons. 2000. Adult prey choice affects chick growth and reproductive success in Pigeon Guillemots. Auk 117:82-91.

Nordström, M., J. Högmander, J. Laine, J. Nummelin, N. Laanetu, and E. Korpimäki. 2003. Effects of feral mink removal on seabirds, waders and passerines on small islands in the Baltic Sea. Biological Conservation 109:359-368.

Nordström, M., J. Högmander, J. Nummelin, J. Laine, N. Laanetu, and E. Korpimäki. 2002. Variable responses of waterfowl breeding populations to long-term removal of introduced American mink. Ecography 25:385-394.

Oakley, K. L., and K. J. Kuletz. 1979. Summer distribution and abundance of marine birds and mammals in the vicinity of Naked Island, Prince William Sound, Alaska, in 1978, and aspects of the reproductive ecology of the Pigeon Guillemot. U.S. Fish and Wildlife Service, Office of Special Studies, Anchorage, AK.

Oakley, K. L., and K. J. Kuletz. 1996. Population, reproduction, and foraging of Pigeon Guillemots at Naked Island, Alaska, before and after the *Exxon Valdez* oil spill. American Fisheries Society Symposium 18:759-769.