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Title: Restoration of Pigeon Guillemot Nesting Habitat Through Removal of Introduced Predators

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Daniel D. Roby

The 1989 Exxon Valdez oil spill (EVOS) in Prince William Sound, Alaska provided impetus for a great deal of research into the ecosystems of the Northern Gulf of Alaska. Buried within the multitude of resulting impacts, which included hundreds of thousands of oiled seabirds and dramatic ecosystem shifts in the North Pacific Ocean, was the steady decline of pigeon guillemots (*Cepphus columba*) at the historically important nesting area in the Naked Island Group of central Prince William Sound. The cause of this decline, however, perplexed researchers for decades, as it both preceded and outlasted the effects attributed to the spill.

Guillemots are a seabird in the auk family (Alcidae) that nest in burrows and other natural crevices. Monitoring of guillemots nesting at the Naked Island Group in Prince William Sound began in 1979, 10 years prior to EVOS, and have continued intermittently until the present. Between 1979 and 2008, the number of guillemots nesting at the Naked Island Group declined by 95%. In 2008, when a remnant population of only about 100 guillemots was still

attending the Naked Island Group, it came to light that American mink (*Neovison vison)*, a voracious predator of ground-nesting birds, had been intentionally introduced to the Naked Island Group throughout the 1970's to provide trapping opportunities.

In 2012, we initiated research to test whether removing mink from the Naked Island Group would allow the local guillemot population to recover. Lethal trapping efforts to remove mink from the islands were initiated in 2014 and continued through 2018. The last mink was captured in the spring of 2016, and the last mink sign (i.e. tracks or scat) was observed in the spring of 2017. By 2018, the Naked Island Group appeared to be free of mink.

Removal of introduced predators is a widespread and effective tool for restoration of island nesting birds. Despite its pervasive use, the effects of predator removal on target species for conservation remains understudied. In addition, no predator removal efforts in North America have targeted American mink. In order to evaluate the effects of mink removal on the guillemot population at the Naked Island Group, I used a Before-After, Control-Impact (BACI) study design. Specifically, I compared trends in population counts of guillemots at the Naked Island Group before and after the removal of mink to the population trends at a number of nearby mink-free islands. To augment this experiment, I measured six variables that have been linked to guillemot nesting success and productivity, due to either predation pressure or forage fish availability. I hypothesized that the abundance of guillemot nests, nestling survival rates, and guillemot use of nest sites vulnerable to land-based predators would all increase following the removal of mink. Also, I predicted that guillemot chick growth rates, diet composition, and meal delivery rates to nests would not be affected by mink removal and would vary instead due to stochastic environmental factors as they affect forage fish availability.

Results from my BACI experimental design indicated that guillemot numbers at the Naked Island Group increased dramatically following the initiation of mink removal efforts, as compared to the control sites. Prior to mink removal, guillemot counts at the Naked Island Group decreased from 146 birds in 2007 to only 69 in 2014. Following mink removal, guillemot counts immediately began to increase, reaching 167 birds by 2018. During this same time period, I observed no clear change in guillemot abundance at control islands where guillemot population counts consistently, though slowly, increased from 2008 to 2018. Concurrent with increases in the number of guillemots at the Naked Island Group following the removal of mink, I also observed increases in guillemot nest abundance, nestling survival rates, and the proportion of guillemot nest in sites vulnerable to mink predation (i.e. burrows instead of crevices in cliffs). These changes in combination suggested that the removal of mink resulted in improved quality of nesting habitat available for guillemots and the initiation of recovery of the guillemot population.

Foraging conditions for guillemots also appeared to have been favorable at the Naked Island Group during my study period, and these would not be expected to be related to mink removal. Guillemot chick growth rates and meal delivery rates were significantly higher than those observed during the period when mink were present at the Naked Island Group, and I found evidence that guillemot diet composition contained a larger percentage of high-quality prey than had been documented in earlier studies. This suggests that foraging conditions guillemots have improved compared to the period when mink predation pressure was at its peak, which coincided with the aftermath of EVOS. As EVOS has been linked to declines in the

abundance of high-quality prey, such as schooling forage fish, the improved foraging conditions that I observed were likely due to the recovery of prey resources following EVOS.

All of these factors, both top-down and bottom-up, indicate recently improved conditions for guillemots nesting at the Naked Island Group and in central Prince William Sound. I expected the guillemot nesting population to grow at the Naked Island Group following the removal of an introduced mammalian predator; however, the observed rate of increase in guillemot numbers at the Naked Island Group exceeded my expectations to such an extent that it is unlikely that intrinsic growth (population growth through reproduction) alone was responsible. This suggests that immigration of guillemots from elsewhere in Prince William Sound drove much of the initial recovery in guillemot numbers at the Naked Island Group following the removal of mink.

In conclusion, I demonstrated that the number of pigeon guillemots nesting at the Naked Island Group had been limited by mink predation, and that the removal of mink initiated the recovery of this historically important sub-population. The initial rate of increase in guillemot numbers was likely primarily the result of immigration to the Naked Island Group from other breeding colonies within the Sound. In addition, currently favorable foraging conditions and positive guillemot population trends at nearby control islands suggest that conditions are conducive to the continued recovery of the sub-population of pigeon guillemots at the Naked Island Group, as well as the Prince William Sound population at large.

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Restoration of Pigeon Guillemot Nesting Habitat Through Removal of Introduced Predators

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Samuel B. Stark

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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.

Samuel B. Stark, Author

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Restoration of Pigeon Guillemot Nesting Habitat Through Removal of Introduced Predators

CHAPTER 1

GENERAL INTRODUCTION

Samuel B. Stark

When the M/V *Exxon Valdez* grounded on Bligh Reef in the northeastern corner of Prince William Sound (PWS), Alaska on March 23, 1989 and began spilling oil, PWS was host to hundreds of thousands of overwintering seabirds. As the oil spread through the Sound and beyond, seabirds were killed by direct oiling of their plumage, ingestion of oil, and starvation. Of the tens of thousands of seabirds that died in the Sound in the immediate aftermath of the spill, between 500 and 1,500 were pigeon guillemots (*Cepphus columba*; Piatt et al. 1990). For more than a decade after the spill, research focused on the declining sub-population of guillemots nesting at the Naked Island Group, an archipelago that was heavily oiled and formerly supported the highest nesting densities of guillemots in PWS (Oakley 1981). It was not until nearly 20 years after the spill that the complexity of factors responsible for the dramatic decline in pigeon guillemots at the Naked Island Group was fully realized.

The most neglected factor in this decline was the introduction of American mink (*Neovison vison*) to the Naked Island Group in the 1970s, followed by the gradual establishment of a population of mink throughout the archipelago during the 1980s. Research on the sub-population of pigeon guillemots at the Naked Island Group during the 2000s concluded that, based on the weight of evidence, mink predation was the primary factor limiting the recovery of pigeon guillemots at the Naked Island Group (Bixler 2010). Subsequently, an attempt was made to remove all mink from current and former guillemot nesting habitat on the archipelago in order to allow the nesting sub-population of guillemots to recover (Irons and Roby 2014). The objective of my thesis research was to measure the response of pigeon guillemots to the attempted removal of mink from their nesting habitat at the Naked Island Group, and thereby

test the hypothesis that mink predation had become the dominant limiting factor for that sub-population of guillemots.

Pigeon guillemots are a medium-sized, primarily piscivorous seabird in the family Alcidae that are native to coastal areas of the North Pacific and Bering Sea. They are pursuit-divers that propel themselves underwater using their wings for locomotion (Ewins 1993). Pigeon guillemots feed on a wide variety of forage fish species, including schooling pelagic fishes and nearshore demersal fishes, plus occasionally crustacea (Oakley and Kuletz 1996, Litzow et al. 1997, Golet et al. 2000). Guillemots nest semi-colonially in crevices on cliff faces, in talus, in soil burrows at the tops of cliffs, and in a variety of anthropogenic structures on marine shorelines (Kuletz 1983, Ewins 1993).

The North American population of pigeon guillemots was estimated at approximately 235,000 individuals, of which roughly 200,000 nested in Alaska (Ewins 1993). Much of the pigeon guillemot's breeding range is infrequently surveyed due to inaccessibility, relatively low guillemot nesting densities, and cryptic nest sites. As a result, there is little information on population-wide trends in guillemot abundance. While the North American population is generally considered to be resilient due to its wide geographic range, local sub-populations are susceptible to declines caused by changes in food availability (Ainley 1990), predation pressure (Emms and Verbeek 1989, Vermeer et al. 1993, Bixler 2010), and oil pollution (Golet et al. 2002).

Surveys conducted in June of 1978 and 1979, prior to the *Exxon Valdez* oil spill (EVOS), counted 1,600 to 1,800 pigeon guillemots around the Naked Island Group (Oakley and Kuletz

1996). The Naked Island Group, comprised of Naked Island (the largest island in the archipelago), Storey Island, Peak Island, and a few small islets, is located in central PWS and was the first shoreline where oil from the EVOS made landfall. Nesting by guillemots had not yet been initiated when the oil arrived at the Naked Island Group during the last week of March and, therefore, it is unlikely that many guillemots were present on or near the islands at that time. It is likely, however, that guillemots that would have nested at the Naked Island Group were killed elsewhere in the Sound due to the direct effects of oiling. The proportion of guillemot carcasses recovered after EVOS that belonged to the sub-population nesting at the Naked island Group is unknown (Oakley and Kuletz 1996).

The sub-population of pigeon guillemots nesting at the Naked Island Group experienced a prolonged decline after EVOS. In 1994, Sanger and Cody (1994) counted 1,118 guillemots during a survey of the Naked Island Group, a ca. 30% decline from counts conducted prior to EVOS. By 2008 that number had fallen to only 101 guillemots (Bixler 2010). Assigning a cause to this decline, however, was complicated by two additional factors. First, the population of guillemots throughout the Sound was in decline prior to EVOS, from an estimated 15,500 birds in 1972 to just 4,400 birds in 1984-85 (Agler et al. 1999). Second, a substantial increase in predation rates on guillemot nests at the Naked Island Group was observed beginning in the mid-1990s (Hayes 1995), likely exacerbating the damage caused by EVOS.

The observed decline in the PWS guillemot population prior to EVOS has been linked to the shift in the Pacific Decadal Oscillation that occurred in the mid-1970s (Oakley and Kuletz 1996, Agler et al. 1999, Golet et al. 2002). This shift, in combination with direct mortality of forage fish likely caused by exposure of adults, eggs, and fry to oil from EVOS (Piatt et al. 1990,

McGurk and Brown 1996, Marty et al. 1999, Irons et al. 2000, Golet et al. 2002), resulted in a decrease in abundance of high-lipid schooling forage fishes, such as juvenile Pacific herring (*Clupea pallasi*) and capelin (*Mallotus villosus*) in PWS (Anderson and Piatt 1999). During this same period a decline in the prevalence of an additional species of high-lipid schooling forage fish, Pacific sand lance (*Ammodytes personatus*), occurred in the diet of guillemots nesting at the Naked Island Group (Oakley and Kuletz 1996, Golet et al. 2000). The sand lance habit of burrowing into sandy sediments at low tide likely made them particularly vulnerable to oiling following EVOS (Golet et al. 2002). While the population-level impacts of EVOS on these fish are not known, it is possible that the reduced abundance of sand lance in guillemot diets in the years following EVOS was a direct effect of oiling (Golet et al. 2002). Golet et al. (2000) found that guillemots that provisioned their chicks with prey of lower lipid content, and therefore lower energy density (e.g., gadids, blennies, sculpins), had lower nestling survival and lower productivity than those that delivered prey of higher energy density, such as sand lance. This decrease in productivity related to a decline in the prevalence of high-lipid forage fish in the diet could have been at least partially responsible for the observed Sound-wide decline in guillemot numbers during this period (Cushing et al. 2017).

The second factor confounding the measurement of the effects of EVOS on the guillemot sub-population nesting at the Naked Island Group were the increasing rates of nest failure due to predation that were observed after EVOS. Nest monitoring efforts in the early 1980s, prior to EVOS, found that guillemot eggs or chicks were on average depredated in 6% (± 2%) of nests, with annual nest predation rates ranging from 0% to 11% (Kuletz 1983). When guillemot research at the Naked Island Group was conducted in the years following EVOS, the

predation rates on nests had increased to an average of 38%, and was even as high as 83% in 1998 (Golet et al. 2002). This increase in nest predation rates was coincident with the first identification of American mink as a predator of guillemot eggs, chicks, and adults at the Naked Island Group (Hayes 1995).

The origin of the mink at the Naked Island Group was not recorded by government officials, as it was on other islands in Prince William Sound. In 1951, the Alaska Department of Fish & Game introduced mink to Montague Island in southern PWS to provide more fur trapping opportunities for local residents (Burris and Knight 1973). Nevertheless, the available evidence provides strong support for the hypothesis that mink were intentionally introduced to the Naked Island Group in the 1970s. The family that homesteaded on Peak Island at the turn of the 19th century and had a fox farm there for years told a biologist with the U.S. Fish and Wildlife Service that they introduced mink to the Naked Island Group because there were previously none present on the archipelago to harvest (D.B. Irons, pers. comm.). This account is supported by several other lines of evidence that indicate mink were introduced to the Naked Island Group prior to EVOS, including the lack of records of mink in historical inventories of wildlife at the Naked Island Group or by area trappers (Irons and Roby 2014). Additionally, analysis of the genetic structure of mink collected at Naked Island during the 2000s confirmed the presence of genetic markers from farmed mink (Fleming and Cook 2010); farmed mink were introduced to Montague Island in 1951, instead of wild stock, and subsequently became established there and on nearby Green Island. This introduced mink population was likely one of the sources for the mink that were introduced to the Naked Island Group (Fleming and Cook 2010).

The pigeon guillemots nesting at the Naked Island Group are not the first seabird population to suffer as a result of the introduction of non-native predators. More than 800 islands worldwide currently host invasive species whose introduction has caused the reduction or extirpation of local seabird populations (Towns et al. 2011, Spatz et al. 2014). Islands are crucial habitat for ground nesting seabirds, such as the those in the family Alcidae, as they are frequently free of land-based predators (Lack 1968). Introduction of terrestrial predators, either intentionally or inadvertently, to these insular habitats has caused population declines and extirpations of seabird populations that rely on islands as secure nesting habitat (Maccarone and Montevecchi 1981, Birkhead and Nettleship 1995, Bright 1998).

Accessibility of guillemot nests to land-based predators has been associated with reduced nesting success and adult survival (Emms and Verbeek 1989, Bixler 2010). Thus predation pressure increases the tendency for guillemots to use nest sites that are either inaccessible or in more insular habitat (Lack 1968, McCullough and Barrett 2012). Prior to the increase in guillemot nest predation by mink, guillemots utilized a variety of nest sites on Naked Island. Kuletz (1983) separated guillemot nest sites into three types based on their location relative to sea cliffs and the surrounding substrate. During her study period of 1979-1981, she found that guillemot nests were roughly evenly distributed among these three substrates (cliff face: 35.6%, cliff top: 39.7%, talus: 24.7%). As predation pressure increased throughout the 1990s and 2000s, nests in readily accessible sites (talus and cliff top substrates) became less frequent. By 2008, Bixler (2010) found that guillemots were no longer nesting in talus substrate and had greatly decreased the frequency of using cliff top nest sites. The majority of active nests (88%, n = 17) were found in the less accessible cliff face nest site type. This switch was

attributed to a change in selection pressure during the 1990s and 2000s in favor of nest sites that were inaccessible to land-based predators due to the increase in predation rates on guillemot nests by mink (Bixler 2010).

Surveys of pigeon guillemots nesting at the Naked Island Group and at other high-density nesting areas for guillemots in western PWS were conducted by Bixler (2010) in 2008. Her work established that the sub-population breeding on the Naked Island Group had experienced greater declines than other sub-populations of guillemots in the Sound that were nesting where mink were absent. Additionally, the guillemot sub-population at the Naked Island Group declined from representing roughly 25% of the Sound-wide population at the time of EVOS to only about 1%. This disproportionate decrease in the guillemot sub-population at the Naked Island Group, especially in proximity to sub-populations that did not experience declines, was evidence that predation by mink was the primary limiting factor for the guillemot sub-population at the Naked Island Group.

Guillemot counts between 1990 and 2008 at the Naked Island Group declined even faster than expected based on models that used estimates of population vital rates from this period (Bixler 2010, Irons and Roby 2014). Using the maximum estimated rates of predation on adults, plus estimated nestling survival rates, the models still predicted a slower decline than the observed decline at the Naked Island Group. In order to produce the trend observed during this period, an emigration rate of 15% needed to be added to the models. High predation rates on guillemot chicks and adults during this period apparently caused emigration of guillemots from the Naked Island Group. Other guillemots could have used this social information to opt for nesting at other nearby breeding colonies, rather than at the Naked Island Group. This rapid

decline of nesting guillemots at the Naked Island Group suggests a high degree of connectivity among sub-populations of nesting guillemots in Prince William Sound.

While the pigeon guillemots nesting at the Naked Island Group have been the primary focus for much of the seabird research conducted there, the Naked Island Group has also seen declines in many of its other ground-nesting marine birds. Arctic terns (*Sterna paradisaea*), parakeet auklets (*Aethia psittacula*), tufted puffins (*Fratercula cirrhata*), horned puffins (*F. corniculata*), and black oystercatchers (*Haematopus bachmani*) have all experienced local reductions in their nesting populations since the 1980s (Bixler 2010; SBS, unpubl. data). Parakeet auklets and arctic terns, which both formerly nested in abundance in the area, have not nested on the Naked Island Group since, at the latest, 2006 (Bixler 2010; SBS, unpubl. data). The numbers of nesting horned and tufted puffins have both declined, from several hundred breeding pairs to only a few pairs of each species, which nest on the largest and most inaccessible cliffs on Naked Island (Bixler 2010; SBS, pers. obs.). These declines in numbers of ground-nesting seabirds at the Naked Island Group provided further evidence that mink predation was the factor limiting guillemot population recovery at the Naked Island Group.

Following EVOS the Exxon Valdez Oil Spill Trustee Council (EVOSTC) was formed "…to oversee restoration of the injured ecosystem…" (EVOSTC 2009). As pigeon guillemots are one of only two seabird species still listed as "not recovering" on the EVOSTC injured resources list (EVOSTC 2014), the recovery of the pigeon guillemot population in Prince William Sound has become a restoration priority. While all the factors mentioned above may have contributed to the long-term decline in numbers of pigeon guillemots nesting at the Naked Island Group, Bixler (2010) concluded that mink predation was the primary factor limiting the recovery of this sub-

population. In response to this conclusion, the U.S. Fish and Wildlife Service (USFWS) contracted with the U.S. Department of Agriculture's Animal and Plant Health Inspection Service (APHIS) to remove all mink from those areas at the Naked Island Group where pigeon guillemots formerly or currently nested. Trapping to remove mink began in the spring of 2014.

The overall goal of my thesis research was to measure the effects of mink removal on the sub-population of pigeon guillemots nesting at the Naked Island Group. To achieve this goal, I compared a number of parameters of pigeon guillemot nesting ecology, use of various nest site types, and the availability of forage fish resources to nesting guillemots at the Naked Island Group during three distinct periods: (1) before the establishment of introduced mink, (2) once mink had become well-established throughout the Naked Island Group, and (3) following the removal of mink from guillemot nesting habitat at the Naked Island Group. I also compared guillemot population trends at the Naked Island Group before and after mink removal, and compared those trends with concurrent trends at nearby control islands where mink were absent. My primary objective was to test the hypothesis that mink predation was the main limiting factor for the guillemot sub-population nesting 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. 1990. Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford University Press, Stanford, USA.

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.

Birkhead, T. R., and D. N. Nettleship. 1995. Arctic fox influence on a seabird community in Labrador: a natural experiment. Wilson Bulletin 107: 397- 412.

Bixler, K. S. 2010. Why aren't pigeon guillemots in Prince William Sound, Alaska recovering from the *Exxon Valdez* oil spill? Unpubl. M.Sc. thesis, Oregon State University, Corvallis, OR. 161 pp.

Bright, C. 1998. Life out of bounds: bioinvasion in a borderless world. W.W. Norton Company, New York, USA.

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

Cushing, D. A., D. D. Roby, and D. B. Irons. 2017. Patterns of distribution, abundance, and change over time in a subarctic marine bird community. Deep-Sea Research II http://dx.doi.org/10.1016/j.dsr2.2017.07.012

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.

Exxon Valdez Oil Spill Trustee Council (EVOSTC). 2009. About us. Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/index.cfm?FA=aboutUs.home

Exxon Valdez Oil Spill Trustee Council (EVOSTC). 2014. Injured Resources and Services: 2014 Update. Unpublished report by the Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/static/PDFs/2014IRSUpdate.pdf

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). Edited by A. Poole and F. Gill. The Birds of North America Online. d.oi:10.2173/bna.49.

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. Final Report to the U.S. Fish and Wildlife Service, Migratory Bird Office, Anchorage, Alaska. 51 pp.

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. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 94173), U.S. Fish and Wildlife Service, Anchorage, Alaska.

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., and D. D. Roby. 2014. Pigeon guillemot restoration research in Prince William Sound, Alaska, FY14 amendment. Project 11100853. Proposal to the Exxon Valdez Trustee Council. Available at: http://www.evostc.state.ak.us/Store/Proposal_Documents/2322.pdf

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

Lack, D. L. 1968. Ecological adaptations for breeding in birds. Methuen Publishing, London, England.

Litzow, M. A., J. F. Piatt, and J. D. Figurski. 1997. Hermit crabs in the diet of Pigeon Guillemots at Kachemak Bay, Alaska. Colonial Waterbirds 21: 242-244.

Marty, G. D., M. S. Okihiro, E. D. Brown, D. Hanes, and D. E. Hinton. 1999. Histopathology of adult Pacific herring in Prince William Sound, Alaska, after the Exxon Valdez oil spill. Canadian Journal of Fisheries and Aquatic Science 53: 2343-2354.

McCullough, D., and R. H. Barrett. 2012. Wildlife 2001: Populations. Springer Science & Business Media, Berlin, Germany.

McGurk, M. D., and E. D. Brown. 1996. Egg-larval mortality of Pacific herring in Prince William Sound, Alaska, after the Exxon Valdez oil spill. Canadian Journal of Aquatic Science 53: 2343-2354.

Maccarone, A. D., and W. A. Montevecchi. 1981. Predation and caching of seabirds by red fox (*Vulpes vulpes*) on Baccalieu Island, Newfoundland. Canadian Field-Naturalist 95: 352-353.

Oakley, K. L. 1981. Determinants of population size of Pigeon Guillemots *Cepphus columba* at Naked Island, Prince William Sound, Alaska. Unpubl. M.Sc. thesis, University of Alaska, Fairbanks. Fairbanks, AK. 82 pp.

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.

Piatt, J. F., 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.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. Restoration Project 93034. Exxon Valdez Oil Spill Restoration Project Final Report. PB--96-194808/XAB. U.S. Fish and Wildlife Service, Anchorage, AK.

Spatz, D. R., K. M. Newton, R. Heinz, B. Tershy, N. D. Holmes, S. H. M. Butchart, and D. A. Croll. 2014. The biogeography of globally threatened seabirds and island conservation opportunities. Conservation Biology 28: 1282-1290.

Towns, D. R., G. V. Byrd, H. P. Jones, M. J. Rauzon, J. C. Russel, and C. Wilcox. 2011. Impacts of introduced predators on seabirds. Pp. 58-90 *in* Seabird islands: ecology, invasion, and restoration. C. P. H. Mulder, D. R. Towns, W. B. Anderson, and P. J. Bellingham (eds.). Oxford University Press, Oxfords, England.

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.

CHAPTER 2

EFFECTS OF INTRODUCED PREDATOR REMOVAL ON A CREVICE-NESTING SEABIRD: A CASE STUDY OF MINK REMOVAL FROM PIGEON GUILLEMOT NESTING HABITAT

Samuel B. Stark, Daniel D. Roby, and David B. Irons

Abstract

Removal of introduced predators is an effective tool for restoration of island-nesting birds. Despite its widespread use, the effects of predator removal on target species for conservation remains understudied and poorly understood for many species. Pigeon guillemots (*Cepphus columba*), a crevice-nesting species in the seabird family Alcidae, have experienced local declines where predators have been introduced to breeding islands. The sub-population of guillemots breeding at the Naked Island Group in Prince William Sound, Alaska declined by 95% from 1979 to 2008, concurrent with the introduction of American mink (*Neovison vison*). We studied guillemot breeding biology at the Naked Island Group spanning mink removal efforts from 2014 to 2018. The guillemot population increased by 38% following the first year of mink removal, and by 2018 the population had increased by 136% to 163 individuals. During the same period, the numbers of breeding guillemots on other nearby islands where mink were absent increased by only 19%. Following mink removal, we also observed an increase in the number of active guillemot nests, an increase in the proportion of active guillemot nests in sites vulnerable to mink predation, and a decrease in predation rates on nestling and breeding adult guillemots at the Naked Island Group. We also observed higher guillemot nestling growth rates and meal delivery rates to nests compared to pre-mink removal, suggesting that greater availability of forage fish may have been a factor in higher nestling survival rates, in addition to mink removal. Our results indicate that the removal of mink from the Naked Island Group has been effective in initiating the recovery of a declining local population of breeding guillemots. The rapid recruitment of guillemots following mink removal suggests that the initial response was driven by immigration from nearby mink-free islands.

Introduction

Non-native predators are one of the major drivers of declines in island bird populations worldwide (Towns et al. 2011). Many seabird species nest colonially on isolated offshore islands where predation pressure from land-based predators is minimal or lacking (Lack 1968). Introduction of terrestrial predators, either intentionally or inadvertently, to these insular habitats has caused major declines and extirpations of seabird populations that rely on islands as secure nesting habitat (Maccarone and Montevecchi 1981, Birkhead and Nettleship 1995, Bright 1998).

Removal of introduced predators is a commonly used technique for restoring populations of island nesting birds (Towns et al. 2011, Whitworth et al. 2014). Predator removal efforts have met with mixed success, however, with some resulting in the immediate recovery of the target prey species, while others show little to no response from the prey (Nordstrom et al. 2003). Based on these variable outcomes and the absence of post-predator removal monitoring studies, restoration teams are left to speculate as to which factors may have been responsible for each observed outcome.

An understanding of the life history of the target species of conservation concern and the ecological context at the time of predator removal efforts are crucial for interpreting and predicting restoration outcomes. Understanding of reproductive rates, time required to reach maturity, and natal and breeding dispersal can all contribute to the probability of success of predator removal efforts. Unlike life history traits, ecological factors, such as food availability, are often highly variable and stochastic (Suryan et al. 2002). How these factors affect the

response of species intended to benefit from predator removal is frequently not monitored due to logistical and funding constraints. Lack of monitoring can severely limit the inferences made from restoration projects as only a single factor influencing population size and reproductive success of the target species is being controlled during the predator removal experiments. Underwood (1992) cites a lack of control of environmental factors as a serious flaw in the use of the Before-After, Control-Impact design in natural systems. An understanding of both life history traits and the current environmental context of the conservation target are necessary to accurately interpret observed changes following the removal of introduced predators.

The pigeon guillemot population nesting on the Naked Island Group in Prince William Sound, Alaska experienced prolonged decline after American mink (*Neovison vison*) were introduced to the islands during the 1970s. While mink were initially presumed to be native to the island, researchers began to suspect otherwise as predation on guillemot eggs, nestlings, and adults by mink increased during the 1990s and 2000s. Comparisons of pigeon guillemot data from islands with and without mink, interviews with local trappers and fishers (DBI, pers. comm.), and an analysis of the genetic structure of mink from the Naked Island Group compared to that of mink from the mainland of Prince William Sound (Fleming and Cook 2010) allowed us to recognize mink as an introduced species at the Naked Island Group (Irons and Roby 2007).

Long-term monitoring of pigeon guillemots at the Naked Island Group has provided unique insights into the effects of introduced predators on a historically abundant sub-population of breeding guillemots. Studies of pigeon guillemot nesting ecology have been conducted at Naked Island over the last 40 years, beginning in 1978 (Kuletz 1983). During this

time, researchers have observed declines in guillemot abundance, numbers of active guillemot nests, guillemot egg and chick survival, as well as changes in nest site use and diet composition. By 2008, the pigeon guillemot population at the Naked Island Group had experienced a 95% decline from more than 1,500 individuals in the early 1980s to as few as 100 individuals (Bixler 2010). During this time, the predation rate on guillemot eggs and nestlings increased from an annual average of 6% of active nests to an average of 39% of active nests following the establishment of the mink population (Kuletz 1983, Oakley and Kuletz 1996, Golet et al. 2000, Bixler 2010).

During the 1990s and 2000s guillemot nesting colonies completely disappeared from portions of the Naked Island Group, and the number of active guillemot nests declined to an estimated 17-22 nests by 2008 (Bixler 2010). The remaining active nests were increasingly in sites that were apparently inaccessible to land-based predators, including mink, sites such as crevices in sheer sea-cliffs (Bixler 2010). Accessibility of guillemot nests to land-based predators has been associated with reduced nesting success and adult survival (Emms and Verbeek 1989, Hayes 1995). Thus, predation pressure from land-based predators can increase the tendency for seabirds to use nest sites that are either inaccessible or in more insular habitats, such as remote islands (Lack 1968, McCullough and Barrett 2012).

The impact of the introduction of mink to the Naked Island Group on the sub-population of pigeon guillemots nesting there was confounded by two other factors that caused changes in the marine food web of Prince William Sound and the northern Gulf of Alaska. First, in 1976 a major regime shift occurred in the marine ecosystem of the northern Gulf of Alaska. This shift was linked to the Pacific Decadal Oscillation and resulted in declines in a number of high-lipid

schooling marine forage fishes across the region (Francis et al. 1998, Agler et al. 1999), including Pacific herring (*Clupea pallasi*), Pacific sand lance (*Ammodytes personatus*), and capelin (*Mallotus villosus*; Van Pelt et al. 1997, Anthony et al. 2000). These three forage fishes were prominent in the diet of pigeon guillemots nesting at the Naked Island Group and elsewhere in Prince William Sound (Golet et al. 2000), and declines in forage fishes were associated with declines in guillemot numbers throughout the Sound (Bixler 2010, Cushing et al. 2017).

Second, in March 1989 the T/V *Exxon Valdez* ran aground on Bligh Reef, 20 nautical miles to the northeast of the Naked Island Group, spilling 11 million gallons of crude oil into Prince William Sound. The prevailing currents transported the oil toward Naked Island and beyond along the coast of the northern Gulf of Alaska (Shabecoff 1989). This resulted in the immediate deaths of 500 - 1500 guillemots and their long-term exposure to oil-derived toxins (Piatt et al. 1990, Oakley and Kuletz 1996, Golet et al. 2002). The spill also contributed to the decline of the local population of Pacific herring to a degree that is still not fully understood (Carl et al. 2002). These direct and indirect effects of the oil spill contributed to the decline in the numbers of pigeon guillemots that nested at the Naked Island Group (Golet et al. 2002).

Both the marine regime shift during the late 1970s and the *Exxon Valdez* oil spill have been implicated in long-term declines in the abundance of high-energy forage fishes in Prince William Sound. These fish are an important food source for pigeon guillemots and other nearshore marine predators in the Sound (Golet et al. 2000, Peterson et al. 2003). Pigeon guillemot nestlings fed a diet high in high-lipid schooling forage fishes had higher survival then nestlings that were fed primarily low-lipid nearshore demersal fishes (Golet et al. 2000).

Declines in the availability of high-lipid forage fish, therefore, likely contributed to the decline in guillemot productivity observed from the late 1980s through the 2000s.

Bixler (2010) posited that mink predation, and not prey availability, was the primary limiting factor for the recovery of the pigeon guillemot sub-population at the Naked Island Group 20 years after the *Exxon Valdez* oil spill. In support of this conclusion, Bixler (2010) cited high predation rates on guillemot nests, decreasing use of nest sites vulnerable to mink predation, and disproportionate declines in the numbers of guillemots at the Naked Island Group compared to other nearby islands where mink were absent. Because pigeon guillemots are one of only two seabird species still considered not to have recovered from the *Exxon Valdez* oil spill by the Exxon Valdez Oil Spill Trustee Council, the effort to restore the breeding population of guillemots in Prince William Sound is considered a priority (EVOSTC 2014). This led to the initiation of a trapping effort in 2014 to (1) remove mink from guillemot nesting habitat throughout the Naked Island Group, (2) restore the numbers of breeding guillemots at the Naked Island Group, and (3) bolster the guillemot population throughout Prince William Sound (Irons and Roby 2007).

In this study, we tested the hypothesis that the size and the reproductive success of the Naked Island population of pigeon guillemots was limited by predation from mink. Based on this primary hypothesis, we predicted that removal of mink from guillemot nesting areas in the Naked Island Group would result in an increase in guillemot numbers relative to trends in guillemot numbers at nearby mink-free islands. We also predicted an increase in the numbers of active guillemot nests at the Naked Island Group and enhanced guillemot nestling survival

during the post-mink removal period. In addition, we predicted an increase in the use by guillemots of nest sites that are more accessible to mink and other land-based predators.

To provide environmental context to the changes we observed following the removal of mink we also measured several parameters that have been used in previous studies as indicators of guillemot prey availability (Oakley and Kuletz 1996, Litzow and Piatt 2002). We were interested in determining if any of these metrics (diet composition, chick provisioning rates, chick growth rates) might indicate that prey availability was still limiting guillemot population growth at the Naked Island Group. We assumed that guillemot foraging conditions at the Naked Island Group were similar to those at mink-free control islands due to their close proximity (9-23 km). Consequently, we predicted that any changes in prey availability would result in similar rates of change in numbers of guillemots counted during surveys at the Naked Island Group (treatment islands) post-mink removal compared to nearby mink-free islands (control islands), and that any differences in guillemot population trends between treatment and control islands could be ascribed to mink removal at the Naked Island Group.

Methods

Study Area

The Naked Island Group is an archipelago consisting of three major islands and a number of smaller islands and islets in central Prince William Sound (Figure 1). The three main islands, Naked, Peak, and Storey, are the most isolated large islands in Prince William Sound, separated from the nearest mainland by more than 15 km of open water and from the nearest island by more than 6 km of open water. This is greater than the maximum distance (4 km) that

mink have been documented to have dispersed across open water (Gerell 1967). The archipelago is surrounded by shallow rocky shelves that extend up to 2 km offshore and by channels in excess of 500 m deep. This insularity combined with abundant foraging habitat provides ideal nesting habitat for nearshore-foraging marine birds such as the pigeon guillemot (Ewins 1993).

Other nearby islands support high densities of nesting pigeon guillemots relative to the mainland. The Smith Island Group (Smith and Little Smith islands), Seal Island, and Fool Island are similarly insular, but are smaller islands than the three main islands in the Naked Island Group. Historically these islands supported similar densities of nesting pigeon guillemots compared to the Naked Island Group prior to mink introduction. While the numbers of pigeon guillemots at the Naked Island Group declined dramatically following the introduction of mink, the Smith Island Group, Seal Island, and Fool Island remained mink-free and experienced relatively small declines in guillemot numbers following the *Exxon Valdez* oil spill (Bixler 2010). We used these three islands as controls to evaluate the effects of mink removal from the Naked Island Group on numbers of nesting guillemots.

Mink Removal

As part of the effort to restore the nesting population of pigeon guillemots in Prince William Sound following the *Exxon Valdez* oil spill, the US Fish and Wildlife Service (USFWS) determined that depredation of pigeon guillemot eggs, nestlings, and adults by mink introduced to the Naked Island Group needed to be reduced (Irons and Roby 2007). To reduce mink predation on guillemots, mink were lethally trapped near historical and current pigeon

guillemot nesting habitat throughout the archipelago. Trapping was conducted during the months of March and April, beginning in 2014 and continued each year through 2018.

Traps were set along the shoreline of the three main islands and one small island (Bass Harbor Island) that comprise the Naked Island Group by a crew of professional trappers employed by the USDA - Animal and Plant Health Inspection Service (APHIS). Both baited sets and trail sets were deployed, depending on conditions at the islands. Body-gripping Conibear kill traps were used to remove mink. To maximize trapping efficacy, factors such as snow depth, availability of carrion for mink to feed on, and density of mink were considered in the selection of trap sites and trap type. Annual trap deployments ranged from 3,234 to 17,274 trap-nights. During the 2016-2018 guillemot breeding seasons, we also deployed camera traps at bait stations and along game trails near guillemot nesting areas to detect the presence of mink. Information gained during each trapping season was incorporated into subsequent trapping protocols to enhance trapping efficacy.

Guillemot Abundance Surveys

We surveyed the pigeon guillemot population annually following the methods described by Ewins (1993) and used during previous surveys for pigeon guillemots at the Naked Island Group (Oakley and Kuletz 1996, Golet et al. 2000, Bixler 2010). We conducted these surveys in late May (the pre-breeding period) during morning high tides (0600-1000 ADT), beginning two hours before high tide and ending two hours after high tide, when guillemot attendance at colony sites is most consistent (Vermeer et al. 1993a). We conducted surveys in each year from 2012 through 2018. We also included surveys conducted during previous work in 2007 and 2008 at our study site, which followed the same protocol, in our analysis (Bixler 2010).

We conducted surveys in vessels deployed with a boat operator and two observers. We counted all guillemots visible during surveys. When guillemots were sighted, we recorded the number of individuals in each group, which side of the vessel guillemots were on (inshore or offshore), and the GPS coordinates. We divided the coastlines of the Naked Island Group (Naked, Peak, and Storey islands), the Smith Island Group (Smith and Little Smith islands), Seal Island, and Fool Island into shoreline transects established by the USFWS – Office of Migratory Birds and used in previous surveys of marine birds in Prince William Sound (Agler et al. 1999, Kuletz et al. 2011, Cushing et al. 2017).

Trends in Guillemot Abundance

Our analysis of guillemot abundance followed a *Before-After, Control-Impact* (BACI) study design (McDonald et al. 2000). First, we separated the annual pre-breeding guillemot surveys into two time periods, *Before* the removal of mink from the Naked Island Group (2007-2014) and *After* mink removal from the Naked Island Group (2015-2018). We placed the survey counts from 2014 in the *Before* period because the survey was conducted less than a month after the end of the first mink trapping session, presumably prior to the earliest opportunity guillemots would have been able to detect a reduction in mink predation pressure from removal efforts. Second, we separated annual guillemot surveys into two groups based on the island groups in central Prince William Sound where the surveys were conducted; the islands in the Naked Island Group where mink were removed were considered the *Treatment* group and nearby islands that were mink-free (the Smith Islands, Seal Island, and Fool Island) were considered the *Control* group.

Our study design deviated in a number of ways from the traditional BACI design outlined by Smith (2014). First and most importantly, the selection of our treatment group (mink removal) was not random, as mink were only removed from the Naked Island Group. Including multiple sites for the treatment group was not possible due to the close proximity of the islands in the Naked Island Group, the extreme difficulty of predator removal, and limited resources. Lastly, the islands in the control group were similar to those in the treatment group during the "after" period, rather than the "before" period. The first two discrepancies from BACI design limit the scope of inference from this study, while the latter discrepancy was addressed in our analytical approach.

We pooled survey counts from the islands of the Naked Island Group and the islands of the Smith Island Group, as they were not sufficiently geographically separate to serve as independent samples within each group. Because the rates of change in numbers of guillemots counted at islands in the control group (Smith Islands, Seal Island, Fool Island) were similar to one another, we further pooled all counts of guillemots at control islands.

Guillemot Nest Abundance

To test for the predicted increase in the number of active guillemot nests at the Naked Island Group following mink removal, we attempted to locate and identify every active guillemot nest in the archipelago. This effort yielded a minimum estimate of the number of active guillemot nests at the Naked Island Group during each year from 2014 through 2018. We surveyed the entire Naked Island Group systematically for active guillemot nests from inflatable skiffs traveling parallel to the shoreline approximately 50 m from shore at least once per week throughout the breeding season (Bixler 2010). When we observed guillemots, we recorded

their location, behavior, and group size. We then observed guillemot behavior for a minimum of 1 min and for up to 1 hour when guillemots were either on land, in groups (> 3 individuals), near previously used nest sites, or carrying fish in their bills. In addition to systematic surveys, we also opportunistically identified sites with active guillemot nests while conducting other fieldwork in the Naked Island Group. Due to time and personnel constraints, nest search effort was reduced in 2014 and 2018 compared to 2015-2017, and likely underestimated the number of active guillemot nests in those two years. During 2015-2017, it was unlikely that the true number of active guillemot nests at the Naked Island Group could have exceeded the number counted by more than 5%, based on the steep decline in nest discovery rates during the nesting season.

We identified potential active guillemot nest sites using behavioral clues and audio playbacks to elicit responses from any incubating guillemots concealed in suspected nest sites. We used the first observed delivery of a nestling meal (bill-load) to a nest site to both confirm that a nest site was active and as a proxy for the hatching date at that nest. This was based on the assumptions that (1) fish are not delivered to the nest site until after the egg(s) hatches and (2) the first chick meal delivery would be observed within 1-4 days of the actual date when the egg(s) hatched.

Guillemot Nestling Survival

To test our prediction that mink removal would decrease mink predation and increase guillemot nest survival, we calculated nestling survival rate during the 2017 nesting season and compared it to nestling survival rates during the period when mink were well-established on the Naked Island Group (1989-2008). To reduce the likelihood of guillemot nest abandonment

during the sensitive incubation period, we did not access active guillemot nests in 2017 until we confirmed hatching by observation of delivery of a fish to the nest crevice by an adult guillemot. This precluded measuring hatching success rate. After hatching, we checked active guillemot nests at least once every five days until the nest failed or the young fledged in order to determine the fate of each nestling. We calculated nestling survival rate (chicks fledged as a proportion of eggs hatched) for all guillemot nests monitored. Guillemot hatch date was estimated as 1 day prior to the first observed nestling meal delivery (Ewins 1993), and was confirmed based on wing length measurements obtained for nestlings during the linear phase of growth and using a regression of wing length vs. age for a sample of known-age nestlings measured by Golet et al. (2000).

If an active nest became inactive prior to the expected earliest fledging date of 30 days post-hatching, we accessed the nest crevice in an attempt to determine the fate of the nesting attempt. When accessed nests did not contain live nestlings, we attempted to identify the cause of nest failure and nestling death. Nestlings missing prior to the earliest possible fledging date were considered depredated and the nest classified as failed. We examined any nestlings found dead in crevices for evidence of predation and we assigned the cause of death to either predation or non-predation.

To aid in identification of nest predators we opportunistically deployed trail cameras at the entrances to six active guillemot nest crevices during the 2017 nesting season to detect causes of potential nest failure. Each camera was set to motion-sensing trigger and took three photos after each trigger.

Guillemot Nest Sites

Pigeon guillemot nest site selection and distribution are shaped by food availability and the local predator community (Emms and Verbeek 1989, Ewins 1993). Guillemots nest semi-colonially in crevices on sea-cliff faces, in coastal talus, in soil burrows at the tops of sea-cliffs or bluffs, and in a variety of anthropogenic structures along marine shorelines (Kuletz 1983, Ewins 1993). The local distribution of active nests is shaped by their susceptibility to predation by land-based predators that can access and enter their nest crevices.

Once we confirmed that a guillemot nest site was active, we classified each guillemot nest into one of three nest site categories. These categories were (1) Burrow, where nest cavities were partially or entirely in soil and located at the top of a shoreline cliff, bluff, or bank; (2) Cliff Face, defined as nest cavities in rocky crevices located on the face of a shoreline cliff; and (3) Talus, where nest cavities were located in rock rubble at the base of shoreline cliffs. We then pooled these three nest site categories into two categories for further analysis, based on relative accessibility to mink: more-vulnerable (Burrow and Talus nest site categories combined) or less-vulnerable (Cliff Face nest site category). In 2017, we deployed trail cameras at six different active nest sites representing all three nest site types (4 Burrow, 1 Cliff Face, 1 Talus).

Guillemot Prey Availability

Guillemots feed on a wide variety of marine forage fishes, including pelagic schooling fishes, nearshore demersal fishes, and occasionally crustacea (Oakley and Kuletz 1996, Litzow et al. 1997, Golet et al. 2000). To better understand the role that food availability played in guillemot population change we measured three metrics of food availability that have been

used in previous studies of pigeon guillemot nest success and nestling survival (Barrett et al. 2002, Litzow et al. 2002). These included nestling growth rates, nestling diet composition, and meal delivery rates to nests.

To assess guillemot nestling growth we accessed guillemot nests during the 2017 breeding season. We accessed each active guillemot nest a minimum of two times during the nestling-rearing period. Our objective was to assess nestling growth and development rates, following methods previously used at the Naked Island Group (Golet et al. 2000, Golet et al. 2002).

The first nest access visit occurred between six and eight days after we observed the first nestling meal delivery at a nest, and the purpose was to document brood size (1 or 2 nestlings), measure body mass of nestlings at 8-10 days post-hatching, and mark individual nestlings for identification in the nest pre-fledging, or on the water post-fledging. The second visit to an active nest occurred between seven and nine days after the first visit (15-19 days post-hatching), and the purpose was to confirm nestling survival, reweigh nestlings, and collect morphometric data on nestlings when they were close to the end of the linear phase of nestling growth in body mass.

We measured nestling body mass using 100-gram (± 1 g), 200-gram (± 5 g), or 500-gram (± 10 g) Pesola^{tm} spring scales, depending on the size of the nestling. We used measurements of nestling body mass (g) obtained during the first two nest visits to estimate growth rates in nestling body mass (g/day) during the linear phase of growth, between 8 and 18 days post-hatching (Ewins 1993, Emms and Verbeek 1993, Golet et al. 2000). We measured relaxed wing chord (± 1 mm) and flattened wing length (± 1 mm) using wing rulers.

For guillemot nests where the hatch date was not precisely known, we estimated nestling age by comparing wing chord length to the regression of wing chord on age (days post-hatching) for known-age nestlings from previous studies at the Naked Island Group (Golet et al. 2000, Golet et al. 2002). Nestling age may not have been precisely known either because the nest was found after hatching or due to logistical constraints in observing active nests for the first nestling meal deliveries.

Pigeon guillemots deliver single prey items to feed their nestlings in the nest site. These prey items are generally held sideways in the bill, and can be visible to nearby observers. We assessed nestling diet composition using visual identification of prey items delivered to the nest crevice by adult birds. We identified fish to the lowest possible taxonomic level, following the protocol used by Golet et al. (2000). We conducted observations of guillemot prey deliveries to active nests using spotting scopes from land-based blinds placed near active nests or using binoculars and digital cameras from inflatable skiffs anchored just offshore of active guillemot nests. We conducted observations of meal deliveries both opportunistically and during three-hour observations sessions. We identified at least 15 prey items delivered to each nest for nests included in our analyses of nestling diet composition. We then calculated the proportions of the nestling diet at each nest that consisted of each prey type. Prey items that are considered high-lipid schooling forage fish, including Pacific sand lance, Pacific herring, capelin, and a variety of other smelt (Osmeridae) species, were lumped together as high-quality prey (Anthony et al. 2000).

From observations that we collected during standardized three-hour nest monitoring sessions, we also calculated delivery rates of nestling meals to each nest (prey items

delivered/hour). We averaged this rate across all nests monitored in a breeding season to determine the average meal delivery rate to nests for each season during 2016-2018. We then compared the mean percentage of high-quality forage fish prey in the nestling diet during 2016-2017 and nestling meal delivery rates measured during 2016-2018 (mink removal period) to those same metrics measured prior to mink establishment at the Naked Island Group (1979-1984) and during the period when mink were well-established (1989-2008).

All procedures outlined in this study involving live animals followed protocols approved by the Institutional Animal Care and Use Committee at Oregon State University under ACUP # 4919.

Statistical Analyses

We used Generalized Linear Models with Poisson distributions for count data to test the effect of treatment (categorical: mink removal vs. control), period (categorical: before [2007-2014] vs. after (2015-2018] mink removal), year (continuous count covariate; year 2007 = year 1), and the interaction of these three explanatory variables on the number of pigeon guillemots counted during pre-breeding surveys at the treatment and control islands (Nordstrom et al. 2003). To determine which combination of these three variables (Treatment, Period, Year, and their interactions) best described the observed variation in numbers of guillemots counted during pre-breeding surveys, we compared models based on all of the combinations of these three factors using Akaike's Information Criterion with correction for small sample sizes (AICc). This resulted in 19 potential models to explain variation in guillemot survey counts (Table 1). We compared these models using the ΔAICc value, which is the difference between a model's AICc score and the lowest (most probable) AICc score of the candidate models. We then used

the best model, given the data, to test for the effect of mink removal at the Naked Island Group on the numbers of guillemots counted during surveys. Based on our primarily hypothesis, that the sub-population of pigeon guillemots nesting at the Naked Island Group was limited by predation from mink prior to mink removal, we predicted that the interaction of Treatment x Period x Year would best explain variation in the number of guillemots counted on surveys during the study period. In other words, trends in guillemot numbers in this BACI design would depend on whether surveys were conducted before or after the treatment (mink-removal) AND whether the surveys were conducted at treatment islands (i.e. Naked Island Group) or control islands (i.e. Smith Islands, Seal Island, Fool Island); year is a key explanatory variable because it defines trends in the survey data.

For the models estimating guillemots counted during pre-breeding surveys, we performed post hoc analyses to estimate the difference in rate of change (slope) of guillemot abundance using the best model identified using AICc. These comparisons were between the two periods (Before and After mink removal) for each treatment group (Control and Treatment) individually, and then the change in the two groups compared to each other. Slopes for each combination of Period and Treatment are reported in units of the model, logit link change in number of guillemots per year.

We also regressed the numbers of active guillemot nests at the Naked Island Group during 2014-2018 as a function of year. We compared the regression fit using a simple linear model and a second order polynomial model to determine which model type provided the best fit. Our primary interest was to assess whether the numbers of active guillemot nests were increasing and, if so, whether the increase was linear or exponential.

To test for the predicted increase in use of vulnerable nest sites by guillemots nesting at the Naked Island Group post-mink removal, we quantified guillemot use of each category of nest site for all active guillemot nests. We then compared the composition of nest site types used during the post-mink removal period (2015-2018) to the composition of nest site types used during a single year prior to the detection of mink at the Naked Island Group (1979), and a single year when mink were present and numerous at the Naked Island Group (2008). We used pairwise Fisher's exact tests and adjusted resultant *p*-values using the Holm-Bonferroni correction for multiple comparisons to test for differences in use of various nest site types among years (Ramsey and Schafer 2002). The first set of comparisons evaluated differences between each of our four study years (2015-2018) and 1979, prior to the establishment of mink. The second set of comparisons evaluated differences between each of our four study years and 2008, when mink were widespread on the Naked Island Group.

We also used Generalized Linear Models (GLM) with Gaussian distributions to investigate potential differences in estimated mean nestling survival, nestling growth rate, nestling meal delivery rate, and the proportion of high-lipid prey in nestling diets across the three periods spanning mink introduction and removal at the Naked Island Group (categorical: (1) period when mink undetected (1978-1984), (2) period when mink well-established (1989-2008), (3) period when mink removed (2016-2018); Appendix B). For each of these comparisons we designated the period when mink were well-established as the reference level. Because our primary interest was testing for differences at the Naked Island Group between the three time periods and not the quality of the model fit, we performed post hoc analyses on all models where there was a significant effect of period at an α level of 0.10.

We performed analyses using R studio (Version 1.1.419 – © 2009-2018 RStudio, Inc.; Ramsey and Schafer 2002). The R packages used in these analyses included: *AICcmodavg, nlme, ggplot2,* and *gmodels*. All post hoc analyses were performed using the "estimable" function from the package *gmodels*.

Results

Mink Removal

Trapping efforts reduced the population of introduced American mink at the Naked Island Group to a level where no mink were detectable in guillemot nesting habitat following five seasons of trapping from 2014 through 2018. A total of 106 mink were removed from guillemot nesting habitat on the Naked Island Group during the first three seasons of trapping (Figure 2). During the fourth trapping season, 2017, a single set of mink tracks was detected on a small island in the Naked Island Group (Bass Harbor Island), but no mink were caught and none were detected using camera traps. During the fifth and final trapping season, 2018, no mink or mink sign were detected by any means on any of the islands in the Naked Island Group. While confirming that all mink were removed from guillemot nesting habitat at the Naked Island Group will require additional monitoring, we expect that the reduction in numbers of mink at the Naked Island Group removed mink predation as a limiting factor for the recovery of the guillemot sub-population nesting there.

Guillemot Numbers in Surveys

Prior to mink removal at the Naked Island Group, guillemot numbers declined from 146 individuals in 2007, to 69 individuals in 2014, a 53% decline over 7 years. In the first year

following the initiation of mink removal, the number of guillemots counted during the pre-breeding survey increased by 38% (Figure 3A). The numbers of guillemots counted during pre-breeding surveys then increased from 2015 to 2018 by 72% (Figure 3A). The last year of our study, 2018, was the only year following mink removal when guillemot counts at the Naked Island Group did not increase from the previous year (Figure 3A). The cause of this lack of increase in 2018 is not known.

At the control islands we observed an increase in guillemot numbers during both the *before* and *after* periods. During the *before* period (2008-2014), guillemot numbers at the control islands increased from 235 individuals in 2008 to 368 individuals in 2014, a 57% increase over 6 years (Figure 3B). This increasing trend in guillemot numbers at the control islands continued during the *after* period (post-mink removal at the Naked Island Group), when guillemot numbers increased from 315 individuals in 2015 to 377 individuals in 2018, a 20% increase over 3 years.

Comparison of Trends in Guillemot Numbers

When we ranked each of the 19 candidate models (Table 1) using ΔAIC_c scores, there was only one competitive model ($\Delta AIC_c < 2$) given the data. The top model included the explanatory variables Year, Period, Treatment, and the interactions between all three variables ($W_i = 0.9999$; Table 2). None of the other 18 candidate models included the three-way interaction of Year x Treatment x Period. In the absence of the three-way interaction no model could explain the large change in the trend in guillemot numbers at the Naked Island Group from the pre-mink removal (*before*) period to the post-mink removal (*after*) period (Figure 3A), while the trend in guillemot numbers at the control islands remained relatively constant (Figure

3B). This is supported by the significance of the three-way interaction term in the best model ($F_{1,8}$ = 8.21, p = 0.02; Table 3). Following model selection, we identified over-dispersion in the variance of the selected model (dispersion factor = 1.9, Z = 2.06, p = 0.01) and addressed this by using a Quasi-Poisson distribution (Appendix A).

Based on the best model, we conducted a three-way comparison of the rates of change in guillemot numbers at the control and treatment islands, including (1) the rate of change at the treatment islands between the *before* period and the *after* period, (2) the rate of change at the control islands between the *before* period and the *after* period, and (3) the difference between treatment and control islands in the change of slope from the *before* period to the *after* period. The first comparison addresses whether there was any change in population trend at the Naked Island Group after the initiation of mink removal; the second comparison addresses whether there was any change in population trend at the control islands coincident with the initiation of mink removal at the Naked Island Group; and the third comparison addresses whether any change in population trend at the Naked Island Group with the initiation of mink removal was different from any change in population trend at the control islands that was coincident with mink removal at the Naked Island Group.

There was a statistically significant increase in the rate of change in guillemot numbers at the Naked Island Group (treatment islands) between the *before* period and the *after* period. Numbers of guillemots at the treatment islands changed from declining at an average annual rate of -0.11 ln(individuals) (SE = 0.03, t_8 = -3.45, p = 0.009) during the *before* period to increasing at an average annual rate of 0.16 ln(individuals) (SE = 0.07, t_8 = 2.21, p = 0.06) during

the *after* period (Figure 3A). This amounted to a net increase in the rate of change by 0.27 ln(individuals/year) (SE = 0.08, t_8= 3.44, p = 0.008; Table 4).

Conversely, the rate of change in numbers of guillemots at the control islands did not differ significantly between the *before* period and the *after* period (estimated difference = -0.001 ln(individuals/year), SE = 0.05, t_8= -0.03, p = 0.97; Figure 3B, Table 4). During the *before* period, the number of guillemots counted at the control islands increased at an average annual rate of 0.06 ln(individuals) (SE = 0.05, t_8 = 2.3, p = 0.03; Table 4). During the *after* period the average annual rate of change at the control islands remained 0.06 ln(individuals) (SE = 0.06, t_8 = 1.26, p = 0.78; Table 4).

There was a significant difference between the treatment islands and the control islands in the change of slope of guillemot numbers from the *before* period to the *after* period (logit link, t_8 = 2.85, p = 0.02). The net effect of mink removal on the rate of change in guillemot numbers was 0.27 ln(individuals/year) (SE = 0.10; Figure 3A & B, Table 4).

Guillemot Nest Abundance

We found a significant increase in guillemot nest abundance at the Naked Island Group following the initiation of mink removal (Figure 4). Both a simple linear model ($F_{1,3}$ = 36.47, p = 0.009, MSE = 18.14, Adj. R^2 = 0.899) and a second order polynomial model ($F_{2,2}$ = 371.88, p = 0.003, MSE = 0.64; Adj. R^2 = 0.995) explained a significant proportion of the variation in nest numbers among years (Appendix C). We selected the second order polynomial model, however, as it was a much better fit to the data, minimized the mean squared error (MSE), and reduced bias in the residuals:

$$N_x = 36.6 + 33.2X + -9.35X^2 \quad (1)$$

In equation 1, the response variable, estimated guillemot nest abundance (N), is dependent upon year (*X*). The negative term in the second order polynomial (-9.35, SE = 1.26, *t* = -7.40, *p* = 0.018) indicates a significant slowing of the rate of increase in numbers of guillemot nests over the study period (Figure 4).

The number of active guillemot nests found at the Naked Island Group increased by 373% during the first five breeding seasons following the initiation of mink removal, from 11 nests in 2014 to 52 nests in 2018. During the 2015 breeding season, the second season after the initiation of mink removal, the increase in number of active guillemot nests was evident throughout much of the Naked Island Group. The minimum estimate of number of active guillemot nests increased by 136%, from 11 nests in 2014 to 26 nests in 2015 (Figure 4). The exception to the general increase in active guillemot nests at the Naked Island Group was the western shoreline of Naked Island, where there were at least 124 guillemot nests in 1997, when the guillemot population at the Naked Island Group was estimated at ca. 500 birds, but only two or three active guillemot nests each year during 2014-2018.

Guillemot Nest Sites

During the post-mink removal period (2015-2018), we observed a change in the percentage of different nest site types used by pigeon guillemots at the Naked Island Group (Figure 5). During the 2015 breeding season, 36% of active guillemot nests were in sites

considered vulnerable to mink predation (Talus and Burrow nest site types), and during the 2016 breeding season 37% of active nests were in vulnerable sites. The proportions of active guillemot nests in sites considered vulnerable to mink predation during 2015 and 2016 were significantly lower (Holm-Bonferroni adj. p = 0.044 and 0.034, respectively) than during 1979, when 64% of active guillemot nests were in sites considered vulnerable to mink predation; 1979 was before mink were first confirmed to be present on the Naked Island Group.

During 2017-2018, however, we observed an increase in the proportion of active guillemot nests that were in sites considered vulnerable to mink predation (Figure 5). This change was due almost entirely to an increase in the proportion of active nests in the Burrow nest site category, which included only 12% of active guillemot nests in 2008 (n = 2 nests), but increased to 46% of active guillemot nests by 2018 (n = 24 nests). In 2018, the proportion of active guillemot nests in sites considered vulnerable to mink predation (48%, n = 25 nests) was significantly greater (Holm-Bonferroni adj. p = 0.038) compared to 2008 (12%), when mink were well-established on the Naked Island Group.

Guillemot Nestling Survival

We found a significant difference in average annual survival rates of guillemot nestlings at the Naked Island Group among the three periods: (1) pre-mink establishment (1978-1984), (2) mink well-established (1989-2008), and (3) post-mink removal (2017) ($F_{2,11}$ = 6.47, p = 0.013*;* Figure 6). In order to test the prediction that average annual nestling survival rates would increase following mink removal, we performed a post hoc analysis to compare guillemot nestling survival rates during 2017, post-mink removal, to the average annual nestling survival rate before mink were well-established on the Naked Island Group (n = 5 years) and after mink

were well-established (n = 8 years). During 2017, the single year following mink removal when guillemot nestling survival rate was measured, nestling survival was 86.4% (n = 36 nestlings). This was 41 percentage points (SE = 17.6) greater than the average annual nestling survival rate when mink were well-established on the Naked Island Group (45.3%, SE = 5.85, n = 8 years; t_{11} = 2.28, p = 0.04). Conversely, the nestling survival rate observed in 2017 (post-mink removal) was not significantly different (t_{11} = 0.55, p = 0.60) from the average annual nestling survival rate observed at the Naked Island Group prior to mink establishment (75.4%, SE = 7.40, n = 5 years; Figure 6), consistent with the prediction that guillemot nestling survival would increase following mink removal.

During the 2017 nesting season, we checked active guillemot nests throughout the nestling period at 21 accessible nests containing a total of 36 nestlings (6 one-nestling broods and 15 two-nestling broods). Five guillemot nestlings were found dead in the nest crevice or disappeared from the nest crevice prior to the earliest expected fledging date, a 13.9% mortality rate. Two nestlings were found dead in their nest crevice (5.5%) with a live sibling and no sign of nest predation; these two mortalities were considered non-predation events. Two other nestlings (5.5%) were apparently killed by predators. The first suffered injuries consistent with depredation by corvids (hole in the anterior cranium with emanating fracture lines, hole in the throat skin, and all breast and throat tissue missing) and its carcass was found at the base of the cliff where the nest crevice was located; several common ravens (*Corvus corax*) were present near the nest when the nest was checked. The second nestling that was apparently killed by predators disappeared from the nest crevice prior to fledging (age $\underset{\sim}{}$ 19 days post-hatching) and was assumed to have been killed by a predator and removed. The fifth nestling

mortality was a nestling that was apparently abandoned by its parents and died of starvation following the depredation of its nest mate, apparently by corvids.

At the six active guillemot nests where we deployed trail cameras, no nests failed due to predation. We did, however, detect potential nest predators at each of the nests where trail cameras were deployed, including common ravens and northwestern crows (*Corvus caurinus*). Based on images from the trail cameras, these potentially predatory corvids appeared to investigate the entrance to the nest crevices without entering, despite the presence of small live guillemot nestlings in each nest crevice.

Food Provisioning to Guillemot Nestlings

We found significant differences ($\alpha = 0.1$) between the three study periods in the three indices of forage fish availability measured at the Naked Island Group: (1) nestling growth rate, (2) percent of nestling diet consisting of high-quality forage fish, and (3) meal delivery rate to nests ($F_{2,9} = 5.51$, $p = 0.024$; Table 5). The three study periods were: (1) pre-mink establishment (1979-1984), (2) mink well-established (1989-2008), and (3) post-mink removal (2016-2018). Based on these results, we proceeded with post hoc analysis of the differences in each of these dependent variables among study periods.

In 2017, guillemot nestling growth rates averaged 24.2 g/day (n = 25 nestlings) during the linear phase of growth. This average nestling growth rate (24.2 g/day) was higher than any previously recorded average nestling growth rate during the 11 years between 1979 and 1998 when guillemot nestling growth rates were measured at the Naked Island Group. In guillemot broods containing two nestlings (n = 11) the average growth rate of beta (second-hatched)

nestlings (22.3 g/day, SE = 1.8) was not significantly different from that of alpha (first-hatched) nestlings (24.2 g/day, SE = 1.7; two-tailed Student's t-test, $t_{19} = 0.86$, $p = 0.40$). Therefore, growth rates of alpha and beta nestlings in two-chick broods and those of singleton nestlings (30.7 g/day, SE = 3.3, n = 3), were combined in calculating average nestling growth rate in 2017.

Average growth rate of guillemot nestlings during the 2017 nesting season was significantly greater (estimated difference = 6.28 g/day, SE = 1.9, $t_9 = 3.27$, $p = 0.009$; Figure 7) than average annual nestling growth rate during the period when mink were well-established on the Naked Island Group (18.0 g/day, SE = 0.68, n = 7 years). There was also a significant difference in average nestling growth rate between 2017 and the period before mink were first confirmed on the Naked Island Group (1979-1981) (20.0 g/day, SE = 0.90, n = 3 years; $t_9 = 2.11$, $p = 0.06$).

The proportion of guillemot nestling meals that consisted of high-quality schooling forage fish (i.e. sand lance, herring, capelin) during the 2016 and 2017 breeding seasons (mean = 28%, SE = 7.55, n = 2 years) was not significantly different than that observed during the period when mink were well-established on the Naked Island Group (mean = 22%, SE = 4.03, n = 7 years; $t_9 = 0.68$, $p = 0.19$). There was, however, a significant difference (estimated difference = -19.80, SE = 9.74, $t_9 = -2.03$, $p = 0.07$) between the average annual proportion of high-quality forage fish in the guillemot diet during 2016-2017 and that observed during the period before mink were well-established on the Naked Island Group (48%, SE = 6.16, n = 3 years; Figure 8). The proportion of the nestling diet that consisted of high-quality forage fish in 2016 (18%, n = 33 nests) and 2017 (38%, n = 38 nests) remained at low to intermediate levels compared to that measured at the Naked Island Group prior to mink becoming well-established.

Following the removal of mink (2016-2018), the estimated average annual rate of nestling meal deliveries was 1.17 deliveries $nest^{-1}$ hr^{-1} (SE = 0.11, n = 3 years). This was significantly greater than the average annual meal delivery rate to nests during the period when mink were well-established at the Naked Island Group (0.84 deliveries $nest^{-1}$ hr^{-1}, SE = 0.07, n = 7 years; t_{10} = 2.41, p = 0.04; Figure 9). This represented a 39% increase in the average meal delivery rate to nests following mink removal at the Naked Island Group. There was no statistically significant difference in nestling meal delivery rates between the pre-mink period at the Naked Island Group (1979-1983; mean = 0.9 deliveries $nest^{-1}$ hr^{-1}, SE = 0.16, n = 3 years) and the period following the removal of mink (t_{10} = 1.68, p = 0.12).

Discussion

Our findings support the primary hypothesis that the size and reproductive success of the population of pigeon guillemots nesting at the Naked Island Group was limited by mink predation prior to the removal of mink starting in 2014, and that the removal of mink removed predation as a primary limiting factor. This is supported by a number of changes at the Naked Island Group following mink removal. These changes include the large increase in the rate of change of guillemots counted during pre-nesting surveys at the Naked Island Group compared to pre-mink removal, increases in the number of active guillemot nests detected at the Naked Island Group during nestling-rearing, the increase in guillemot nestling survival rate at the Naked Island Group, and increased use by guillemots of nest sites vulnerable to mink predation. This evidence suggests that the sub-population of pigeon guillemots at the Naked Island Group has begun to recover as a result of the removal of mink.

The trapping of mink at the Naked Island Group was successful in reducing the number of mink in guillemot nesting habitat to undetectable levels by 2018. While trapping only took place in areas of current or historical guillemot nesting, this trapping coverage apparently included the seasonal ranges of the entire mink population on the Naked Island Group during the trapping period. The effort to remove mink was effectively complete before the 2016 guillemot nesting season, when we initiated intensive monitoring of active guillemot nests. The success of the mink trapping effort was integral to evaluating the response of the guillemot population to mink removal.

We tested whether mink predation was limiting pigeon guillemot numbers at the Naked Island Group by comparing trends in guillemot numbers at the Naked Island Group to those at the control islands, where mink were absent, using a BACI design. In the six years prior to mink removal, guillemot numbers at the Naked Island Group were in decline. In contrast, during this same 6-year period, guillemot numbers at the control islands were increasing. After mink removal commenced at the Naked Island Group, guillemot numbers began increasing, while the trend at the control islands remained unchanged. The effect of mink removal is evident based on the change in trend from the *before* period to the *after* period at the Naked Island Group compared to the control islands. This comparison is strong evidence that mink predation was limiting the numbers of pigeon guillemots at the Naked Island Group, rather than food availability.

The role of mink removal in the recent increase in the guillemot sub-population nesting at the Naked Island Group is supported by the increase in nestling survival and the decrease in adult mortality post-mink removal. Bixler (2010) identified mortality of nestling and adult

guillemots as limiting the growth of the guillemot population at the Naked Island Group in 2008. Following the removal of mink, we observed a substantial decline in mortality of both guillemot nestlings and adults at the nest site. Guillemot nestling survival at the Naked Island Group, which Golet et al. (2002) found to be negatively correlated with predation rates on nestlings, returned to levels observed prior to the detection of mink on the Naked Island Group (1978-1981; Kuletz 1983) following mink removal. Predation on adult guillemots at active nests, which was confirmed at 9% of monitored nests in 1998 (Golet et al. 2002) and at 10% of monitored nests in 2008 (Bixler 2010), was not observed during this study. The mortality rates of guillemots nesting at the Naked Island Group and their nest success rates have apparently returned to the levels observed pre-mink establishment (Kuletz 1983), levels expected at guillemot colonies that are free of mammalian predators (Ainley and Boekelheide 1990).

Both the rate of growth in guillemot numbers and the nest recruitment rate at the Naked Island Group exceeded expectations following mink removal. The high growth rate in guillemot numbers following the initiation of mink removal was inconsistent with intrinsic growth in a closed population. Most or all of the observed growth was likely the result of immigration to the Naked Island Group from other nearby guillemot colonies that make up the larger meta-population in Prince William Sound.

The rapid response to reduction in mink predation is incompatible with intrinsic growth of the guillemot sub-population breeding at the Naked Island Group. The pre-breeding count of guillemots at the Naked Island Group increased substantially in 2015, immediately following the second year of spring mink trapping. Guillemots do not reach maturity and initiate breeding until at least their 3rd year and many may not breed for the first time until their 5th or 6th year

(Ewins 1993). During this immature period, sub-adult guillemots do not attend breeding colonies in the nest initiation period (late May and early June), and would not have been counted by surveys during the pre-breeding period (Nelson 1982, Vermeer et al. 1993). Therefore, we would not expect an increase in recruitment through intrinsic reproduction following mink removal until after at least a 3-year time lag. The observed rapid recruitment response by guillemots at the Naked Island Group suggests that immigrants were the primary factor responsible for the increase in numbers during the first five breeding seasons following the initiation of mink removal.

In addition to the short time lag for the recruitment response, the magnitude of response following mink removal was unanticipated. The average annual population growth rate (λ) observed at the Naked Island Group during 2014-2018 was 1.27. This is much greater than the increase in numbers of breeding pigeon guillemots following the removal of introduced arctic foxes (*Vulpes lagopus*) from islands in the Aleutian Archipelago, Alaska, where the average λ was 1.13 over six years (Byrd 2001). The rate observed in this study is far above the estimated maximum intrinsic rate of increase (r_{max}) for a pigeon guillemot population (Russell 1999, Sæther and Bakke 2000).

Bixler (2010) found that the guillemot sub-population at the Naked Island Group declined at a rate greater than predicted based on the observed low nesting success and rate of adult mortality due to predation at the nest site. The additional decline was best accounted for by breeding guillemots emigrating from the Naked Island Group to other colonies. It is likely that the reverse of this process drove the observed rapid rate of increase by pigeon guillemots in both this study and following removal of arctic foxes from some Aleutian Islands.

The increase in numbers of guillemots counted at the Naked Island Group during the pre-breeding period corresponded with an increase in the number of active guillemot nests during the first five years following the initiation of mink removal. During this period, the average annual recruitment rate of breeding pairs to the Naked Island Group population (λ) was 1.19 (19%/year). Such a high recruitment rate has not been previously documented in a recovering guillemot population (Byrd et al. 1997, Byrd 2001, Nordstrom et al. 2003).

Following the removal of mink from the Naked Island Group, the number of pigeon guillemots counted during pre-breeding surveys and the number of active guillemot nests increased immediately. Over the subsequent three years, however, these rates of increase slowed, rather than accelerated as would be expected based on exponential population growth. Both of these attributes of the early response by guillemots to mink removal at the Naked Island Group support recruitment of immigrants as the driver of immediate population growth.

One possible source of these immigrating birds is from a cohort of “floaters” at other colonies in central Prince William Sound. These floaters would have likely been unable to find suitable nest sites at existing colonies nearby (Kokko and Sutherland 1998). Following the removal of mink from the Naked Island Group, however, these individuals could have quickly responded to the increase in productivity by the few remaining pairs of nesting guillemots and the social attraction afforded by other new recruits. Based on the increased reproductive success among conspecifics, these new recruits could have driven the observed immediate increase in both the numbers of individuals in the sub-population and the numbers of active nests (Danchin et al. 1998). As the number of guillemots unable to find suitable nest sites in

central Prince William Sound declined, however, the rate of increase in numbers of guillemots counted during pre-breeding surveys and in numbers of active nests slowed at the Naked Island Group. While quantifying guillemot movements among colonies was beyond the scope of this study, this scenario provides a plausible explanation for the observed trends in guillemot numbers at the Naked Island Group following mink removal.

The abundance of guillemot nests at the Naked Island Group decreased following the introduction and establishment of mink on the archipelago, but has begun to recover following mink removal. Prior to mink establishment, guillemot nests were found in talus rubble at the base of sea-cliffs, in crevices on the face of sea-cliffs, and in burrows in root wads at the top of sea-cliffs and bluffs. Once mink were well-established on the Naked Island Group, however, 88% of active guillemot nests were found in crevices on sea-cliffs that were apparently inaccessible to terrestrial predators such as mink (Kuletz 1983, Bixler 2010). This shift in nest site selection by guillemots nesting at the Naked Island Group appears to have been reversed by the removal of mink; guillemot nest sites that are more accessible to mink are apparently no longer being selected against due to mink predation pressure. This change has resulted in a trend toward greater utilization of nest site types whose use by guillemots was more prevalent at the Naked Island Group prior to the introduction of mink. This supports the hypothesis that mink predation caused a shift in the types of nest sites used by guillemots at the Naked Island Group (Bixler 2010) and is consistent with our prediction that mink removal would result in guillemots reoccupying nest site types that are more vulnerable to mink predation.

A similar change in nest site use was observed following rat removal from nesting colonies of Scripps's murrelet (*Synthliboramphus scrippsi*) on the Channel Islands of California

(Whitworth et al. 2013). In their study, nests sites that were accessible to rats had been vacant, but were reoccupied following rat removal. The decrease in predation pressure in that study, as in the present study, allowed for successful nesting in these previously unoccupied nest site types.

Long-term monitoring of pigeon guillemots nesting at the Naked Island Group provided a unique opportunity to evaluate potential changes in prey availability concurrent with removal of mink. This also allowed us to address some of the concerns with the BACI study design raised by Underwood (1992) and related to the lack of control of confounding environmental variables not addressed in studies of the restoration of island bird populations through the removal of introduced predators (Nordstrom 2000, Whitworth 2014). In the present study, we tested for changes in prey availability compared with earlier periods of guillemot research at the Naked Island Group by evaluating food provisioning to guillemot nestlings, including measuring diet composition, meal delivery rates, and growth rates. Such changes in prey availability could contribute to guillemot population growth irrespective of mink removal.

In addition to the effect of mink removal at the Naked Island Group, the increasing trend in guillemot numbers counted at the control islands suggests that nesting conditions for guillemots in central Prince William Sound improved during the study period. During the first two decades following the *Exxon Valdez* oil spill, the Sound-wide population of pigeon guillemots was in decline (Bixler 2010). One explanation for the recent improvement in nesting conditions is enhanced food supply, and this is supported by the high provisioning rates at guillemot nests and high chick growth rates observed at the Naked Island Group following mink removal. This suggests that future increases in the guillemot population in Prince William Sound

are possible beyond the growth at the Naked Island Group driven by immigration. Under these conditions, the removal of mink from the Naked Island Group has the potential to restore a formerly large sub-population of nesting guillemots that likely served as a source for the regional meta-population.

High guillemot nestling growth rates and meal delivery rates to nests suggest that foraging conditions for guillemots nesting at the Naked Island Group have improved compared to the first two decades following the *Exxon Valdez* oil spill, when the numbers of guillemots nesting at the Naked Island Group were in steep decline, and to a lesser degree were in decline throughout Prince William Sound. Enhanced food availability likely improved breeding success for guillemots nesting at the Naked Island Group and at nearby control islands. This is supported by the increase in guillemots counted during pre-breeding surveys at control islands. Despite the increasing trend in guillemot numbers at the control islands during 2007-2014, guillemot numbers at the Naked Island Group continued to decline during this period. Not until mink were removed did counts of guillemots at the Naked Island Group began to increase. The evidence suggests that the recruitment of guillemots to the Naked Island Group was driven by improved conditions for successful nesting that resulted from the removal of mink. Prior to the decrease in nest predation rates resulting from the removal of mink, the effects of improved foraging conditions were not realized. While enhanced foraging conditions facilitated the increase in the sub-population of breeding guillemots at the Naked Island Group, it was the removal of mink that triggered the increase.

Conclusions

The removal of American mink from the Naked Island Group was successful in lifting the primary limiting factor for growth of this sub-population of breeding pigeon guillemots. Immediate population growth at the Naked Island Group following mink removal was likely driven by immigration from other nearby breeding colonies in central Prince William Sound, rather than intrinsic growth. High guillemot nesting success following mink removal and the social attraction provided by the presence of conspecifics still nesting at the Naked Island Group likely encouraged floater guillemots to nest. Future intrinsic growth of the sub-population of pigeon guillemots at the Naked Island Group may benefit from the improved foraging conditions evident from this study and associated enhancement of guillemot nestling survival. Current conditions in central Prince William Sound appear favorable for the gradual recovery of the entire Prince William Sound guillemot population. Future efforts to remove introduced predators to benefit pigeon guillemots are likely to elicit rapid and early success if the focus is on historical colonies where remnant breeders remain to provide social attraction and evidence of conditions conducive to reproductive success.

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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* Seabirds of the Farallon Islands, D. G. Ainley and R. J. Boekelheide (eds.). Stanford University Press, Stanford, California.

Anthony, J. A., D. D. Roby, and K. R. Turco. 2000. Variation in lipid content of forage fishes and its effect on energy provisioning rates to seabird nestlings. Journal of Experimental Marine Biology 248: 53-78.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458-473.

Barraquand, F., T. T. Hoye, J. A. Henden, N. G. Yoccoz, O. Gilg, N. M. Schmidt, B. Sittler, and R. A. Ims. 2014. Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and arctic lemmings. Journal of Animal Ecology 83: 375-387.

Barrett, R. T. 2002. Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. Marine Ecology Progress Series 230: 275-287.

Birkhead, T. R., and D. N. Nettleship. 1995. Arctic fox influence on a seabird community in Labrador: a natural experiment. Wilson Bulletin 107: 397- 412.

Bixler, K. S. 2010. Why aren't pigeon guillemots in Prince William Sound, Alaska recovering from the *Exxon Valdez* oil spill? Unpubl. M.Sc. thesis, Oregon State University, Corvallis, OR. 161 pp.

Bright, C. 1998. Life out of bounds: bioinvasion in a borderless world. W.W. Norton Company, New York, USA.

Burke, C. M., and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. Journal of Zoology 278: 354-361.

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.

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.

Carls, M. G., G. D. Marty, and J. E. Hose. 2002. Synthesis of the toxicological impacts of the *Exxon Valdez* oil spill on Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 59: 153-172.

Cushing, D. A., D. D. Roby, and D. B. Irons. 2017. Patterns of distribution, abundance, and change over time in a subarctic marine bird community. Deep-Sea Research II http://dx.doi.org/10.1016/j.dsr2.2017.07.012

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.

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

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.

Exxon Valdez Oil Spill Trustee Council (EVOSTC). 2014. Injured Resources and Services: 2014 Update. Unpublished report by the Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/static/PDFs/2014IRSUpdate.pdf

Ewins, P. J. 1985. Colony attendance and censusing of Black Guillemots *Cepphus grylle* in Shetland. Bird Study 32: 176-185.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). Edited by A. Poole and F. Gill. The Birds of North America Online. d.oi:10.2173/bna.49.

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. Final Report to the U.S. Fish and Wildlife Service, Migratory Bird Office, Anchorage, Alaska. 51 pp.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 2003. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7: 1-21.

Gerell, R. 1967. Dispersal and acclimatization of the mink (*Mustela vison*) in Sweden. Viltrevy 4: 1-38.

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. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 94173), U.S. Fish and Wildlife Service, Anchorage, Alaska.

Isleib, M. E., 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.

Irons, D. B., and D. D. Roby. 2007. Pigeon guillemot restoration research in Prince William Sound, Alaska. Unpublished research proposal to the Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/Store/Proposal_Documents/2190.pdf Accessed: August 21, 2019.

Kokko, H., and W. J. Sutherland. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. American Naturalist 152: 354-366.

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

Kuletz, K. J., C. S. Nations, B. Manly, A. Allyn, D. B. Irons, and A. McKnight. 2011. Distribution, abundance, and population trends of Kittlitz's murrelet *Brachyramphus brevirostris* in Prince William Sound, Alaska. Marine Ornithology 39: 97–109.

Lack, D. L. 1968. Ecological adaptations for breeding in birds. Methuen Publishing, London, England.

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., J. F. Piatt, and J. D. Figurski. 1998. Hermit crabs in the diet of Pigeon Guillemots at Kachemak Bay, Alaska. Colonial Waterbirds 21: 242-244.

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. 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.

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, 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.

Maccarone, A. D., and W. A. Montevecchi. 1981. Predation and caching of seabirds by red fox (*Vulpes vulpes*) on Baccalieu Island, Newfoundland. Canadian Field-Naturalist 95: 352-353.

McDonald, T.L., W.P. Erikson, and L.L. McDonald. 2000. Analysis of count data from before-after control-impact studies. Journal of Agricultural, Biological, and Environmental Statistics. 5: 262-279.

Nelson, D. A. 1982. The communication behavior of the Pigeon Guillemot *Cepphus columba*. Unpubl. Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan.

Nordstrom, M., J. Hogmander, J. Nummelin, N. Laanetu, and E. Korpimaki. 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. 1981. Determinants of population size of Pigeon Guillemots *Cepphus columba* at Naked Island, Prince William Sound, Alaska. Unpubl. M.Sc. thesis, University of Alaska, Fairbanks. Fairbanks, Alaska. 82 pp.

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.

Piatt, J. F., 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.

Peterson, C. H., S. D. Rice, J. W. Short, D. Esler, J. L. Bodkin, B. E. Ballachey, and D. B. Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302: 2082-2086.

Ramsey, F. L., and D. W. Schafer. 2002. The statistical sleuth: a course in methods of data analysis, 2nd edition. Duxbury Press, Pacific Grove, California.

Russell, R. W. 1999. Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. Pp. 51-76 *in* Life in the slow lane: ecology and conservation of long-lived marine animals. J. A. Musick (ed.). Symposium 23, American Fisheries Society, Bethesda, Maryland.

Sæther, B., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642-653.

Shabecoff, P. 1989, March 25. Exxon vessel hits reef, fouling water that is rich in marine life. The New York Times, 1, 42.

Smith, E. P. 2014. BACI Design. Wiley StatsRef: Statistics Reference Online. Edited by N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri and J.L. Teugels. Available at: https://doi.org/10.1002/9781118445112.stat07659. Acessed December 16, 2019.

Suryan, R. M., D. B. Irons, M. Kaufman, J. Benson, P. G. R. Jodice, D. D. Roby, and E. D. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla.* Marine Ecological Progress Series 236: 273-287.

Towns, D. R., G. V. Byrd, H. P. Jones, M. J. Rauzon, J. C. Russel, and C. Wilcox. 2011. Impacts of introduced predators on seabirds. Pp. 58-90 *in* Seabird islands: ecology, invasion, and

restoration. C. P. H. Mulder, D. R. Towns, W. B. Anderson, and P. J. Bellingham (eds.). Oxford University Press, Oxford, England.

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology 161: 145-178.

Van Pelt, T. I., J. F. Piatt, B. K. Lance, and D. D. Roby. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comparative Biochemistry and Physiology 119: 1–6.

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.

Votier, S. C., G. W. James, S. Patrick, and J. Newton. 2010. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Marine Biology 158: 355-362.

Whitworth, D. L., H. R. Carter, and F. Gress. 2013. Recovery of a threatened seabird after eradication of an introduced predator: Eight years of progress for Scripps's murrelet at Anacapa Island, California. Biological Conservation 162: 52-59.

Figures

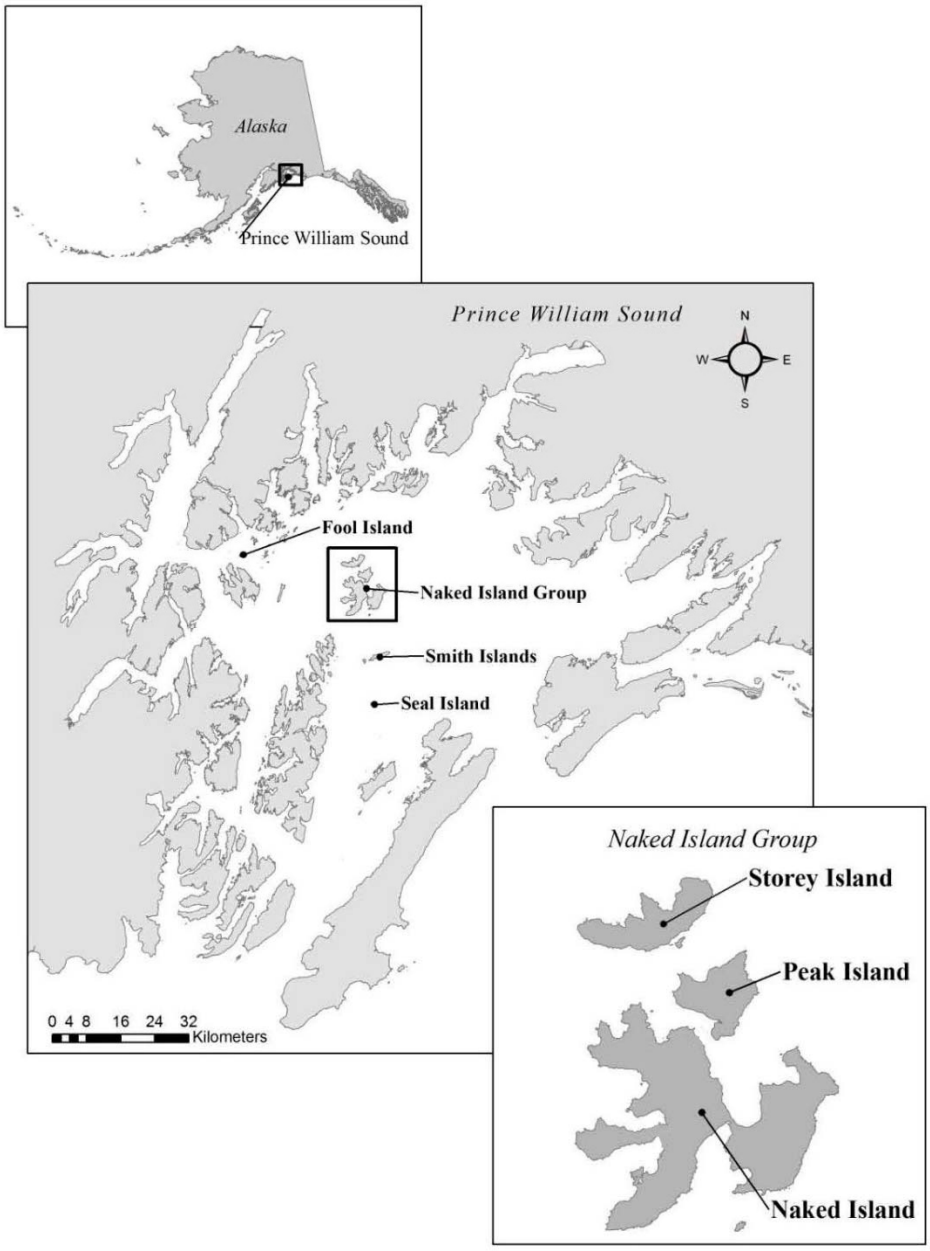

Figure 1. Map of the study area showing the location of Prince William Sound (PWS) in Alaska (top left), the four island groups in central PWS where pigeon guillemots were monitored (middle), and the three main islands that comprise the Naked Island Group (bottom right; after Bixler 2010).

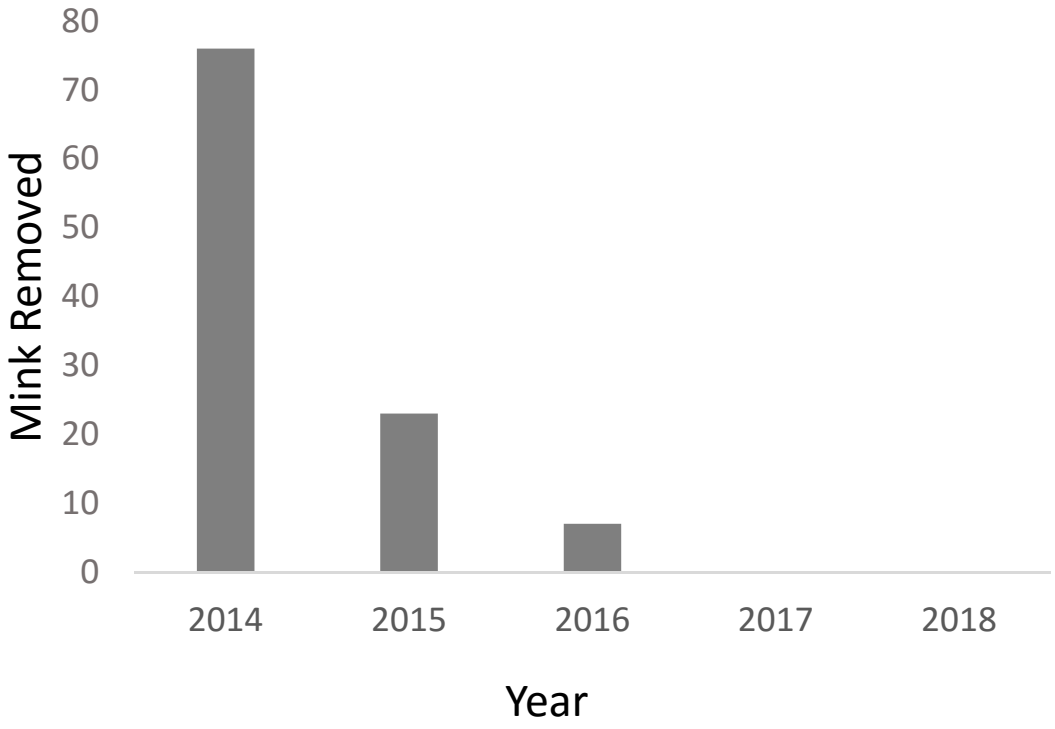

Figure 2. Number of introduced American mink removed from the Naked Island Group, Prince William Sound, Alaska, during each year of trapping effort in March and April of 2014 through 2018.

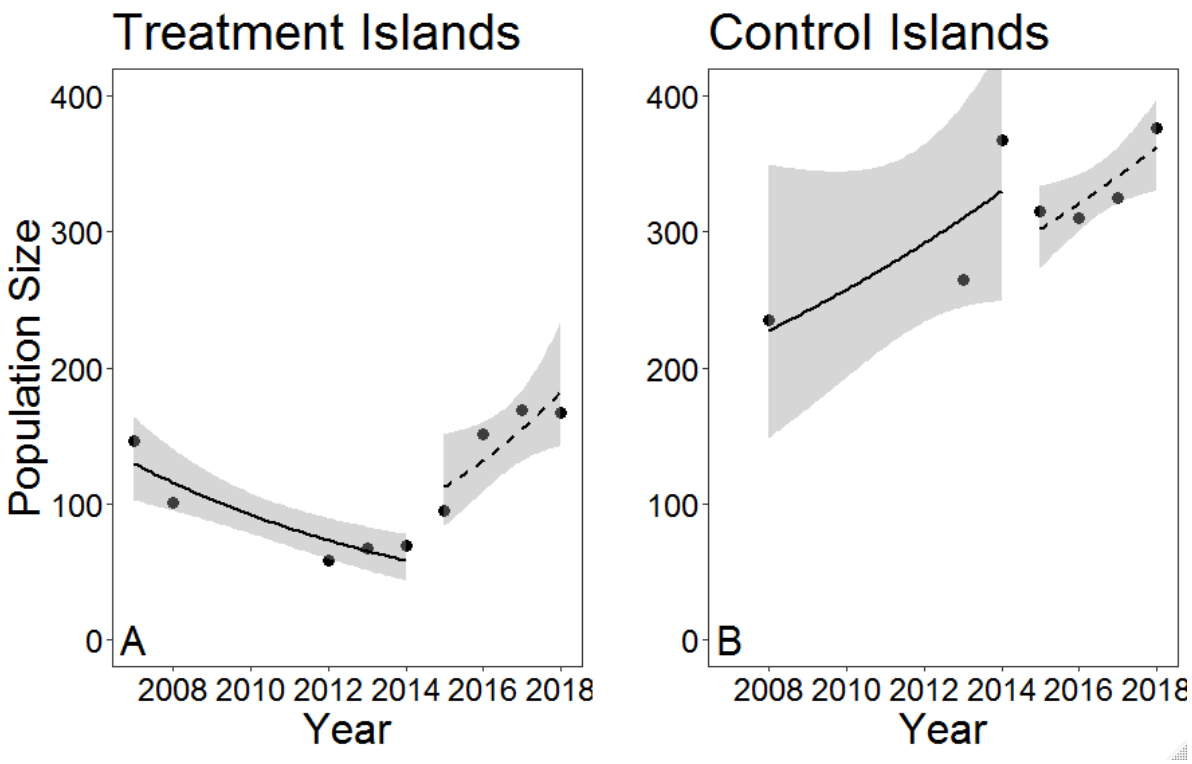

Figure 3. Total numbers of pigeon guillemots counted during pre-nesting surveys at islands in Prince William Sound, Alaska that were either in the treatment group (A: Naked Island Group, where mink removal occurred) or the control group (B: Smith Islands, Seal Island, Fool Island, where mink were not present) before and after the reduction in predation on guillemot nests resulting from mink removal at the treatment islands initiated in 2014. Trend lines indicate the estimated rate of change (individuals/year) during the pre-mink removal period (solid lines) and the period following the initiation of mink removal (dashed lines); estimated trends are based on the slopes of regression lines from a generalized linear model.

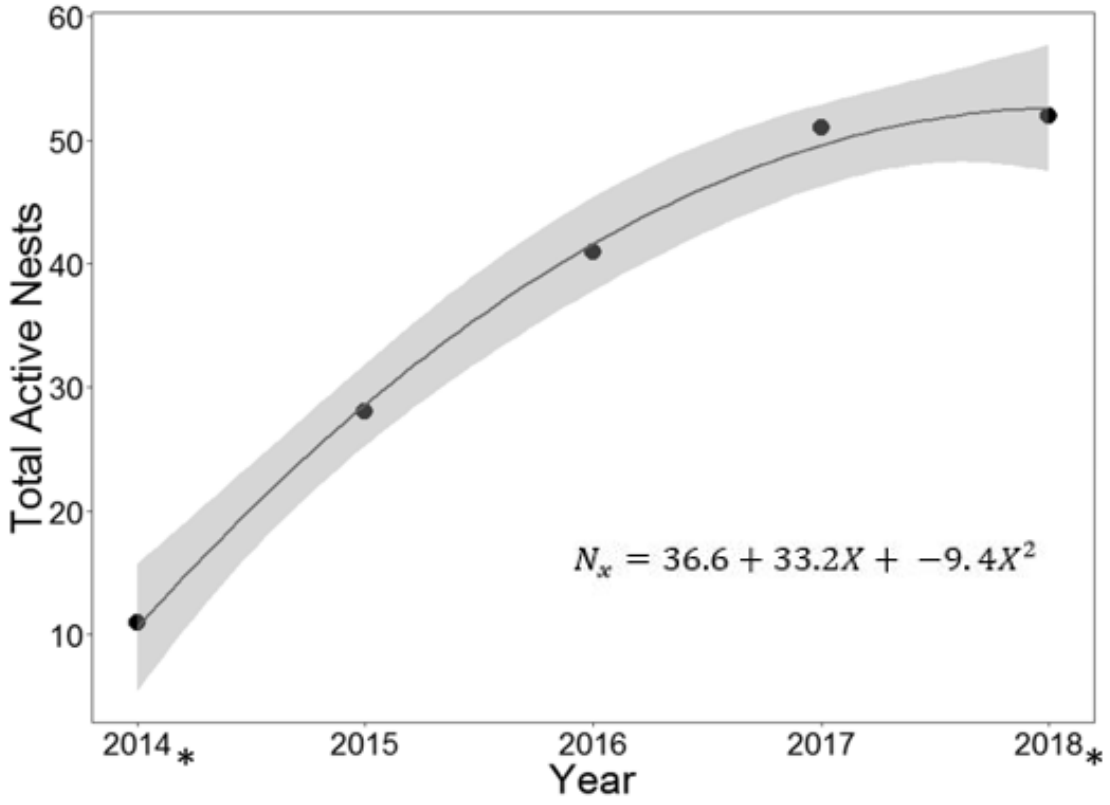

Figure 4. Number of active pigeon guillemot nests at the Naked Island Group, Prince William Sound, Alaska, in each breeding season during 2014-2018, following the initiation of mink removal. The best-fit 2nd order polynomial model of nest counts as a function of year is depicted as a solid line, and the 95% confidence intervals for the rate of increase in number of active guillemot nests is depicted by gray shading. Estimates of intercept, first and second order constants describing the relationship between year (*X*) and the number of observed nests (*N*) in that year. * indicates reduced nest search effort compared to the other three years of the study.

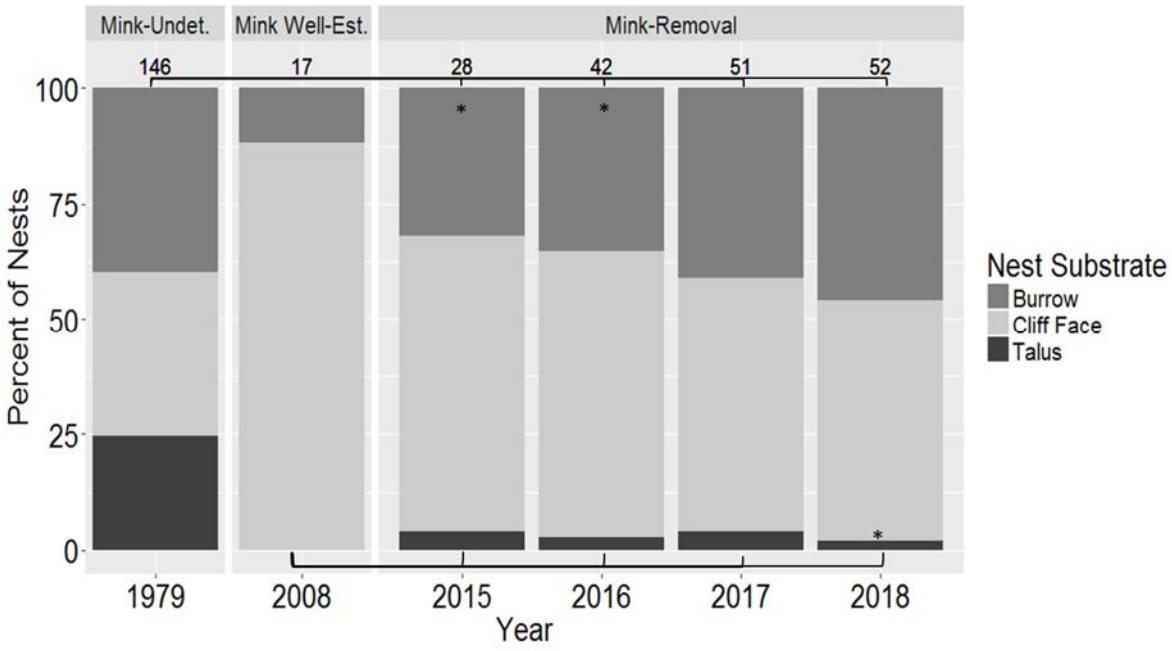

Figure 5. Percent of pigeon guillemot nests at the Naked Island Group, Prince William Sound, Alaska in each of the three categories of nest site type during four years following mink removal (2015-2018). Use of the three nest site types in these four years are compared with nest site use in a year before mink were first detected (1979) and a year when mink were well-established (2008) at the Naked Island Group. Pairwise comparisons of the proportion of nests in sites vulnerable to mink predation (Burrow, Talus) vs. less vulnerable (Cliff Face) using Fisher's exact tests are shown with brackets. * indicates a significant difference; sample size of nests in each year are presented above the bars.

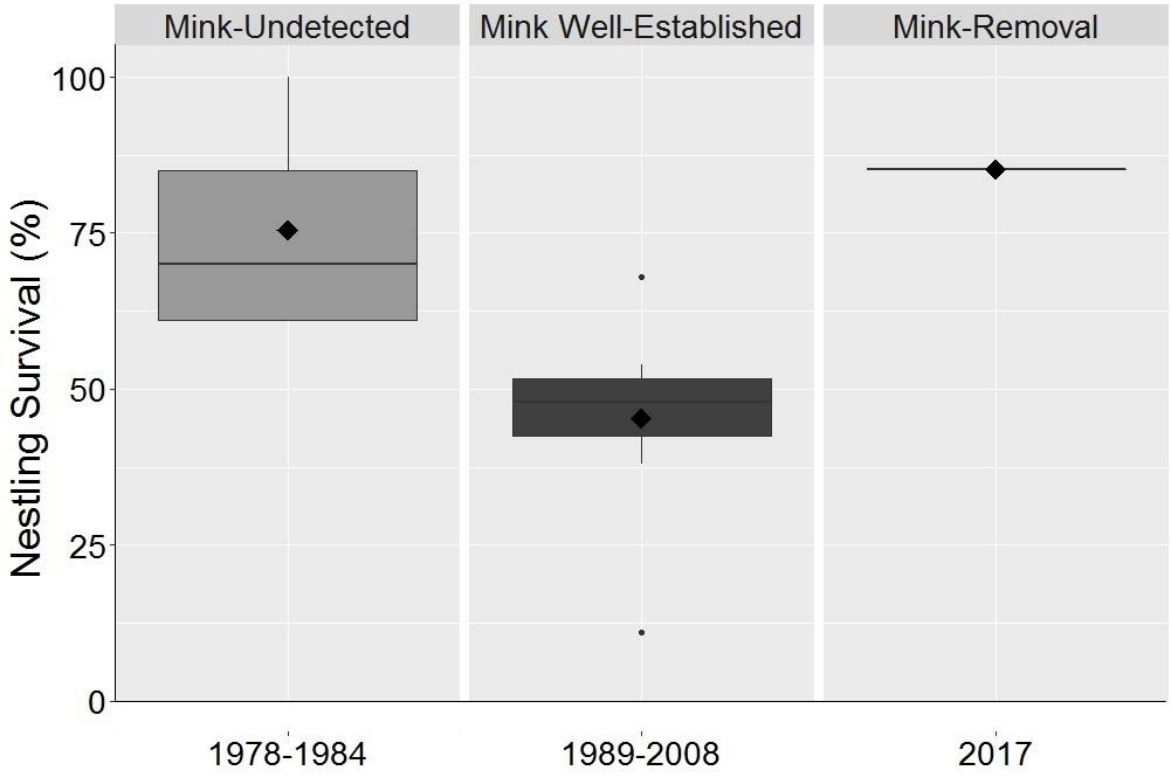

Figure 6. Box plots showing estimated mean (diamonds) and distribution of annual survival rates of pigeon guillemot nestlings during three periods when mink abundance differed at the Naked Island Group, Prince William Sound, Alaska: (1) mink undetected (1979-1984), (2) mink well-established (1989-2008), and (3) after mink removal (2017) following four years of intensive mink trapping.

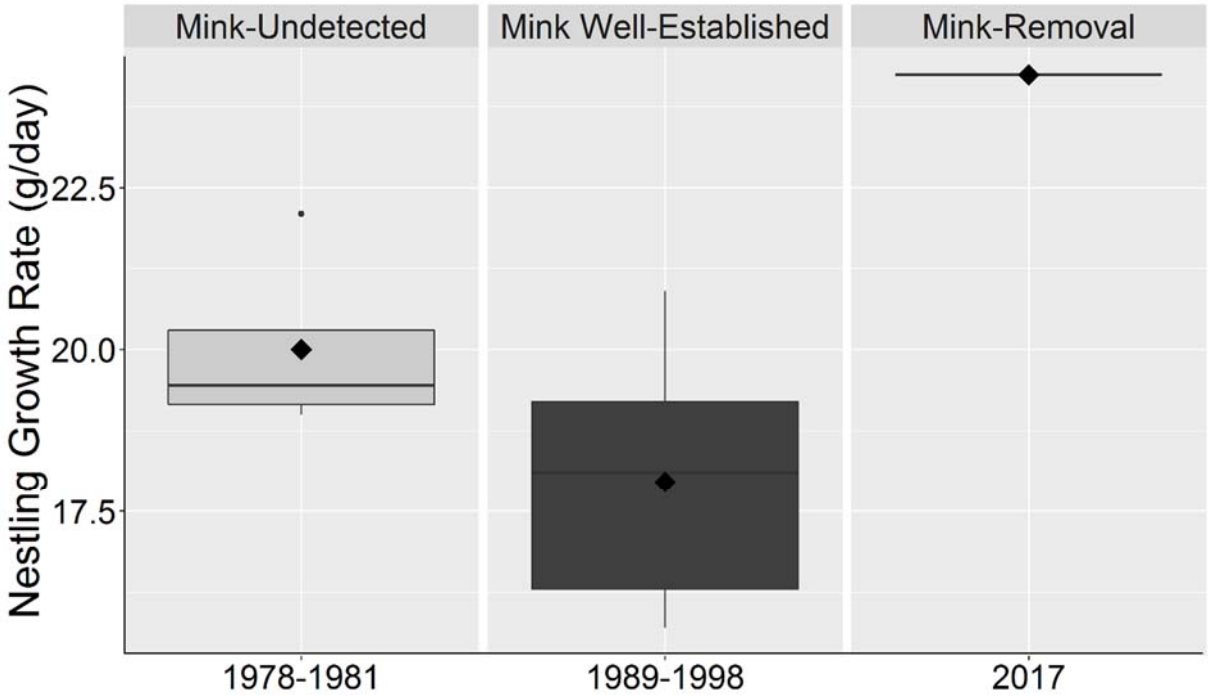

Figure 7. Box plots of nestling growth rates in body mass (g/day) during the linear phase of growth for pigeon guillemot nestlings, showing mean growth rate (diamonds) and distribution of average annual growth rate during three periods when mink abundance differed at the Naked Island Group, Prince William Sound, Alaska: (1) mink undetected (1978-1981), (2) mink well-established (1989-1998), and (3) after mink removal (2017) following four years of intensive mink trapping.

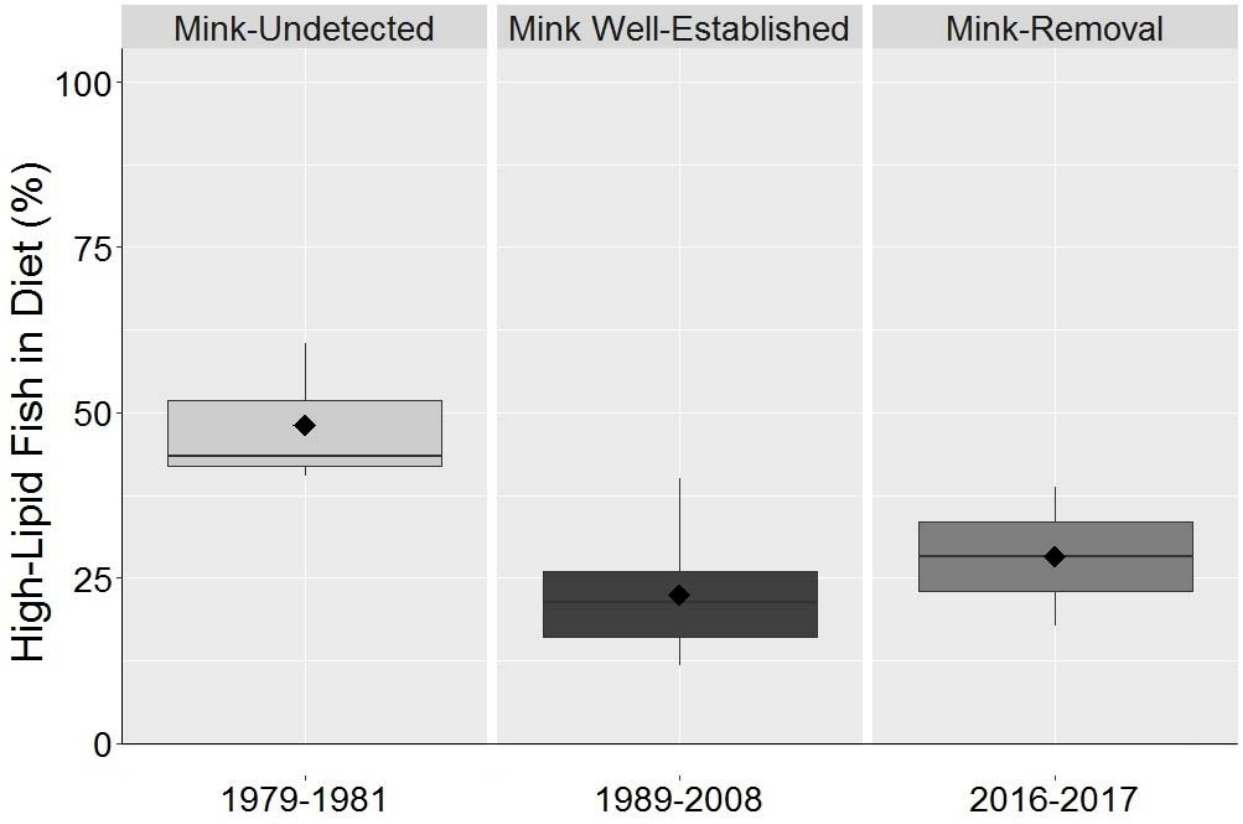

Figure 8. Box plots of the annual average proportion of pigeon guillemot nestling diets (by prey item) that consisted of high-lipid schooling forage fish, showing the mean (diamonds) and distribution during three periods when mink abundance differed at the Naked Island Group, Prince William Sound, Alaska: (1) mink undetected (1979-1981), (2) mink well-established (1989-2008), and (3) after mink removal (2016-2017) following 3-4 years of intensive mink trapping.

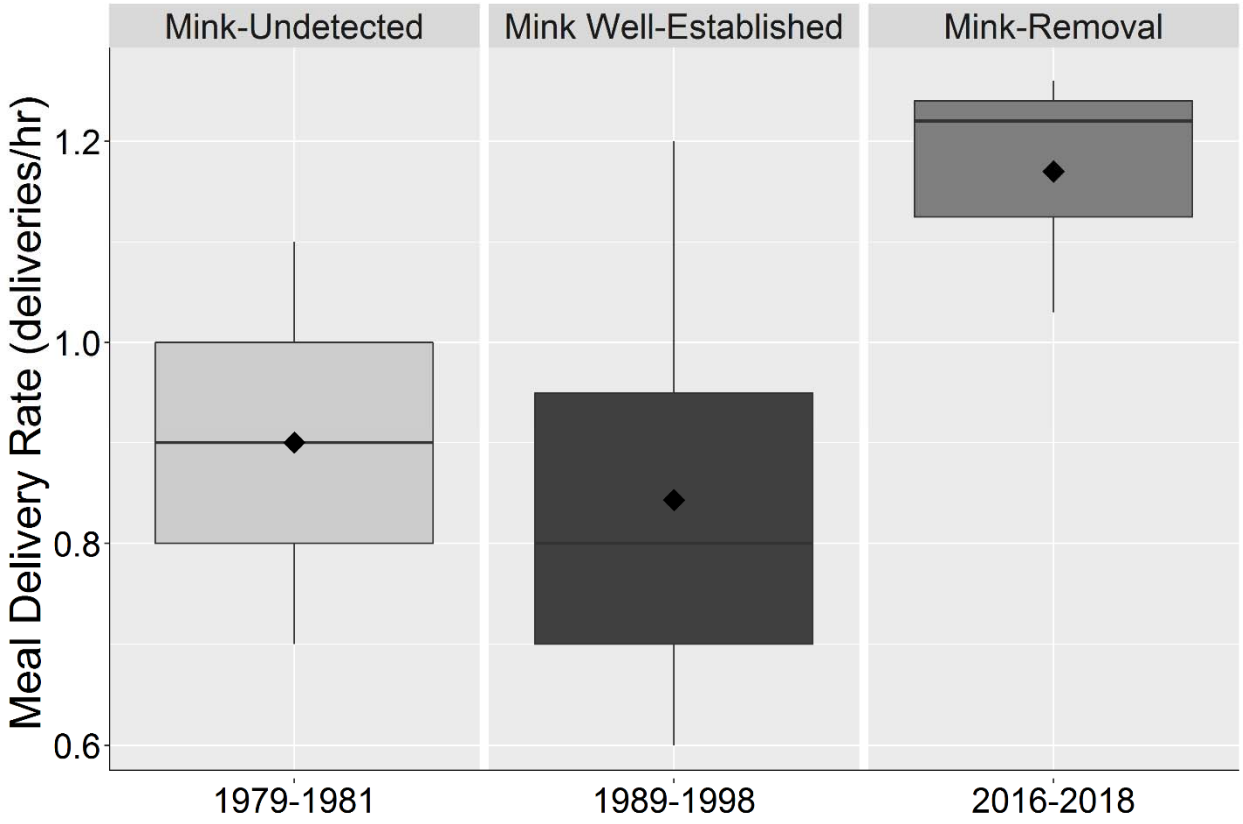

Figure 9. Box plots of the annual average meal delivery rate to pigeon guillemot nests, showing the mean (diamonds) and distribution during three periods when mink abundance differed at the Naked Island Group, Prince William Sound, Alaska: (1) mink undetected (1979-1981), (2) mink well-established (1989-1998), and (3) after mink removal (2016-2018) following 3-4 years of intensive mink trapping.

Table 1. List of 19 generalized linear models developed based on *a priori* hypotheses for the factors explaining variation in numbers of pigeon guillemots counted during pre-breeding surveys at study sites in central Prince William Sound, Alaska, between 2007 and 2018. These models are listed in order of increasing number of explanatory variables, and were ranked based on model selection using Akaike's Information Criterion adjusted for small sample sizes (AICc).

	Model
1	Null
2	Period
3	Treatment
4	Year
5	Period + Treatment
6	Period+ Year
7	Treatment +Year
8	Period + Treatment+ Year
9	Period + Treatment + (Period x Treatment)
10	Period + Year + (Period x Year)
11	Treatment + Year + (Treatment x Year)
12	Period + Treatment + Year + (Period x Treatment)
13	Period + Year + Treatment (Period x Year)
14	Treatment + Year + Period (Treatment x Year)
15	Period + Treatment + Year + (Period x Treatment) + (Period x Year)
16	Period + Year + Treatment + (Period x Year) + (Treatment x Year)
17	Treatment + Year + Period + (Treatment x Year) + (Treatment x Period)
18	Treatment + Year + Period + (Treatment x Year) + (Treatment x Period) + (Period x Year)
19	Period + Treatment + Year + (Period x Treatment) + (Period x Year) + (Treat x Year) + (Period x Treatment x Year)

Table 2. The top four generalized linear models explaining variation in number of pigeon guillemots counted during pre-breeding surveys at study sites in central Prince William Sound, Alaska, between 2007 and 2018. Models were ranked using Akaike's Information Criterion adjusted for small sample sizes (AICc) and based on the ΔAICc value, the difference between an individual model's AICc score and the lowest AICc score of all the candidate models. None of the models ranked 2-4 were competitive (ΔAICc ≤ 2.0) with the top model, given the data. Also included are the number of parameters estimated in each model (K), the test statistic of -2X the log likelihood ratio (-2x(loglik.)), and the AIC_c model weights (W_i).

Rank	***Model***	***K***	***-2x (loglik.)***	***AIC_c***	***ΔAIC_c***	***W_i***
1	Period + Treatment + Year + (Period x Treatment) + (Period x Year) + (Treatment x Year) + (Period x Treatment x Year)	8	142.45	178.92	0	0.99999
2	Treatment + Year + Period + (Treatment x Year) + (Treatment x Period) + (Period x Year)	7	195.59	201.70	22.78	0.00001
3	Treatment + Year + Period + (Treatment x Year) + (Treatment x Period)	6	203.70	209.47	30.55	<0.00001
4	Period + Treatment + Year + (Period x Treatment) + (Period x Year)	6	214.75	2235.83	56.91	<0.00001

Table 3. Results of the best-fit generalized linear model explaining variation in the number of pigeon guillemots counted during pre-breeding surveys at study sites in central Prince William Sound, Alaska, between 2007 and 2018. Estimates of the two categorical variables (Period and Treatment) are for the shift in the response variable from the reference level (Period: before mink removal; Treatment: mink removal site [Naked Island Group]) to the alternate level (Period: after mink removal; Treatment: control sites [Smith Islands, Seal Island, Fool Island]). Estimates from this model are in logit link output.

Coefficients	Estimate	SE	*t*	*p*
(Intercept)**	4.864	0.134	36.29	<0.0001
Year**	-0.115	0.033	-3.45	0.0086
Period	-1.440	0.727	-1.98	0.0832
Treatment*	0.500	0.202	2.47	0.0386
Year x Period**	0.277	0.080	3.44	0.0088
Year x Treatment**	0.177	0.043	4.13	0.0033
Period x Treatment	1.301	0.876	1.49	0.1757
Year x Treatment x Period*	-0.278	0.098	-2.86	0.0213

* $p < 0.05$, $p > 0.01$

** $p < 0.01$

Table 4. Estimates of logit link rates of change (slope of regression) in numbers of individual pigeon guillemots counted per year (ln(individuals/year)) during pre-breeding surveys at treatment islands (mink removal) and control islands (no mink present) in central Prince William Sound, Alaska. Annual counts were divided into two periods, pre-mink removal and post-mink removal within each of the two treatment groups. In each group, the change in slope between the before and after periods, and the difference between treatment and control in the change of slope was compared using post hoc analysis based on the best fit Generalized Linear Model of guillemot numbers counted during pre-breeding surveys.

Control Islands					
Rate of Change	Estimate	SE	*t*-value	df	*p*
Before	0.062	0.029	2.31	8	0.049
After	0.061	0.048	1.26	8	0.242
Before/After Difference	0.001	0.055	-0.02	8	0.979
Treatment Islands					
Rate of Change	Estimate	SE	*t*-value	df	*p*
Before	-0.115	0.033	-3.44	8	0.008
After	0.162	0.073	2.21	8	0.058
Before/After Difference	0.277	0.080	3.44	8	0.007
Before/After Difference between Treatment and Control					
	Estimate	SE	*t*-value	df	*p*
	0.278	0.027	2.85	10	0.021

Table 5. ANOVA table for the effect of period (pre-mink detection, mink well-established, post-mink removal) on four variables that serve as indicators of the availability of forage fish for nesting pigeon guillemots at the Naked Island Group in central Prince William Sound, Alaska.

Model	df	*F*-value	*p*	Adj. R
Nestling Survival Rate				
Period	2,11	6.478	0.013	0.457
Nestling Growth Rate				
Period	2,9	6.014	0.022	0.477
Rate of Nestling Meal Deliveries				
Period	2,10	2.951	0.098	0.245
Proportion of High-Quality Prey in Diet				
Period	2,9	5.506	0.024	0.48

Appendix A. Equation describing the relationship between the number of guillemots observed in a given survey, the year that survey was conducted, the treatment (mink removal vs. control) of the site surveyed, and the period in which the survey took place (before vs. after mink removal) at islands in central Prince William Sound, Alaska.

$$Yt \sim \text{Quasi} - \text{Poisson}\ (Gt)$$

$$\eta(G_t) = \beta_0 + \beta_1 T_c + \beta_2 P_a + \beta_3 Y_k + \beta_4 T_c P_a + \beta_5 Y_k T_c + \beta_6 Y_k P_a + \beta_7 Y_k T_c P_a$$

$$Var(Y_t) \ = \ \mu\Theta$$

G_t = number of guillemots observed during pre-breeding surveys during the t^{th} survey

β_0 = intercept of the regression of the number of guillemots observed during pre-breeding surveys at the treatment islands during the period prior to mink removal

β_1 = incremental shift in the intercept of the regression of the number of guillemots observed during spring surveys at the control islands during the period prior to mink removal at the treatment islands

β_2 = incremental shift in the intercept of the regression of the number of guillemots observed during spring surveys at the treatment islands during the period following the initiation of mink removal

β_3 = average annual rate of change in the number of guillemots observed during pre-breeding surveys at the treatment islands in the period prior to mink removal

β_4 = additional incremental shift in the intercept of the regression of numbers of guillemots observed during pre-breeding surveys at the control islands during the period after the initiation of mink removal from the treatment islands

β_5 = incremental shift in the average annual rate of change in the number of guillemots observed during pre-breeding surveys at the control islands in the period prior to mink removal at the treatment islands

β_6= incremental shift in the average annual rate of change in the number of guillemots observed during pre-breeding surveys at the treatment islands in the period following the initiation of mink removal.

β_7 = additional incremental shift in the average annual rate of change in the number of guillemots observed during pre-breeding surveys at the control islands in the period following the initiation of mink removal.

T_c = 1 when the treatment is *control* and zero otherwise

P_a = 1 when the period is *after* the initiation of mink removal and zero otherwise

Y_k = year when the tth survey was conducted

Θ = quasi-Poisson over dispersion parameter

η = logit function linking the estimate to the linear model

Appendix B. General equation describing the relationship of the response variables *nestling survival*, *nestling growth rate*, *meal delivery rates*, and *percentage high-quality forage fish in the nestling diet* and the predictive variable *Period* for pigeon guillemots nesting at the Naked Island Group, Prince William Sound, Alaska.

$$R_{vt} = \beta_{0v} + \beta_{1v}B_x + \beta_2 A_y + \varepsilon_{vt}$$

R_{vt} = value of the v[th] response variable from t[th] observation

β_0 = value of the v[th] response variable during the period when mink were well-established at the Naked Island Group

β_1 = incremental change in the v[th] response variable during the period before mink were detected at the Naked Island Group

β_2 = incremental change in the v[th] response variable during the period after the initiation of mink removal from the Naked Island Group

B_x = 1 when the observation is from the period before mink were detected and zero otherwise

A_y= 1 when the observation is from the period after the initiation of mink removal and zero otherwise

ε_t = random error term for the t[th] observation of the v[th] response variable

v = response variable of the equation, including *nestling survival*, *nestling growth rate*, *meal delivery rate*, and *percentage high-quality forage fish in the nestling diet*

Appendix C. Equation describing the relationship between the number of active pigeon guillemot nests detected at the Naked Island Group in each breeding season and the continuous covariate Year.

$$N_t = \beta_0 + \beta_1 X + \beta_2 X^2 + \varepsilon_t$$

N_t = number of guillemot nests detected during the t^{th} breeding season

β_0 = intercept of the regression of the number of guillemot nests detected per breeding season

β_1 = average annual rate of change in the number of guillemot nests detected per breeding season

β_2 = additional average annual rate of change in the number of guillemot nests detected per breeding season described by the second order polynomial

X = year when the t^{th} breeding season took place

ε_t = random error term for the t^{th} breeding season

CHAPTER 3

Synopsis and Conclusions

Samuel B. Stark

The number of pigeon guillemots (*Cepphus columba*) nesting at the Naked Island Group in Prince William Sound, Alaska underwent a dramatic decline during the 30-year period from 1979 to 2008 (Kuletz and Oakley 1996, Bixler 2010). The sub-population of guillemots nesting at the Naked Island Group began to increase for the first time since 1979 following the trapping and removal of introduced American mink (*Neovison vison*), as part of efforts to restore this sub-population to historical levels. As part of this restoration effort, I monitored the response of guillemots to the removal of mink at the Naked Island Group during the 2012-2018 breeding seasons. Results from my study showed that the guillemot sub-population nesting at the Naked Island Group began to grow immediately and substantially following the initiation of mink removal efforts in 2014, while the numbers of guillemots nesting at nearby mink-free control islands continued to increase slowly. Following mink removal at the Naked Island Group, I also documented an increase in the number of active guillemot nests, an increase in guillemot nestling survival rates, and the return of nesting guillemots to some nest sites vulnerable to land-based predators.

Although guillemots nesting at the Naked Island Group are also subject to bottom-up factors that limit nesting success, such as local prey availability, my study design evaluated the response of guillemots to the removal of mink while controlling for inter-annual changes in foraging conditions near the islands. Comparison of the rates of change in guillemot numbers at the Naked Island Group before and after mink removal supported my primary hypothesis that predation by mink on pigeon guillemots attempting to nest at the Naked Island Group was the primary limiting factor for the recovery of this sub-population of pigeon guillemots. Further supporting the hypothesis were the increases in guillemot nest abundance, nest success, and

use of nest substrates that are accessible to land-based predators at the Naked Island Group. Alone, each of these additional findings does not provide proof of cause and effect; however, in combination they provide a clear picture of a recovering sub-population of guillemots that is no longer subject to intense nest predation by mink. The continued growth and recovery of this sub-population following the removal of mink would make an important contribution toward restoring the overall population of pigeon guillemots in Prince William Sound.

Although the removal of mink has initiated the recovery of guillemots at the Naked Island Group, my research was conducted in a complex natural system and there were some unexpected results from my study. I expected and found that mink removal at the Naked Island Group lead to increased nesting success for pigeon guillemots due to decreased predation on eggs and nestlings. My expectation was that this increase in guillemot productivity would subsequently result in an increase in numbers of nesting guillemots over an extended period following improvements in nesting success. Pigeon guillemots, like many other long-lived seabirds, have delayed maturation and typically attempt to nest for the first time when they are 3-5 years old (Ewins 1993). Based on this life history trait, I expected at least a 3-5 year delay in the recruitment of breeding guillemots to the Naked Island Group following mink removal.

Contrary to my expectations, I observed a rapid increase in the total number of guillemots present at the Naked Island Group during the pre-breeding period, as well as an increase in the number of guillemots nesting there following the first year of mink trapping. This increase in the number of guillemots and active guillemot nests the first year following the initiation of mink removal suggests that prospecting adult guillemots quickly detected the change in local nesting success and immigrated to the Naked Island Group from other nearby

nesting areas. During the course of my fieldwork, I observed on several occasions adult guillemots carrying prey in their bills that departed the Naked Island Group and flew toward other nearby islands, suggesting that guillemots nesting at nearby islands were collecting information about guillemot nesting colonies and forage fish resources at the Naked Island Group. Furthermore, I noted a large spike in guillemot attendance at nesting colonies in the Naked Island Group during the chick-rearing period, suggesting that prospecting adults were evaluating potential nest sites and the contents of active nests, as has been observed for black guillemots (*C. grylle*; Ewins 1985). This peak in attendance also suggests that guillemots that were not prospecting at the Naked Island Group during the pre-breeding season were prospecting and gathering information on local nesting success during the chick-rearing period. Adult guillemots likely gain this information by way of interactions with conspecifics, as has been observed in other seabirds (Votier et al. 2010). This information gathering may result in some individuals enhancing their fitness by immigrating to higher quality nesting habitat soon after it becomes available.

Guillemots prospecting for nest sites at the Naked Island Group were able to detect the increased nesting success following the removal of mink and may have been motivated to immigrate there because there was a small remnant population of nesting guillemots that had persisted despite the high nest predation rates preceding mink removal. The introduction of non-native predators to seabird nesting islands has, in many cases, resulted in the complete extirpation of ground-nesting birds (Vitousek 1988). Once extirpated, these islands are frequently not recolonized even once the predator is removed due to the absence of conspecifics providing evidence of secure nesting habitat and risk aversion by individuals that

could potentially re-establish a nesting population (Forbes and Kaiser 1994, Parker et al. 2007, Munilla et al. 2016). The presence of even a few active and successful guillemot nests likely provided prospecting conspecifics with evidence of suitable nesting habitat following mink removal and acted as a nucleus near which breeding adults recruited and colonies grew. Without these social cues, it is unlikely that guillemot numbers would have rebounded as soon or as rapidly. Guillemot colonies at nearby islands in central Prince William Sound likely provided sources for recruits to bolster the immediate growth of the guillemot sub-population at the Naked Island Group and expedite its initial recovery.

As guillemots recolonized the Naked Island Group following the removal of mink, I found that there was an increase in the use of historical nest sites in substrates vulnerable to land-based predators, such as cliff-top burrows and crevices in talus at the base of coastal cliffs. When mink were present at the Naked Island Group, these two nest site types were apparently more accessible to mink than cliff-face nest sites, which likely resulted in decreased use by nesting guillemots of nest sites accessible to mink due to heavy predation pressure. Following mink removal, this trend was reversed, although not entirely along the lines with my expectations; guillemots only started to re-occupy one of the two nest site types that were vulnerable to mink predation. My results showed an increase in the use of cliff-top burrow nest sites following mink removal, but very limited use of talus nest sites; by the last year of this study burrow nest sites represented 46% of active guillemot nests, while talus nest sites represented only 2% of active guillemot nests. Prior to mink establishment at the Naked Island Group, 40% of monitored guillemot nests were located in cliff-top burrow nest sites, while 24% were located in talus nest sites (Kuletz 1983).

The limited use of talus nest sites even before mink were well-established at the Naked Island Group suggests that guillemots nested more frequently in cliff-top burrows and cliff face crevices than in talus crevices, even in the absence of predation pressure from introduced mink. This preference for burrow and cliff face nest sites over talus nest sites at the Naked Island Group was likely driven by the native assemblage of nest predators before mink introduction. Northwest crows (*Corvus caurinus*), common ravens (*Corvus corax*), black-billed magpies (*Pica hudsonia*) and river otters (*Lontra canadensis*) are all known to depredate guillemot nests (Emms and Verbeek 1989, Ewins 1993), and were all historically present at the Naked Island Group (Kuletz 1983, Bixler 2010).

This native suit of predators may still reduce the relative quality of talus nest sites despite the removal of American mink. Trail cameras deployed at a small number of opportunistically selected nests (n = 6) showed corvids investigating the entrances to guillemot nests containing young nestlings. Despite being undefended by adult guillemots, none of these nests failed due to depredation, which suggests that nest predation by corvids is limited by the depth and accessibility of crevice entrances, and not by the ability of corvids to locate active guillemot nests. Predation by river otters may also discourage guillemots from nesting in talus substrate locations. River otters are common at the Naked Island Group and they forage primarily in the inter-tidal and sub-tidal zones in the nearshore environment (Melquist et al. 2003). They frequent talus habitat for defecating, socializing, and resting. While seabird eggs may not be an important component of otter diets, their use of similar habitats would put them in regular contact with guillemot nests located in talus. Accessibility of guillemot nests located in talus to a suite of predators may make these nest sites less secure for nesting guillemots. It is

possible that guillemots use talus nest sites only when nest sites for guillemots are limited and more secure nest substrates are unavailable.

In addition to a faster than expected increase in the number of guillemots and a lower than expected use of talus nest sites, I also observed unexpectedly high growth rates in guillemot nestlings post-mink removal. Average guillemot chick growth rate during the 2017 nesting season was the highest recorded during any year when growth rates were measured at the Naked Island Group between 1979 and 2017. Based on the observed guillemot chick growth rates, local foraging conditions for nesting guillemots during my study were likely more favorable compared to the period post-Exxon Valdez oil spill (EVOS), when mink were well-established at the Naked Island Group (1989-2008). Previous studies of guillemots nesting at the Naked Island Group have linked decreased prevalence of high-lipid forage fishes in the diet of guillemots following EVOS with decreased chick growth rates and lower nesting success (Oakley and Kuletz 1996, Golet et al. 2002). During the present study, I also detected higher chick meal delivery rates compared to the period when mink were well-established on the Naked Island Group. I noted that guillemot chicks in two-chick broods had similar growth rates, indicating that food availability was sufficient for adults to adequately provision both chicks in 2-chick broods and suggesting that foraging conditions were favorable for guillemots during 2017.

Guillemot chick growth rates can serve as an umbrella indicator for the availability of forage fish to guillemots provisioning their young and sheds light on local foraging conditions (Cairns 1987, Kuletz 1996, Golet et al. 2000). While valuable as an overall assessment of the status of food availability, it does not provide any specific indication of what factors may have

caused the unusually high rates of chick growth that I observed in 2017. Factors including availability of high-lipid forage fish (Golet et al. 2000), reduced competition for prey resources with conspecifics (Dann and Norman 2006), distance to high-quality foraging areas, and carry-over effects of winter foraging conditions on adult condition pre-breeding (Sorenson et al 2009) can all impact chick growth rates. While I did not measure any of these factors directly, I was able to measure meal delivery rates and the percentage of prey items delivered to nests that are considered high-quality prey. Chick meal delivery rates in pigeon guillemots have been linked to prey availability (Litzow and Piatt 2003), while chick diet composition has been linked to the relative availability of high-quality prey (Golet et al. 2002). Both of these factors provide more insight into what may have caused the unusually high chick growth rates that I observed in 2017.

Average nestling meal delivery rates at the Naked Island Group during the 2016-2018 nesting seasons were higher than both the period prior to the establishment of mink and the period when mink were well-established on the Naked Island Group. This may be the result of increased availability of nearshore demersal forage fish during the present study due to major declines in the size of the guillemot sub-population nesting at the Naked Island Group during the 1990s and 2000s (Bixler 2010). The reduction in guillemot abundance likely reduced competition for nearshore demersal forage fishes, a major prey resource for guillemots, in a density-dependent manner (Ashmole 1963, Cairns 1987). Litzow and Piatt (2003) found that the highest nestling meal delivery rates by guillemots were observed in areas where they fed primarily on nearshore demersal fishes in years when these prey types were highly available. The observed decrease in the Prince William Sound guillemot population during the 1990s and

2000s also likely resulted in reduced commuting times to foraging areas (Lewis et al. 2001, Burke and Montevecchi 2009), further reducing the parental effort required for higher chick meal delivery rates. The high rates of nestling meal deliveries observed during the present study likely indicate an increase in the availability of prey and contributed to the high guillemot nestling growth rates measured in 2017.

In addition to increased nestling meal delivery rates, I also observed changes in the composition of the chick diet during my study. Prey items that guillemots delivered to nests during the 2016 and 2017 breeding season consisted of 17% and 38% high-lipid prey types (i.e. sand lance, herring, capelin), respectively. Although diet composition in the two years differed considerably, my observations were consistent with the high inter-annual variability observed during earlier studies of guillemot diet at the Naked Island Group (Kuletz 1983, Golet et al. 2000). Because of the high natural variability in the diet composition of pigeon guillemots at the Naked Island Group, I was not able to detect a significant difference in diet composition during the present study compared with the diet of guillemots following EVOS.

Despite the lack of a statistically significant difference between the diet composition of pigeon guillemots at the Naked Island Group pre- and post-mink removal, a biologically important change in the diet of guillemots nesting at the Naked Island Group appears to have taken place since diet composition was last measured in 2008. During the first breeding season following EVOS the diet composition of guillemots still contained 40% high-lipid fish (Oakley and Kuletz 1996) and, during the same year, herring returns from the commercial fishery in Prince William Sound were also relatively unaffected by the oil spill. In the following years, however, both the herring fishery and the proportion of high-lipid prey in guillemot diets declined

appreciably (Golet et al. 2002, Thorne and Thomas 2007). The time lag between the oil spill and the decline in availability of high-lipid forage fishes has been attributed to the toxic effects of oil contamination on larval fishes and eggs (McGurk and Brown 1996). The relatively low proportion of high-lipid schooling fishes in guillemot diets persisted at the Naked Island Group at least until the mid-1990s (Golet et al. 2000). During this time only an average of 10-12% of meal deliveries to guillemot nests consisted of high-lipid prey types. By 1995, high-lipid prey types had increased to between 19% and 30% of the guillemot diet (Golet et al. 2002), where it remained in 2008 (Bixler 2010). Chick meals delivered to guillemot nests at the Naked Island Group in 2017 had the highest proportion of high-lipid prey types since 1989 (Oakley and Kuletz 1996). Conversely, the proportion of high-lipid prey types in 2016 was the lowest recorded since 1994. While this inter-annual variability in guillemot diet composition makes any trend in the availability of high-lipid forage fish less clear, it is likely that foraging conditions for guillemots nesting at the Naked Island Group have improved compared to the decade following EVOS.

Further evidence for the increasing availability of high-quality forage fish for guillemots at the Naked Island Group during my study period was provided by the similarity in the growth rates between alpha and beta chicks in 2017. Such similarity in growth rates between nest mates in 2-chick broods has been shown to be correlated with favorable conditions for guillemot foraging that include either diets consisting mostly of high-lipid prey (Golet et al. 2000) or overall increases in prey availability (Ainley et al. 1990). At the Farallon Islands, growth rates of alpha and beta chicks in pigeon guillemot nests were more similar during years when upwelling resulted in increased abundance of juvenile rockfish and subsequent high guillemot

nesting success (Ainley et al. 1990). Guillemot nests at the Naked Island Group where a greater proportion of high-lipid forage fish were delivered also had more similar growth rates for alpha and beta chicks than nests where low-lipid forage fish were delivered (Golet et al. 2000). The high rates of chick growth that I observed in 2017 were likely the result of the combination of high meal delivery rates to chicks and the greater proportion of high-lipid prey in chick diets during the 2017 breeding season.

The high rates of chick growth, high meal delivery rates, improvements in diet composition, and similarity in growth rates of alpha and beta chicks all suggest that foraging conditions have improved in Prince William Sound form the period following the EVOS. This is in concurrence with the gradual increase in population size we observed at control islands during this study. This increase further supports my conclusion that foraging conditions are conducive to continued growth of the Naked Island Group guillemot sub-population and the Prince William Sound guillemot population at large.

My study was able to detect a significant effect of mink removal on the numbers of pigeon guillemots at the Naked Island Group, while controlling for the potential effects of bottom-up factors by surveying for changes in guillemot numbers at nearby islands where mink were not present. This evidence, as well as increases in numbers of active nests, nesting success, and distribution of nesting guillemots at the Naked Island Group following mink removal, all support my conclusion that mink predation has been removed as the primary limiting factor to the growth of the guillemot sub-population. In addition to the release from mink predation, increases in guillemot abundance at control islands, chick growth rates, availability forage fish prey, and the proportion of high-lipid prey in the diet measured during

my study all suggest that foraging conditions for pigeon guillemots in central Prince William Sound have improved since the 1990s, and are more favorable for guillemot nestling survival (Graves 1984) and overall productivity (Golet et al. 2000). Based on both the elimination of mink predation and improved foraging conditions, the guillemot sub-population at the Naked Island Group should grow intrinsically after the pool of potential immigrants from other nearby islands has been exhausted. The removal of mink from the Naked Island Group combined with enhanced forage fish availability to guillemots position this guillemot sub-population to continue its recovery and eventually contribute to the recovery of the regional population of pigeon guillemots in Prince William Sound.

Methodological Recommendations

When designing a study using a Before-After, Control-Impact (BACI) study design, the control group and the experimental group are usually expected to be similar during the period prior to the application of the treatment and differ after the treatment is applied to the experimental group. In this study, however, the starting state of my experimental group was a population of guillemots in the presence of mink and my control islands were mink free throughout my study. This meant that it was actually the period after the treatment of mink removal was applied to experimental group that the control and the experimental group were under similar conditions. This means my BACI study was effectively backwards, with the before treatment period at the experimental group effectively taking the place of the after treatment.

We choose control islands that were free of mink as no islands with mink in Prince William Sound support populations of guillemots comparable to the Naked Island Group. This is likely because the arrival of predators on island colonies of seabirds often results in their

complete extirpation (Towns et al. 2011). This may have been the case at the Naked Island Group in the next decade if mink removal intervention had not taken place. Future studies should consider using control islands where introduced predators are present and not removed, if available. If unavailable, it is important to recognize that the role of the before and after period may be reversed when analyzing data using a BACI study design.

An additional challenge of my BACI study design, was its reliance on very small sample sizes of guillemot surveys, especially at the control islands. Further, the three large islands that comprise the Naked Island Group do not function as independent survey units due to their close proximity. Because guillemots can easily and quickly move between the three main islands in the Naked Island Group, my ability to designate biologically meaningful survey subunits within the two treatment groups was impaired. As such, it was necessary for me to pool counts from individual islands in annual pre-breeding surveys within both the mink-removal (Impact) group and the Control group. This reduced both sample sizes and statistical power to distinguish a difference between control and treatment islands. Future studies would gain substantial statistical power by identifying biologically meaningful sub-units for surveys within the study area and monitoring the numbers of guillemots in each sub-unit.

For any future studies of pigeon guillemots in this study area, once sampling sub-units have been identified at the Naked Island Group, I recommend using similar criteria for designating sub-units in the control group. In this study, I included multiple islands within a single island group in the treatment group and multiple islands within multiple island groups in the control group. This difference in sampling design precluded any use of mixed-models to investigate the closer relationships between islands within a group. Despite an extremely small

sample size, I was nevertheless able to detect a statistically significant effect of mink removal on trends in guillemot numbers at the Naked Island Group. This was due to the dramatic and immediate response of guillemots to mink removal, but such a rapid response should not be expected in all situations. Without the movement of guillemots from other colonies in Prince William Sound to the Naked Island Group, I would likely not have been able to detect a difference in population trends pre- and post-mink removal. If future studies maintain a similar sampling scheme between treatment and control groups, they may be able to avoid pooling counts within island groups and thereby enhance sample size and the power to detect differences in population trends.

Based on my results, I recommend that future efforts to evaluate the effectiveness of predator removal at seabird colonies consider the availability of source populations of birds that may immigrate to the predator removal site when designing monitoring protocols. If a source population of adult seabirds is available and predator removal is efficient, some responses to predator removal may be expected to occur within a year or two. If a small number of remnant breeders is expected to grow the population through intrinsic recruitment alone, however, then a time lag on the population level response should be expected as young birds raised post-predator removal grow to reproductive age and recruit into the local breeding population. As many seabird restoration projects are limited by funding and monitoring is frequently difficult and expensive, it may behoove researchers to delay monitoring until sufficient time has elapsed so that an intrinsic population-level response can be expected. Because it is important to establish a baseline in order to evaluate the effects of management actions, monitoring should began prior to the application of predator removal. Following

predator removal, it may be more cost-effective to delay monitoring for several years in order to detect the intrinsic effect of predator removal on the target seabird population.

Management Implications

While those interested in and entrusted with seabird conservation do not have the power to manipulate climatic and oceanographic shifts due to human activity, nesting habitat can be restored through removal of introduced predators, as demonstrated by my study. Predator removal is an important, practical, and effective tool for the restoration of seabird colonies. While it may not be effective in restoring all colonial nesting seabirds, this study provides additional evidence of a seabird species and a set of historical and environmental circumstances when predator removal has proven successful.

My study also demonstrates the importance of remnant breeders and nearby colonies of nesting seabirds to drive short-term recovery of historical seabird nesting colonies following predator removal. The few pairs of pigeon guillemots still nesting at the Naked Island Group likely provided information to prospecting adult guillemots of improved nesting success following mink removal. When considering conducting predator removal to restore nesting habitat for seabirds, choosing sites where at least a few nesting seabirds remain and there is a source of immigrants from other nearby colonies may bolster the immediate recovery of the target seabird population.

Literature Cited

Ainley, D. G., R. J. Boekelheide, S. H. Morrell, and C. S. Strong. 1990. Pigeon Guillemot. Pages 276–305 *in* Seabirds of the Farallon Islands, D. G. Ainley and R. J. Boekelheide (eds.). Stanford University Press, Stanford, California.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458-473.

Bixler, K. S. 2010. Why aren't pigeon guillemots in Prince William Sound, Alaska recovering from the *Exxon Valdez* oil spill? Unpubl. M.Sc. thesis, Oregon State University, Corvallis, OR. 161 pp.

Burke, C. M., and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. Journal of Zoology 278: 354-361.

Cairns, D. K. 1987. The ecology and energetics of chick provisioning by black guillemots. Condor 89: 627-635.

Dann, P. and F.I. Norman. 2006. Population regulation in little penguins (*Eudyptula minor*): the role of intraspecific competition for nesting sites and food during breeding. EMU-Austral Ornithology 106: 289-296.

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.

Ewins, P. J. 1985. Colony attendance and censusing of Black Guillemots *Cepphus grylle* in Shetland. Bird Study 32: 176-185.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). A. Poole and F. Gill (Eds.). The Birds of North America Online. d.oi:10.2173/bna.49.

Forbes, L. S., and G. W. Kaiser. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. Oikos 70: 377–384.

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.

Graves, S. 1984. Chick growth, sibling rivalry, and chick production in American black oystercatchers. Auk 101: 525-531.

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

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.

McGurk, M. D. and E. D. Brown. Egg larval mortality of Pacific herring in Prince William Sound, Alaska after the Exxon Valdez oil spill. Canadian Journal of Fisheries and Aquatic Sciences 53: 2343-2354.

Melquist, W. E., P. R. Polechla, Jr, and D. Toweill. 2003. River otter (*Lontra canadensis*). Pp. 708-734 *in* Wild mammals of North America: biology, management, and conservation, 2nd ed. Feldhamer, G. A., B. C. Thompson, and J. A. Chapman (Eds.). Johns Hopkins University Press, Baltimore, Maryland.

Munilla, I., M. Genovart, V. H. Paiva, and A. Velando. 2016. Colony foundation in an oceanic seabird. PLoS ONE 1:2. e0147222. https://doi.org/10.1371/journal.pone.0147222

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.

Parker, M. W., S. W. Kress, R. T. Golightly, H. R. Carter, E. B. Parsons, S. E. Schubel, J. A. Boyce, G. J. McChesney, and S. M. Wisely. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. Waterbirds 30: 17–28.

Sorensen, M. C., J. M. Hipfner, T. K. Kyser, and D. R. Norris. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. Journal of Animal Ecology 78: 460-467.

Thorne, R. E., and G. L. Thomas. 2008. Herring and the "Exxon Valdez" oil spill: an investigation into historical data conflicts. *ICES Journal of Marine Science* 65: 44–50.

Towns, D. R., G. V. Byrd, H. P. Jones, M. J. Rauzon, J. C. Russel, and C. Wilcox. 2011. Impacts of introduced predators on seabirds. Pp. 58-90 *in* Seabird islands: ecology, invasion, and restoration. C. P. H. Mulder, D. R. Towns, W. B. Anderson, and P. J. Bellingham (eds.). Oxford University Press, Oxford, England.

Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. Pp. 181 – 189 *in* Biodiversity. Wilson, E. O. (Ed.). National Academy Press, Washington, D.C.

Votier, S. C., G. W. James, S. Patrick, and J. Newton. 2010. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Marine Biology 158: 355-362.

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. 1990. Seabirds of the Farallon Islands: ecology, dynamics, and structure of an upwelling-system community. Stanford University Press, Stanford, USA.

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. Variation in lipid content of forage fishes and its effect on energy provisioning rates to seabird nestlings. Journal of Experimental Marine Biology 248: 53-78.

Ashmole, N. P. 1963. The regulation of numbers of tropical oceanic birds. Ibis 103: 458-473.

Barraquand, F., T. T. Hoye, J. A. Henden, N. G. Yoccoz, O. Gilg, N. M. Schmidt, B. Sittler, and R. A. Ims. 2014. Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and arctic lemmings. Journal of Animal Ecology 83: 375-387.

Barrett, R. T. 2002. Atlantic puffin *Fratercula arctica* and common guillemot *Uria aalge* chick diet and growth as indicators of fish stocks in the Barents Sea. Marine Ecology Progress Series 230: 275-287.

Birkhead, T. R., and D. N. Nettleship. 1995. Arctic fox influence on a seabird community in Labrador: a natural experiment. Wilson Bulletin 107: 397- 412.

Bixler, K. S. 2010. Why aren't pigeon guillemots in Prince William Sound, Alaska recovering from the *Exxon Valdez* oil spill? Unpubl. M.Sc. thesis, Oregon State University, Corvallis, OR. 161 pp.

Bright, C. 1998. Life out of bounds: bioinvasion in a borderless world. W.W. Norton Company, New York, USA.

Burke, C. M., and W. A. Montevecchi. 2009. The foraging decisions of a central place foraging seabird in response to fluctuations in local prey conditions. Journal of Zoology 278: 354-361.

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

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.

Cairns, D. K. 1987. The ecology and energetics of chick provisioning by black guillemots. Condor 89: 627-635.

Carls, M. G., G. D. Marty, and J. E. Hose. 2002. Synthesis of the toxicological impacts of the *Exxon Valdez* oil spill on Pacific herring (*Clupea pallasi*) in Prince William Sound, Alaska, U.S.A. Canadian Journal of Fisheries and Aquatic Sciences 59: 153-172.

Cushing, D. A., D. D. Roby, and D. B. Irons. 2017. Patterns of distribution, abundance, and change over time in a subarctic marine bird community. Deep-Sea Research II http://dx.doi.org/10.1016/j.dsr2.2017.07.012

Danchin, E., T. Boulinier, and M. Massot. 1998. Conspecific reproductive success and breeding habitat selection: implications for the study of coloniality. Ecology 79: 2415–2428.

Dann, P. and F.I. Norman. 2006. Population regulation in little penguins (*Eudyptula minor*): the role of intraspecific competition for nesting sites and food during breeding. EMU-Austral Ornithology 106: 289-296.

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

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.

Ewins, P. J. 1985. Colony attendance and censusing of Black Guillemots *Cepphus grylle* in Shetland. Bird Study 32: 176-185.

Ewins, P. J. 1993. Pigeon Guillemot (*Cepphus columba*). Edited by A. Poole and F. Gill. The Birds of North America Online. d.oi:10.2173/bna.49.

Exxon Valdez Oil Spill Trustee Council (EVOSTC). 2009. About us. Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/index.cfm?FA=aboutUs.home

Exxon Valdez Oil Spill Trustee Council (EVOSTC). 2014. Injured Resources and Services: 2014 Update. Unpublished report by the Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/static/PDFs/2014IRSUpdate.pdf

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. Final Report to the U.S. Fish and Wildlife Service, Migratory Bird Office, Anchorage, Alaska. 51 pp.

Forbes, L. S., and G. W. Kaiser. 1994. Habitat choice in breeding seabirds: when to cross the information barrier. Oikos 70: 377–384.

Francis, R. C., S. R. Hare, A. B. Hollowed, and W. S. Wooster. 2003. Effects of interdecadal climate variability on the oceanic ecosystems of the NE Pacific. Fisheries Oceanography 7: 1-21.

Gerell, R. 1967. Dispersal and acclimatization of the mink (*Mustela vison*) in Sweden. Viltrevy 4: 1-38.

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.

Graves, S. 1984. Chick growth, sibling rivalry, and chick production in American black oystercatchers. Auk 101: 525-531.

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.

Irons, D. B., and D. D. Roby. 2007. Pigeon guillemot restoration research in Prince William Sound, Alaska. Unpublished research proposal to the Exxon Valdez Oil Spill Trustee Council. Available at http://www.evostc.state.ak.us/Store/Proposal_Documents/2190.pdf

Irons, D. B., and D. D. Roby. 2014. Pigeon guillemot restoration research in Prince William Sound, Alaska, FY14 amendment. Project 11100853. Proposal to the Exxon Valdez Trustee Council. Available at: http://www.evostc.state.ak.us/Store/Proposal_Documents/2322.pdf

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.

Isleib, M. E., 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.

Kokko, H., and W. J. Sutherland. 1998. Optimal floating and queuing strategies: consequences for density dependence and habitat loss. American Naturalist 152: 354-366.

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

Kuletz, K. J., C. S. Nations, B. Manly, A. Allyn, D. B. Irons, and A. McKnight. 2011. Distribution, abundance, and population trends of Kittlitz's murrelet *Brachyramphus brevirostris* in Prince William Sound, Alaska. Marine Ornithology 39: 97–109.

Lack, D. L. 1968. Ecological adaptations for breeding in birds. Methuen Publishing, London, England.

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., J. F. Piatt, and J. D. Figurski. 1997. Hermit crabs in the diet of Pigeon Guillemots at Kachemak Bay, Alaska. Colonial Waterbirds 21: 242-244.

Litzow, M. A., J. F. Piatt, and J. D. Figurski. 1998. Hermit crabs in the diet of Pigeon Guillemots at Kachemak Bay, Alaska. Colonial Waterbirds 21: 242-244.

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. 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.

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.

Maccarone, A. D., and W. A. Montevecchi. 1981. Predation and caching of seabirds by red fox (*Vulpes vulpes*) on Baccalieu Island, Newfoundland. Canadian Field-Naturalist 95: 352-353.

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

McCullough, D., and R. H. Barrett. 2012. Wildlife 2001: Populations. Springer Science & Business Media, Berlin, Germany.

McDonald, T.L., W.P. Erikson, and L.L. McDonald. 2000. Analysis of count data from before-after control-impact studies. Journal of Agricultural, Biological, and Environmental Statistics. 5: 262-279.

McGurk, M. D., and E. D. Brown. 1996. Egg-larval mortality of Pacific herring in Prince William Sound, Alaska, after the Exxon Valdez oil spill. Canadian Journal of Fisheries and Aquatic Science 53: 2343-2354.

Melquist, W. E., P. R. Polechla, Jr, and D. Toweill. 2003. River otter (*Lontra canadensis*). Pp. 708-734 *in* Wild mammals of North America: biology, management, and conservation, 2nd ed. Feldhamer, G. A., B. C. Thompson, and J. A. Chapman (eds.). Johns Hopkins University Press, Baltimore, Maryland.

Munilla, I., M. Genovart, V. H. Paiva, and A. Velando. 2016. Colony foundation in an oceanic seabird. PLoS ONE 1:2. e0147222. https://doi.org/10.1371/journal.pone.0147222

Nelson, D. A. 1982. The communication behavior of the Pigeon Guillemot *Cepphus columba*. Unpubl. Ph.D. dissertation, University of Michigan, Ann Arbor, Michigan.

Nordstrom, M., J. Hogmander, J. Nummelin, N. Laanetu, and E. Korpimaki. 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. 1981. Determinants of population size of Pigeon Guillemots *Cepphus columba* at Naked Island, Prince William Sound, Alaska. Unpubl. M.Sc. thesis, University of Alaska, Fairbanks. Fairbanks, Alaska. 82 pp.

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.

Parker, M. W., S. W. Kress, R. T. Golightly, H. R. Carter, E. B. Parsons, S. E. Schubel, J. A. Boyce, G. J. McChesney, and S. M. Wisely. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. Waterbirds 30: 17–28.

Peterson, C. H., S. D. Rice, J. W. Short, D. Esler, J. L. Bodkin, B. E. Ballachey, and D. B. Irons. 2003. Long-term ecosystem response to the Exxon Valdez oil spill. Science 302: 2082-2086.

Piatt, J. F., 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, 2nd edition. Duxbury Press, Pacific Grove, California.

Russell, R. W. 1999. Comparative demography and life history tactics of seabirds: implications for conservation and marine monitoring. Pp. 51-76 *in* Life in the slow lane: ecology and conservation of long-lived marine animals. J. A. Musick (ed.). Symposium 23, American Fisheries Society, Bethesda, Maryland.

Sæther, B., and Ø. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology 81: 642-653.

Sanger, G. A., and M. B. Cody. 1994. Survey of Pigeon Guillemot colonies in Prince William Sound, Alaska. Restoration Project 93034. Exxon Valdez Oil Spill Restoration Project Final Report. PB--96-194808/XAB. U.S. Fish and Wildlife Service, Anchorage, AK.

Shabecoff, P. 1989, March 25. Exxon vessel hits reef, fouling water that is rich in marine life. The New York Times, 1, 42.

Smith, E. P. 2014. BACI Design. Wiley StatsRef: Statistics Reference Online. Edited by N. Balakrishnan, T. Colton, B. Everitt, W. Piegorsch, F. Ruggeri and J.L. Teugels. Available at: https://doi.org/10.1002/9781118445112.stat07659. Accessed December 16, 2019.

Sorensen, M. C., J. M. Hipfner, T. K. Kyser, and D. R. Norris. 2009. Carry-over effects in a Pacific seabird: stable isotope evidence that pre-breeding diet quality influences reproductive success. Journal of Animal Ecology 78: 460-467.

Spatz, D. R., K. M. Newton, R. Heinz, B. Tershy, N. D. Holmes, S. H. M. Butchart, and D. A. Croll. 2014. The biogeography of globally threatened seabirds and island conservation opportunities. Conservation Biology 28: 1282-1290.

Suryan, R. M., D. B. Irons, M. Kaufman, J. Benson, P. G. R. Jodice, D. D. Roby, and E. D. Brown. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the black-legged kittiwake *Rissa tridactyla.* Marine Ecological Progress Series 236: 273-287.

Thorne, R. E., and G. L. Thomas. 2008. Herring and the “Exxon Valdez” oil spill: an investigation into historical data conflicts. *ICES Journal of Marine Science* 65: 44–50.

Towns, D. R., G. V. Byrd, H. P. Jones, M. J. Rauzon, J. C. Russel, and C. Wilcox. 2011. Impacts of introduced predators on seabirds. Pp. 58-90 *in* Seabird islands: ecology, invasion, and restoration. C. P. H. Mulder, D. R. Towns, W. B. Anderson, and P. J. Bellingham (eds.). Oxford University Press, Oxford, England.

Underwood, A. J. 1992. Beyond BACI: the detection of environmental impacts on populations in the real, but variable, world. Journal of Experimental Marine Biology and Ecology 161: 145-178.

Van Pelt, T. I., J. F. Piatt, B. K. Lance, and D. D. Roby. 1997. Proximate composition and energy density of some North Pacific forage fishes. Comparative Biochemistry and Physiology 119: 1–6.

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.

———. 1993b. Nesting biology and predation of Pigeon Guillemots in the Queen Charlotte Islands, British Columbia. Colonial Waterbirds 16: 119–127.

Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. Pp. 181 – 189 *in* Biodiversity. Wilson, E. O. (ed.). National Academy Press, Washington, D.C.

Votier, S. C., G. W. James, S. Patrick, and J. Newton. 2010. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. Marine Biology 158: 355-362.

Whitworth, D. L., H. R. Carter, and F. Gress. 2013. Recovery of a threatened seabird after eradication of an introduced predator: Eight years of progress for Scripps's murrelet at Anacapa Island, California. Biological Conservation 162: 52-59.