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Predation by Mink Prevented Recovery of Pigeon Guillemots (*Cepphus columba*) After the *Exxon Valdez* Oil Spill in Prince William Sound, Alaska

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Abstract.—Pigeon Guillemot (*Cepphus columba*) populations in Prince William Sound, Alaska, USA were damaged by the 1989 *Exxon Valdez* oil spill, with no sign of recovery after 20 years. The continued decline was unexpected because by 2004 there was no evidence of direct exposure to residual oil. The large guillemot population nesting at the Naked Island Group in central Prince William Sound declined by 12% per year during 1990–2008 but was stable at nearby islands. Mortality rates for eggs and chicks at the Naked Island Group increased after the spill, largely due to introduced American mink (*Neovison vison*). Prevalence of lipid-rich fish in the diet of chicks at the Naked Island Group in 2008 was similar to post-spill levels, but lipid-rich fish abundance from aerial surveys was greater in 2008 than after the spill. Evidence suggests that, although residual oil impacted guillemots and their prey for at least a decade post-spill, mink predation gradually became the primary limiting factor at the Naked Island Group during the late 1990s and into the 2000s. The magnitude and persistence of guillemot declines at the Naked Island Group indicate that this population is unlikely to recover without management to reduce predation from non-indigenous mink. *Received 13 May 2024, accepted 13 Nov 2024.*

Key words.—diet composition, forage fish, introduced predator, nesting habitat, nest success, oil spill damage, population decline, seabird restoration

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Despite the continued degradation of coastal marine ecosystems across the globe (Hoffmann *et al.* 2010; McCauley *et al.* 2015; Bugnot *et al.* 2021), notable conservation successes and even large-scale recovery have occurred for a number of marine animals following timely and effective interventions (see Duarte *et al.* 2020). However, successful interventions depend upon understanding factors that cause population declines and prevent recovery (Lotze *et al.* 2006). Evaluation of these factors is complicated by multiple stressors acting in concert, with new threats emerging and their relative importance changing through time (McCauley *et al.* 2015; O'Hara *et al.* 2021).

Seabirds are particularly sensitive to changes in marine ecosystems, with nearly one half of all species experiencing population declines (Dias *et al.* 2019). In waters of Alaska, USA, where approximately 20% of all seabird species have been recorded (Smith *et al.* 2014), seabird populations have been impacted by multiple stressors over the last half century, including invasive predators (Ebbert and Byrd 2002; Byrd *et al.* 2005; Towns *et al.* 2011), effects of regime shifts and climate change on ocean conditions (Anderson and Piatt 1999; Goyert *et al.* 2018; Litzow *et al.* 2020), and oil spills (Peterson *et al.* 2003; Esler *et al.* 2018). Invasive species, primarily mammals, are considered the single greatest threat to seabirds globally (Dias *et al.* 2019) and seabird mammalian predators, mostly foxes (*Alopex lagopus* and *Vulpes vulpes*), were intentionally introduced to several hundred islands in Alaska from the late 18th to the mid-20th century to supply the fur trade (Ebbert and Byrd 2002). These introductions caused rapid and persistent declines in seabird populations (Ebbert and Byrd 2002), especially for species that nest in accessible habitats (Byrd *et al.* 2005). In many cases, eradication of introduced predators has resulted in rapid population responses by impacted seabirds (Ebbert and Byrd 2002).

A major regime shift occurred in the ecosystem of the northeastern Pacific Ocean in 1976, from a negative (cool) phase to a positive (warm) phase in the Pacific Decadal Oscillation

(PDO; Anderson and Piatt 1999). This led to major changes in marine ecosystem structure and function in the northern Gulf of Alaska, including long-term reductions in lipid-rich schooling forage fishes (e.g., Pacific herring [*Clupea pallasii*] and capelin [*Mallotus villosus*]), and subsequent population declines in multiple species of piscivorous seabirds (Anderson and Piatt 1999). Forage fish stocks and several populations of their predators have yet to recover to pre-regime shift levels (Agler *et al.* 1999; Cushing *et al.* 2018), apparently due to persistent climate warming and its impact on ocean conditions (Goyert *et al.* 2018; Litzow *et al.* 2020).

More recently, the grounding of the T/V *Exxon Valdez* in March 1989 resulted in 42 million liters of crude oil spilling into Prince William Sound (hereafter, PWS), Alaska, killing an estimated 250,000 seabirds during the acute oiling event (Piatt and Ford 1996). Chronic exposure to oil that lingered in the system and reductions in prey abundance continued to impact seabirds for at least a decade after the spill (Golet *et al.* 2002; Esler *et al.* 2018). Of marine bird species damaged by the spill, the Pigeon Guillemot (*Cepphus columba*) is one of just two species that have not yet recovered (Esler *et al.* 2018; Kaler and Irons 2023). Although the global threat status of Pigeon Guillemots is "Least Concern" and the population is considered stable, estimates of population size and trends are based on poor quality and incomplete data (Birdlife International 2024). The majority of the world-wide population of Pigeon Guillemots (hereafter, guillemots) nests in Alaska (Ewins 1993), and PWS is the only location in Alaska where a long-term, systematic dataset for the species is available (DBI, pers. obs.). Consequently, estimates of population trends and evaluation of potential drivers are of value, not just for informing oil spill damage assessment and recovery strategies, but also for identifying factors that may regulate guillemot populations elsewhere.

The *Exxon Valdez* oil spill (EVOS) caused the immediate mortality of 500–1,500 guillemots (Piatt *et al.* 1990). In July 1989, 4 months after EVOS, the estimated breeding population of guillemots in PWS was 4,000 individuals (McKnight *et al.* 2008). At that time, about one quarter of all guillemots nesting throughout PWS were located at the Naked Island Group in central PWS (McKnight *et al.* 2008). Numbers of guillemots in PWS declined by an additional 41% from July 1989 to July 2012, after the acute mortality event caused by EVOS (Cushing *et al.* 2018). Elevated levels of hepatic cytochrome P4501A, a detoxification enzyme that was the most reliable indicator of exposure to residual oil in guillemots (Trust *et al.* 2000), indicated that they were still exposed to residual oil from the EVOS a decade after the spill (Seiser *et al.* 2000; Golet *et al.* 2002). By 2004, however, there was no longer evidence that guillemots sampled in PWS were directly exposed to residual oil from the spill (Esler *et al.* 2018). Despite no evidence for direct exposure to residual oil after 1999, the guillemot population in PWS continued to decline over the subsequent two decades (*Exxon Valdez* Oil Spill Trustee Council 2014; Cushing *et al.* 2018; Kaler and Irons 2023). Chronic impacts to guillemot health after the period when individuals were directly exposed to oil have not been studied (Esler *et al.* 2018).

Concurrent with the direct and indirect impacts of EVOS on the guillemot population in PWS, changes in prey availability apparently drove a longer-term guillemot population decline in PWS, from an estimated 15,500 individuals in 1972 (95% CI = ±5,100 individuals; Agler *et al.* 1999) to about 2,100 in 2007 (95% CI = ±650 individuals; McKnight *et al.* 2008). One proposed explanation for the continued lack of recovery by guillemots in PWS nearly 20 years post-spill was a reduction in the abundance of food, specifically lipid-rich schooling forage fishes. This could have been due to either the impact of residual oil from the spill, long-term disruption of the food web from the PDO regime shift, or some combination of the two (Agler *et al.* 1999; Golet *et al.* 2002). The proportion of lipid-rich schooling forage fishes in the diet of guillemot nestlings at the Naked Island Group declined following EVOS, and the proportion of those prey types in their diets had significant positive effects on both chick growth rates and overall reproductive success (Golet *et al.* 2000, 2002).

A second possible explanation for the failure of the guillemot population to recover from EVOS was an increase in predation rates on guillemot nests at the Naked Island Group (Hayes 1996; Oakley and Kuletz 1996; Golet *et al.* 2002). Across 12 nesting seasons prior to 1999, guillemot nest productivity at the Naked Island Group was found to be significantly negatively related to nest predation rate (Golet *et al.* 2002). Known nest predators for guillemots at the Naked Island Group included several avian predators, such as Black-billed Magpies (*Pica hudsonia*), American (Northwestern) Crows (*Corvus brachyrhynchos*), and Common Ravens (*Corvus corax*); as well as mammalian predators, such as river otters (*Lontra canadensis*), and American mink (*Neovison vison*; Hayes 1996; Oakley and Kuletz 1979, 1996). In particular, mink predation rates on guillemot nests increased appreciably at the Naked Island Group during the 1990s (Hayes 1996; Oakley and Kuletz 1996; Golet *et al.* 2002). Furthermore, genetic evidence (Fleming and Cook 2010) and interviews with local fur trappers (DBI, unpubl. data) indicated that mink were introduced by trappers to the Naked Island Group during the 1970s and did not previously occur there.

The goal of our study, conducted in 2007 and 2008, was to determine why, almost 20 years after the *Exxon Valdez* oil spill, a damaged and formerly large breeding population of guillemots at the Naked Island Group had not recovered, and instead continued to decline precipitously. We investigated two potential factors that may have prevented population recovery of guillemots at the Naked Island Group following the apparent cessation of exposure to spilled oil in the early to mid-2000s: food availability (bottom-up control) and nest predation (top-down control; Suryan *et al.* 2006). To do this, we collected data at the Naked Island Group during 2007 and 2008 on (1) whether mink were present on each of the three main islands at the Naked Island Group; (2) the numbers of nesting guillemots and nest site use; (3) rates of guillemot chick predation and overall mortality; (4) abundance of lipid-rich schooling forage fishes in adjacent waters; and (5) diet composition and growth performance of guillemot chicks (Table 1). In addition, we collected data at the Smith Islands, 11 km to the south of the Naked Island Group, and Fool Island, 23 km to the west of the Naked Island Group for comparison because guillemots have historically nested on these islands and continued to nest at high densities compared to

Table 1. Summary of datasets and years collected by location in central Prince William Sound, Alaska, USA between 1978 and 2008. Locations include Naked Island Group (A), Smith Island Group (B), and Fool Island (C). Data were collected both before (1978-1981) and after (1989-2008) the *Exxon Valdez* oil spill (EVOS) in March 1989. Abundance of lipid-rich fish was measured in surface area density (SAD) and catch per unit effort (CPUE).

	Pre-EVOS				Post-EVOS												
Dataset	1978	1979	1980	1981	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2007	2008
Mink presence/ absence																	A, B, C
Number of adults						A, B	A, B	A, B	A, B	A, B	A, B	A, B				A, B	A, B
Number of nests													A				A, C
Mortality of eggs, chicks	A	A	A	A	A	A				A	A	A	A	A	A		A, C
Nest site type	A																A
SAD lipid-rich fish														A, B	A, B		A, B
CPUE lipid-rich fish												A	A				A
% lipid-rich fish in chick diet		A	A	A	A	A				A	A	A	A	A	A		A, C
Chick growth index	A			A		A				A	A	A	A	A	A		A, C

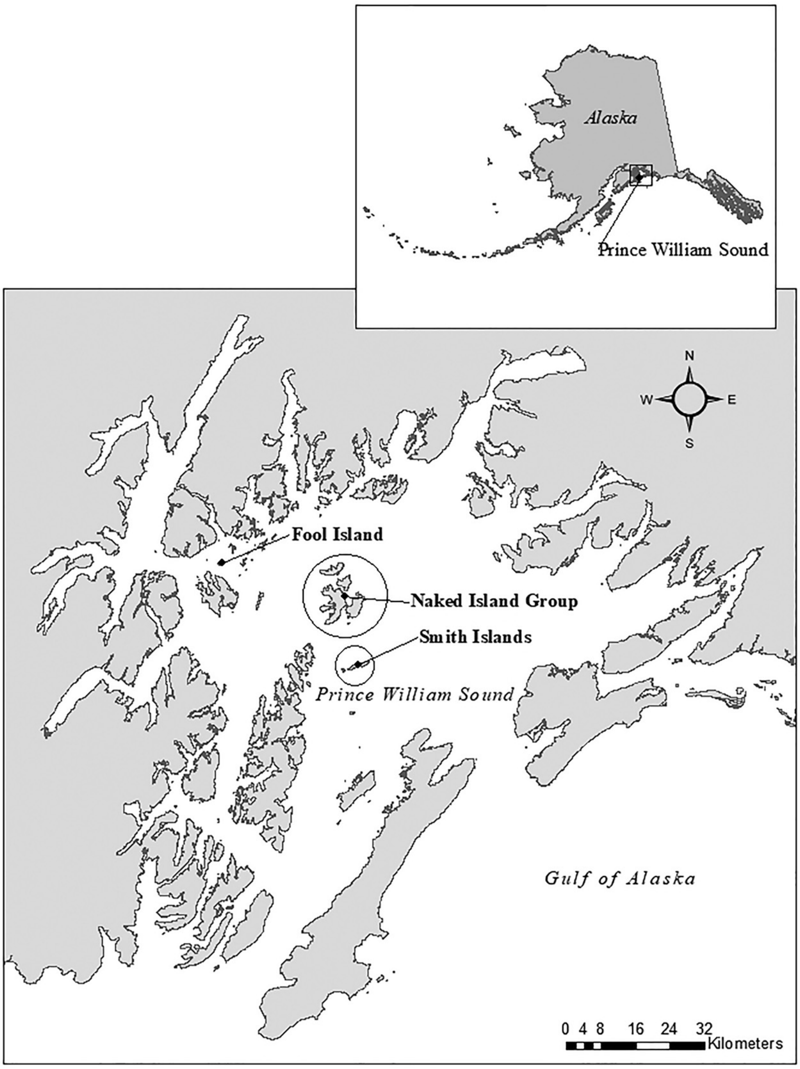

Figure 1. Location of Prince William Sound within Alaska, USA (upper box) and the locations of the Naked Island Group, the Smith Islands, and Fool Island within Prince William Sound (lower box).

the Naked Island Group (Fig. 1; Table 1). We also compared our results to studies conducted in the same areas during 1978–1981 and 1989–1999 (Table 1; Kuletz 1983; Oakley and Kuletz 1996; Golet *et al.* 2002).

METHODS

Study Area

Prince William Sound is a complex fjord-estuarine system with about 5,000 km of coastline, high levels of freshwater input, and bathymetry ranging from shallow glacial moraines and tidal flats to deep fjords and basins (maximum depth > 800 m; Niebauer *et al.* 1994; Vaughan *et al.* 2001). Guillemots are widely distributed throughout PWS during the breeding season, which extends from late May to late August. The Naked Island Group, our primary study area, is located in central PWS and includes three main islands: Naked, Storey, and Peak. We collected data on guillemots at the Naked Island Group, the Smith Islands (Smith Island and Little Smith Island) and Fool Island in 2007 and 2008 (Fig. 1). Kuletz (1983), Oakley and Kuletz (1996), and Golet *et al.* (2002) collected similar data at the Naked Island Group and the Smith Islands during 1978–1981, 1984, and 1989–1999.

Surveys and Measurements

Presence/Absence of Mink. To assess whether mink were present on all six studied islands in 2008, we set lethal Conibear® 110 and 120 traps inside black plastic

Table 2. Number of traps, trap density, and trapping effort for study islands in central Prince William Sound, Alaska, USA during 2008 to determine presence/absence of American mink (*Neovison vison*).

Location	Traps set (number)	Effort (trap nights)	Shoreline length (km)	Density (traps/km)	Mink captured
Fool Island	6	174	1.8	3.3	0
Little Smith Island	3	90	2.7	1.1	0
Smith Island	10	300	12.7	0.8	0
Storey Island	21	42	17.5	1.2	2
Peak Island	7	14	14.2	0.5	5
Naked Island	124	323	72.8	1.7	22

motor route newspaper tubes, baited with herring and ground beaver castor lure, just above high tide line along the shoreline. Traps were checked once per day or as weather conditions permitted and total trapping effort at each island was determined by the number and length of beaches, travel time to trap sites, and weather (Table 2). We assumed that an island was mink-free for the duration of the study if no mink were captured during the trapping effort.

Guillemot Numbers and Nest Site Use. We conducted nearshore boat-based surveys to assess guillemot numbers along the entire shorelines of Naked, Storey, Peak, Smith, and Little Smith islands. Surveys were conducted between 04:00 hr and 10:00 hr, between 24 May and 6 June during 1990–1996 and 2007–2008. We surveyed during early morning high tides in the pre-laying stage, when guillemot colony attendance is least variable (Vermeer *et al.* 1993a). Surveys were conducted at speeds of 10–20 km/h from either 3.7-m inflatable boats or 7.7-m skiffs traveling 100 m from shore. Two observers counted guillemots on the water or flying within 100 m on either side of, ahead of, and above the vessel, as well as on the shoreline rocks and cliffs. We limited surveys to periods of good conditions for observation, when wave heights were less than 0.6 m, but usually when wave heights were less than 0.3 m. Surveys were not conducted when rain and/or fog significantly reduced visibility.

We attempted to locate all active guillemot nests throughout the Naked Island Group and at Fool Island during the chick-rearing stage (late June–early August) in 2008. We found nests opportunistically during boat-based surveys by observing parental behavior. Adults were conspicuous because they frequently staged in the water below the nest prior to entering the nest crevice. Because there were so few active nests, we confirmed activity by accessing nests after observing deliveries of prey items to the nest crevice to minimize the risk of nest abandonment. Where the crevice or nest was not accessible, due to either location, depth, or shape of the crevice, we confirmed nests were active by observing repeated deliveries of prey items (nestling meals), indicating the presence of at least one nestling. In contrast, in 1997, observers counted and accessed most of the active guillemot nests at 19 colonies across Naked and Storey islands during the incubation and chick-rearing stages (May–August; GHG, unpubl. data).

In 2008 we described and classified active guillemot nest sites at the Naked Island Group into three types, following Oakley and Kuletz (1979): talus, cliff face, and cliff top. Talus nest sites were located amidst rocks or boulders at the base of or on a wide ledge of a cliff and the nest chamber was often relatively close to the surface. Cliff face nest sites were on a cliff and varied from nests in narrow cracks extending several meters into a cliff face to nests on a narrow cliff ledge concealed by vegetation. Cliff top nest sites were at the top of a cliff or steep rocky bank, usually at the end of a burrow in soil, often among tree roots, and usually the nest chamber was a meter or more back from the entrance. Oakley and Kuletz (1979) conducted a comparable survey of active guillemot nest sites on the Naked Island Group in 1978.

Predation and Overall Mortality of Guillemot Eggs and Chicks. In 2008 we monitored the contents of active guillemot nests during the chick-rearing stage at the Naked Island Group and at Fool Island until either fledging or nest failure using methods employed at the Naked Island Group during 12 years between 1978 and 1999 (Oakley and Kuletz 1996; Golet *et al.* 2000). To determine overall chick mortality rates, we checked nest contents at least twice during the nestling period and monitored nest activity (prey deliveries) more frequently, no more than five days apart. Eggs or chicks were assumed to be depredated if they disappeared prior to hatching/fledging or if found with signs of predation (e.g., puncture wounds, partially consumed). The cause of a nest failure was "other" if we found dead chicks in the nest without signs of predation. Chicks were considered fledged if they survived until at least 30 days post-hatch. We removed eggs and chicks from the analysis if observers were unsure of their fate. Researchers were unable to distinguish between scavenged and depredated nest contents. There may have been a small number of incorrectly assigned fates; eggs or chicks may have disappeared from their nest for reasons other than predation or chicks may have been depredated late in the chick-rearing period and assumed to have fledged. Consequently, chick mortality rates were estimates; however, methods of assigning mortality were consistent across all periods of study.

During 2008, we checked nest contents only during the chick-rearing stage, and this along with small sample size (Hensler and Nichols 1981) precluded any statistical

Table 3. Average and standard deviation (SD) of effort per aerial survey and number (*n*) of aerial surveys completed during 1998, 1999, and 2008 to estimate abundance of lipid-rich schooling forage fish at the Naked Island Group and the Smith Islands in central Prince William Sound, Alaska, USA. Data courtesy of E. D. Brown.

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

comparison with data from previous years. Similar to previously published studies of guillemots at the Naked Island Group (Golet *et al.* 2000, 2002), the present study reports causes of guillemot egg and/or chick mortality (as opposed to overall productivity [chicks fledged/eggs laid] and rate of nest predation).

Abundance of Lipid-rich Schooling Forage Fishes. The relative abundance of lipid-rich schooling forage fishes in central PWS was measured during the guillemot chick-rearing period in July and August of 1998, 1999, and 2008 by E. Brown (Flying Fish, Ltd). Each survey included a strip transect about 455 m wide and < 1 km from shore encircling Naked, Peak, Storey, Smith, and Little Smith islands. The surveyor counted schools of forage fish within the upper 20 m of the water column and measured the horizontal surface area of each school. This yielded an estimate of surface area density (m^2/km^2) of schooling forage fish in the survey area. Methods are described in detail by Brown and Moreland (2000), Ainley *et al.* (2003), and Suryan *et al.* (2006). The effort per survey was similar across all three years, although the total number of surveys completed in each year differed (Table 3).

Aerial surveys are an appropriate method to assess the relative abundance of both Pacific sand lance (*Ammodytes personatus*) and juvenile Pacific herring in PWS because they are primary guillemot prey types and guillemots are largely associated with nearshore water (< 1 km from shore; Kuletz 1983; Robards and Piatt 1999; Norcross *et al.* 2001). Aerial survey data provide an index of sand lance and juvenile herring density but cannot be converted to a biomass estimate without a measure of depth distribution. Our abundance index does not include schools at depths > 20 m, and thus underestimates what is potentially available to foraging guillemots.

We also measured the relative abundance of nearshore lipid-rich forage fishes at Naked Island based on catch per unit effort (CPUE) of sand lance and herring in beach seine nets during the 1996, 1997, and 2008 nesting seasons (GHG, unpubl. data). We seined opportunistically during each nestling-rearing period, within 1.5 hrs of low tide, at three beaches located close to historical guillemot breeding colonies. We used 3.7-m inflatable boats to set the 37-m variable-mesh net, measuring 0.5 m wide at the ends and 2.4 m wide in the center with a 6-mm mesh bunt, parallel to shore.

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

Diet Composition and Growth Performance of Guillemot Chicks. We estimated the diet composition of guillemots during the chick-rearing period in 2008 at the Naked Island Group by identifying prey items brought to the nest by adults, a method used to collect comparable data during 11 years between 1979 and 1999 at Naked Island. In 2008, diet composition was also estimated at Fool Island. Observers in either a small anchored skiff or an onshore blind identified individual prey items using binoculars or spotting scopes. Guillemot prey items, which are held crosswise in the bill, were identified to species, if feasible, but otherwise the most detailed taxonomic group possible. We grouped items into larger categories consisting of either lipid-rich schooling forage fishes (i.e. Pacific sand lance, Pacific herring, and smelt [Osmeridae, including capelin]) or low-lipid demersal fishes, including cods (Gadidae), pricklebacks (Stichaeidae), gunnels (Pholidae), ronquils (Bathymasteridae), sculpins (Cottidae), rockfish (*Sebastes* spp.), greenling (*Hexagrammos* spp.), and salmon (*Oncorhynchus* spp.). Lipid-rich schooling forage fish generally have energy densities in the range of 6–8 kJ/g fresh mass, while low-lipid demersal fish have energy densities generally less than 5 kJ/g (Anthony *et al.* 2000). We identified at least 10 prey items delivered to each active nest over several days to avoid bias due to short-term prey preferences and to represent chick diet composition over a range of chick ages (8–30 days post-hatch).

We developed an index of guillemot chick growth performance based on measurements of nestling body mass and wing chord length. We measured total body mass (g) and flattened wing chord (mm) of each accessible guillemot nestling in monitored nests at the Naked Island Group and at Fool Island in 2008, using methods employed during 1978, 1981, 1990, and 1994–1999 at Naked Island (Golet *et al.* 2000). Chicks were measured during the linear phase of growth, generally between 8 and 18 days post-hatch (Emms and Verbeek 1991; Ewins 1993; Golet *et al.* 2000). We then calculated an index of chick growth performance based on the residuals of the regression of chick body mass on chick wing chord length (Benson *et al.* 2003). Chicks with a positive residual had put on mass at a higher rate than average for a chick their age, while those with a negative residual had put on mass at a lower rate than average for a chick their age.

Statistical Analysis

We used multiple linear regression analysis to test for differences in guillemot population trends between islands with and without mink (Ramsey and Schafer 2002). To meet assumptions of normality and equal variance, we log-transformed the response variable (number of guillemots counted). We estimated the odds of a nest receiving a lipid-rich, schooling prey item (sand lance, herring, or smelt) rather than a low-lipid, demersal prey item between years and between locations (Naked Island Group vs. Fool Island) using logistic regression. We performed a one-way analysis of variance followed by a Tukey post hoc test to compare chick growth indices across time periods (1978–1981, 1989–1999, and 2008).

Due to small sample sizes, we performed permutation tests to compare (1) chick growth indices at the Naked Island Group vs. Fool Island in 2008; (2) overall egg/chick mortality rates, mortality caused by predation, and mortality due to other causes between time periods on Naked Island; and (3) the number of active guillemot nests assigned to each nest site category between 1978 and 2008 on Naked Island (Ramsey and Schafer 2002). We also used permutation tests to compare the surface area density of fish (as measured during aerial surveys) between 1998–1999 and 2008 for both the Naked Island Group and the Smith Islands, and to compare these two island groups in 2008. We used a Wilcoxon Rank Sum test with normal approximation and continuity correction (Ramsey and Schafer 2002) to compare the surface area density of fish between 1998 and 1999 for both island groups, as well as between island groups during 1998–1999. We pooled surface area density data from 1998 and 1999 at the Naked Island Group and at the Smith Islands because they were not significantly different ($z = 0.99$, $P = 0.32$ and $z = -0.38$, $P = 0.70$, respectively). We used permutation tests to assess the spatial and temporal differences in CPUE of lipid-rich forage fish caught per beach seine haul. Data on the CPUE from seine hauls in 1996 and 1997 were pooled because there was no difference between years ($z = 0.81$, $P = 0.54$). There were also no differences in CPUE of lipid-rich forage fish among months (June, July, and August) ($\chi^2 = 0.37$, $P = 0.86$) or among beach seine sites ($\chi^2 = 1.26$, $P = 0.57$); therefore, these explanatory variables were not included in further analyses.

All tests were two-tailed and when multiple comparisons were completed, Bonferroni corrected. Results were considered statistically significant if $P \leq 0.05$ and marginally significant if $0.05 < P \leq 0.10$. All analyses were conducted using SAS 9.2 software (SAS Institute 2008).

RESULTS

Presence/Absence of Mink

We set traps for mink between 28 April and 28 May 2008 at an average frequency of 1.5 traps/km of shoreline on each island. We caught mink on Naked, Storey, and Peak islands, the three main islands in the Naked Island Group, in 2008 (Tables 1, 2). We did not catch mink on Smith, Little Smith, or Fool islands in 2008 despite high trapping effort; therefore, we concluded that mink were not present on those islands. Average trapping effort was 126 trap nights/island at islands where mink were captured and 165 trap nights/island where mink were not captured.

Guillemot Numbers and Nest Site Use

The total number of guillemots counted at the Naked Island Group (Naked, Storey, and Peak islands; mink present) during the pre-breeding season declined from 1,124 individuals in 1990 to 101 individuals in 2008, a decline of 91%. The median rate of change in guillemot population size at the three main islands in the Naked Island Group was a decline of 12% per year between 1990 and 2008 (95% CI = −13% to −11%, $t = -19.83$, $P < 0.0001$; Fig. 2). The median rate of change in guillemot population size at the two nearby Smith Islands (Smith and Little Smith islands; mink absent) was not different than zero during this period ($t = -0.52$, $P = 0.61$; estimated annual change = −0.4%, 95% CI = −2.0–1.2%), indicating a stable guillemot population. The difference between the Naked Island Group and the Smith Islands in the annual rate of change in guillemot population size was highly significant ($t = 15.03$, $P < 0.001$).

Along with the total number of guillemots, the number of active guillemot nests also declined at the Naked Island Group from the 1990s to 2008. Despite intensive,

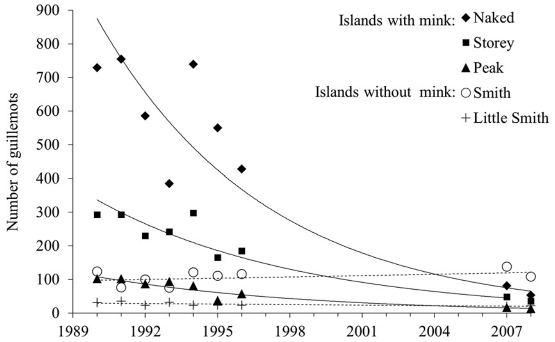

Figure 2. Size of local Pigeon Guillemot breeding populations at islands with mink (Naked, Storey, and Peak islands) and islands without mink (Smith and Little Smith islands) between 1990 and 2008 in central Prince William Sound, Alaska, USA.

systematic searches throughout the shoreline of the Naked Island Group in 2008, we found only 17 active guillemot nests: 8 nests on Storey Island, 2 on Peak Island, and 7 on Naked Island. Because guillemot nests are cryptic, the number of nests found was a minimum estimate of the number of active nests present, but we are confident that we found nearly all active nests that survived to the chick-rearing period. Adults observed loafing on the water adjacent to or flying towards or away from potential nesting habitat were conspicuous, especially when holding fish, and all such observations were thoroughly and repeatedly investigated throughout the breeding season. Some additional active nests may not have been discovered because they failed during the incubation period. We estimated that as many as five additional active guillemot nests may have been present but undetected, based on observations of adult guillemots loafing on the water adjacent to potential nesting habitat. Although there were no attempts to count the total number of guillemot nests across the entire Naked Island Group before 2008, observers counted 114 active nests in 19 colonies on Naked and Storey islands in 1997 (GHG, unpubl. data). We found only four active guillemot nests along the same shoreline areas in 2008, a 96.5% decline from 1997.

We found 18 active guillemot nests at Fool Island in 2008, and there may have been as many as five more active nests that were not confirmed, based on the number of adult guillemots seen loafing near potential nesting habitat. Although the number of guillemot nests found at Fool Island was similar to the number found at the Naked Island Group in 2008, the density of guillemot nests at Fool Island (10 nests/km of shoreline) was more than 140 times greater than at the Naked Island Group (0.07 nests/km). All entrances to guillemot nests were accessible to researchers, but due to deep, complex burrows, mostly in cracked granite cliffs, the nest contents were confirmed in just 28% of active nests.

At the Naked Island Group, we observed a proportionately greater decline between 1978 and 2008 in the number of guillemot nests in talus compared to on cliff faces (P = 0.003; Table 4). There was also a proportionately greater decline in the number of nests in cliff tops compared to on cliff faces between 1978 and 2008 (P = 0.005). There was no difference in the proportionate decline in nests in talus compared to cliff tops (P = 1.00). In 2008, 76% of active guillemot nest sites and their contents were accessible to observers, whereas in 1997 approximately 94% of active nest sites were accessible and nest contents were confirmed in 88% of nest sites. This decline in accessibility is consistent with guillemots selecting nest sites less accessible to mink in 2008 compared to 1997.

Predation and Overall Mortality of Guillemot Eggs and Chicks

The mortality rate of guillemot chicks at the Naked Island Group in 2008 (n = 22 individual chicks monitored in 12 nests) was 31.8%. Most (86%) of this chick mortality

Table 4. Number and percent of Pigeon Guillemot nests in different nest site types at the Naked Island Group, Prince William Sound, Alaska, USA in 1978 and 2008. Guillemot nests were classified as one of three types: (1) cliff face, located in a rock crevice on a cliff face; (2) cliff top, in overhanging soil at a cliff top; and (3) talus, under boulders at the base of a cliff or amidst rocks on a broad cliff ledge.

	1978		2008	
Nest type	Number	Percent	Number	Percent
Cliff face	52	35.6%	15	88.2%
Cliff top	58	39.7%	2	11.8%
Talus	36	24.7%	0	0.0%

was due to predation. Mink predation was confirmed through necropsy as the cause of chick mortality at the Naked Island Group in two cases by Alaska Veterinary Pathology Services (unpubl. data), despite the extremely low number of active guillemot nests.

These results represent a minimum estimate of mortality for 2008 because they do not include mortality during the egg stage and, in several cases, early in the chick-rearing stage. The percentage of all chicks that died due to predation in 2008 was similar to that of the mean annual percentage of eggs and chicks that were depredated during 1989–1999 and 6.7 times greater than the mean annual percentage of eggs and chicks depredated during 1978–1984. We found no dead adult guillemots in nests at the Naked Island Group during 2008. We also discovered no evidence of guillemot chick or adult mortality at Fool Island in 2008, although the sample of monitored guillemot chicks was small ($n = 7$).

The mean annual mortality rate for guillemot eggs and chicks at the Naked Island Group increased from 41% during 1978–1981 to 65% during 1989–1999 ($P = 0.001$; Fig. 3). The predation rate on guillemot eggs and chicks increased from 4% in 1978–1981 to 38% in 1989–1999 ($P = 0.001$). The rate of egg and chick mortality due to causes other than predation was similar in 1978–1981 and 1989–1999 ($P = 0.15$; 37% and 27%, respectively). During 1989–1999, the majority (62.6%) of all egg and chick mortality was due to predation.

Researchers found carcasses of adult guillemots in the nest with signs of depredation for the first time in 1996 (D. L. Hayes, U.S. Fish and Wildlife Service, unpubl. data). During that breeding season, a dead adult was found in 5% of monitored nests. Depredated adults were found in 0%, 9%, and 4% of monitored nests in 1997, 1998, and 1999, respectively (GHG, unpubl. data).

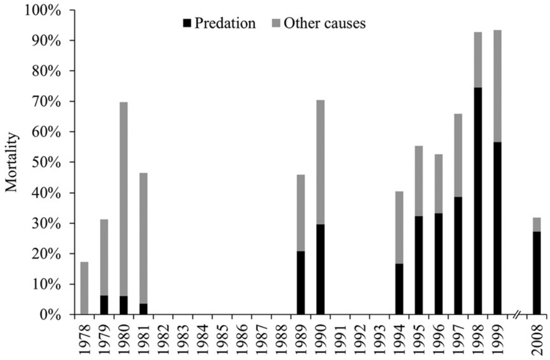

Figure 3. Percent mortality of Pigeon Guillemot eggs and chicks caused by predation and other factors for nests monitored between 1978 and 1999 at the Naked Island Group, central Prince William Sound, Alaska, USA. Eggs and chicks were considered depredated if they disappeared prior to hatching/fledging or if found with signs of predation (e.g., puncture wounds, partially consumed). The cause of nest failure was recorded as "other" if chicks were found dead in the nest crevice without signs of predation. In 2008 nest contents were checked only during the chick-rearing phase and percent mortality includes chicks only.

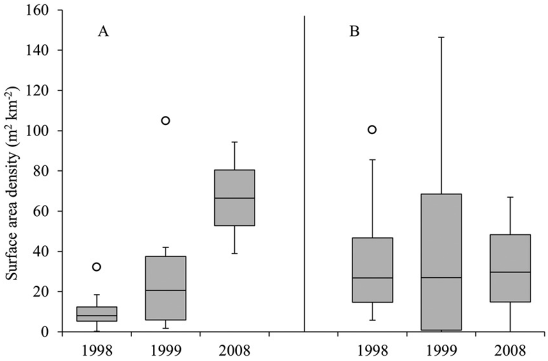

Figure 4. Boxplots of surface area density (m^2 km^{-2}) of lipid-rich schooling fishes visible during aerial surveys at (A) the Naked Island Group and (B) the Smith Islands in central Prince William Sound, Alaska, USA during July–August in 1998, 1999, and 2008. Boxplots show median values (horizontal line), first and third quartile (box outline), values between the third quartile and 1.5 times the interquartile range (whiskers), and outlier values (open circles). Data courtesy of E. D. Brown.

Abundance of Lipid-rich Schooling Forage Fish

Measurements of surface area density of schooling forage fish during aerial surveys demonstrated that there were more schooling forage fish in the waters near the Naked Island Group in 2008 compared with 1998–1999 ($s = 62.0$, $P = 0.01$; Fig. 4). At the Smith Islands, however, 11 km to the south, the abundance of schooling forage fish did not change ($s = 30.5$, $P = 0.73$).

We collected beach-seined samples of lipid-rich schooling forage fish between 4 June and 17 August in 2008 ($n = 14$) during the guillemot chick-rearing period; beach seine samples in 1996 ($n = 7$) and 1997 ($n = 3$ samples) were also collected during this date range. We caught a total of 355 lipid-rich schooling forage fish in 14 beach seine hauls in 2008, compared with 108 lipid-rich schooling forage fish captured in 10 beach seine hauls during 1996 and 1997 (GHG, unpubl. data). The median CPUE of lipid-rich forage fish was 0.5 in 1996–1997 (range = 0–85 fish) and 13.5 in 2008 (range = 0–103 fish), a 26-fold increase. Despite this difference in average CPUE, the difference between 1996–1997 and 2008 was not statistically significant ($z = -1.12$, $P = 0.27$) because of small sample sizes and high variability in CPUE among beach-seined samples.

Diet Composition and Growth Performance of Guillemot Chicks

We identified a mean of 33.1 prey items delivered to each active guillemot nest in 2008 (range = 10–163). The odds that a guillemot chick received a lipid-rich forage fish at Naked Island during 1979–1981 (pre-EVOS) was 3.4 times greater (95% CI = 2.2 to 5.3 times; Wald $\chi^2 = 29.10$, $P < 0.001$) than during 1989–1999 (post-EVOS) and 4.6 times greater (95% CI = 1.5 to 14.0 times; Wald $\chi^2 = 6.98$, $P = 0.01$) than in 2008 (Fig. 5). There was no difference between 2008 and 1989–1999 (Wald $\chi^2 = 0.25$, $P = 0.62$) in the odds that a chick received a lipid-rich forage fish. In 2008, the odds that a chick received a lipid-rich fish was 7.2 times greater (95% CI = 2.6 to 20 times; Wald $\chi^2 = 14.45$, $P < 0.001$) at Fool Island (mink absent) than at the Naked Island Group (mink present).

There was no difference in the index of growth performance of guillemot chicks from the Naked Island Group in 2008 compared to chicks from the Naked Island Group during 1990–1999 (post-EVOS; $t = -0.71$, $P = 0.90$) or during 1978–1981 (pre-EVOS; $t = 1.62$, $P = 0.37$). Also, there was no difference in the growth performance index of chicks between the Naked Island Group (mink present) and Fool Island (mink absent) in 2008 ($t = 0.58$, $P = 0.94$; Fig. 6).

DISCUSSION

The guillemot breeding population at the Naked Island Group showed no sign of recovery from the *Exxon Valdez* oil spill by

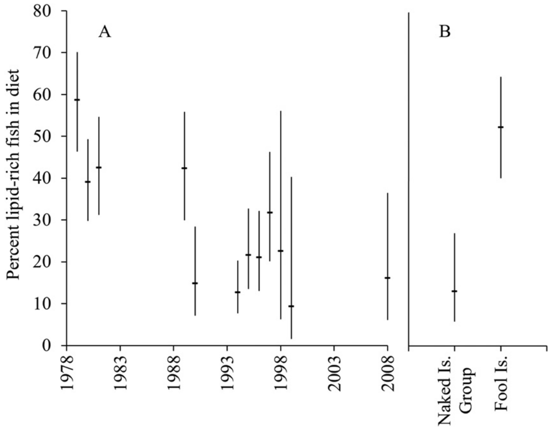

Figure 5. The mean and 95% confidence interval of the proportion of prey delivered to Pigeon Guillemot nests that were lipid-rich schooling forage fishes (i.e. sand lance, herring, and smelt spp.) at A) Naked Island in 1979–1981 (before the *Exxon Valdez* oil spill), 1989–1990, 1994–1999 (after the *Exxon Valdez* oil spill), and 2008; and B) the Naked Island Group and Fool Island in 2008.

2008, 19 years after the spill. Instead, numbers of breeding guillemots at the Naked Island Group continued to decline and were very low compared to pre-spill (1978–1981) or post-spill (1990–1999) population levels. We found evidence of a shift in the relative importance of factors contributing to population decline since the oil spill. Ingestion of weathered crude oil had apparently ceased by 15 years after the spill; cytochrome P4501A, a mixed function oxidase induced by crude oil consumption, was no longer elevated in guillemots sampled in 2004 (Esler *et al.* 2018). We found evidence of recovery in the abundance of lipid-rich forage fish at the Naked Island Group in 2008, at least relative to the 1990s. The proportion of lipid-rich fish in the guillemot diet and guillemot chick growth performance, however, had not increased in 2008 compared to the 1990s. Nevertheless, the mortality of guillemot chicks not attributable to predation was very low in 2008. This suggests that while foraging conditions for guillemots at the Naked Island Group had not returned to pre-spill levels by 2008, prey availability was sufficient to support nesting success.

Mink predation rates on guillemot nests (Golet *et al.* 2002) and nesting adults (GHG, unpubl. data) were high in the late 1990s compared to pre-EVOS. The mortality rate of guillemot chicks attributable to predation at the Naked Island Group remained high

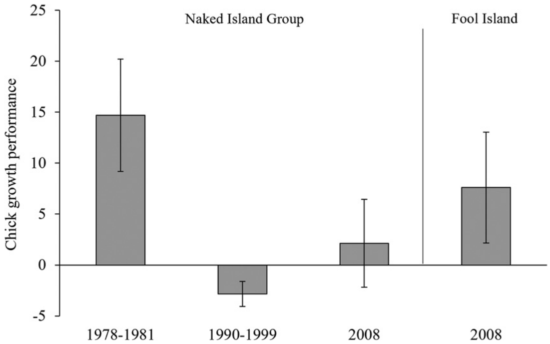

Figure 6. Chick growth performance indices for Pigeon Guillemots in Prince William Sound, Alaska, USA based on one-time measurements of body mass and wing chord length during the linear growth phase (8 to 18 days post-hatch) at the Naked Island Group in 1978–1981, 1990–1999, and 2008, and at Fool Island in 2008. Chick growth performance indices are the residuals of the regression of body mass on wing chord length, presented as the percent of predicted body mass. Bars represent the mean (± 1 standard error) chick growth performance.

in 2008, and the few remaining active guillemot nests were located in less accessible nest sites, indicating that predation pressure on guillemot nests also remained high. Together with the rapid decline in the guillemot breeding population and the very low numbers of nesting guillemots remaining in 2008, we surmise that mink predation gradually became the primary factor preventing population recovery at the Naked Island Group. This inference is supported by the presence of mink during the crash of the guillemot breeding population at the Naked Island Group compared to the absence of mink and a stable guillemot breeding population at the nearby Smith Islands during 1990–2008. We conclude that predation by introduced mink was key to the divergent population trends on the two island groups. As further support for the high relative impact of mink predation on guillemot productivity at the Naked Island Group in 2008, we detected no guillemot chick mortality at monitored nests on Fool Island ($n = 5$); this despite the presence of the same suite of nest predators as at the Naked Island Group with one exception: mink. All guillemot nests found on Fool Island in 2008 were considered readily accessible to mink had they been present.

Mink were present but quite rare at the Naked Island Group during 1978–1981, about 10 years before EVOS (K. Kuletz, U.S. Fish and Wildlife Service, unpubl. data). This is consistent with information obtained from local residents that mink were introduced by one fur-trapper over a period of years during the 1970s in order to establish a trappable population (DBI, unpubl. data). A genetic study of mink from the Naked Island Group revealed that the population possessed genes from eastern North American populations, and concluded the mink released on the Naked Island Group were descended in part from non-native fur farm stock (Fleming and Cook 2010).

Predation on guillemot eggs and chicks at the Naked Island Group grew from negligible during 1978–1981 to approximately two thirds of all mortality during the 1990s. Golet *et al.* (2002) found that overall guillemot productivity at the Naked Island Group was highly correlated with the rate of nest predation. An unknown portion of depredated eggs and chicks were depredated by predators other than mink, but researchers noted when mink sign (e.g., scat, tooth puncture marks) were present in remains; thus, estimates of mink predation rates on guillemot nests are likely minimums. The highest predation rate on guillemot nests at the Naked Island Group was recorded in 1998, when 82% of monitored guillemot nests ($n = 66$) were depredated and at least 60% of monitored nests were depredated by mink (GHG, unpubl. data). Also in 1998, adult guillemots were found depredated by mink inside or near the nest crevice at 9% of all monitored nests (GHG, unpubl. data). Compared to other breeding colonies of this species, this magnitude of predation is high (Ewins 1993; Vermeer *et al.* 1993b). Predation on adult guillemots likely had a disproportionate impact on the local population due to the species K-selected life history traits of high annual adult survival and low reproductive rates (Terborgh 1974; McKinney 1997; Groom *et al.* 2006).

Guillemots select nests that provide some protection against nest predators (Emms and Verbeek 1989), and they may adapt to an increase in predation pressure by selecting safer nest sites, as has been demonstrated in other birds (Forstmeier and Weiss 2004; Eggers *et al.* 2006). We found a correlation between increasing nest predation by mink and changes in guillemot nest site use at the Naked Island Group, suggesting that increasing mink predation pressure caused a large shift in the types of nest sites used. Talus nest sites, located on relatively moderate slopes were readily accessible to mink and were no longer used by guillemots in 2008. Mink are also able to access cliff top nest sites in soil burrows, either via the burrow entrance(s) or by digging an access hole to the nest chamber. Although mink were able to access a few guillemot nests on nearly vertical cliff faces, a high proportion of cliff face nest sites were likely inaccessible to mink.

Increased nest predation by mink apparently had a negative effect on other seabirds nesting at the Naked Island Group. Arctic Terns (*Sterna paradisaea*) were the only surface-nesting colonial seabird breeding at the Naked Island Group in 1978, but the species no longer nested there in 2008. Other crevice- or burrow-nesting seabirds present at the Naked Island Group in 1978 (Oakley and Kuletz 1979) either no longer nested there in 2008 (i.e. Parakeet Auklet, *Aethia psittacula*) or nested in greatly reduced numbers (i.e. Tufted Puffins, *Fratercula cirrhata,* and Horned Puffins, *F. corniculata*). The few pairs of puffins that still nested on the Naked Island Group in 2008 were confined to the highest cliffs (80–100 m) on the islands.

We have made a strong case that predation by introduced mink had become the primary limiting factor for the guillemot population at the Naked Island Group by 2008. There is considerable evidence, however, that mink predation was not the sole factor limiting recovery of guillemot populations 19 years after EVOS, either in PWS generally or at the Naked Island Group in particular. Food supply has apparently remained a limiting factor for guillemots and other piscivorous seabirds nesting in PWS since the 1976 PDO regime shift (Cushing *et al.* 2018). The Sound-wide population of guillemots declined for 40 years, from 1976 to at least 25 years after the EVOS. Populations of other marine birds in PWS that specialize on schooling forage fish also experienced long-term declines (Cushing *et al.* 2018).

Pacific herring, an important prey item for guillemots nesting in PWS (Golet *et al.* 2000), experienced large population declines in PWS after 1989 that were attributed to both EVOS and a long-term warming trend in the Sound (Cushing *et al.* 2018). Little information is available on populations of sand lance, historically the most common lipid-rich prey type in the diet of guillemots at the Naked Island Group (Golet *et al.* 2002). Sand lance were likely negatively impacted by the oil spill due to their close association with shallow beaches that accumulated oil (Golet *et al.* 2002). Sand lance abundance increases with plankton productivity that in turn is positively associated with ocean temperature in Alaska (Litzow *et al.* 2002, Robards *et al.* 2002), but negatively associated with high temperature anomalies (i.e. marine heatwaves; von Biela *et al.* 2019). The relative impact to forage fish populations in PWS from EVOS and warming oceans remains obscure (Esler *et al.* 2018).

Aerial surveys near the Naked Island Group that targeted nearshore schools of herring and sand lance demonstrated that the abundance of lipid-rich schooling forage fish was greater in 2008 compared to the 1990s. Although there was not a statistically significant increase in CPUE of lipid-rich forage fish in nearshore beach seine samples from the 1990s to 2008, small sample sizes, high variability among catches, and the limited area sampled (10s of m^2) severely limited our power to detect a difference. At a minimum, the beach seine samples confirmed that lipid-rich forage fish persisted at a few beaches at the Naked Island Group in 2008, and we think the 26 times higher average CPUE in 2008 is biologically significant.

The proportion of lipid-rich schooling forage fish in the diet of guillemot chicks and the average chick growth index in 2008 suggested that prey abundance had not returned to pre-spill levels at the Naked Island Group. Foraging conditions were presumably better at Fool Island, where the diet of chicks was similar to that at Naked Island prior to the spill. For nesting guillemots, a greater proportion of lipid-rich fish in the diet has been associated with higher chick growth rates, higher nestling survival, less brood reduction, and higher overall productivity (Golet *et al.* 2000; Litzow *et al.* 2002). Nevertheless, guillemots nesting at the Naked Island Group that specialized on a particular prey type had higher reproductive success than did generalists, regardless of the lipid content of the prey (Golet *et al.* 2000). With few remaining guillemots nesting at the Naked Island Group in 2008, there was likely less intra-specific competition for nearshore demersal fish prey, which are relatively sedentary, territorial, and thus more predictable. Under these conditions, nearshore demersal fish may have been more available to nesting guillemots than lipid-rich schooling forage fish, even with an increase in abundance of the latter. A low proportion of lipid-rich schooling forage fish in the diet of guillemot chicks does not necessarily result in a declining guillemot population. Most other monitored guillemot populations rely heavily on low-lipid fish (Golet *et al.* 2000). Ainley *et al.* (1990) documented a stable population of guillemots at the Farallon Islands, California, with no lipid-rich schooling forage fish in the chick diet.

The increase in abundance of lipid-rich schooling forage fish near the Naked Island Group was contrary to prediction if food supply was the primary cause of the rapid decline in the guillemot population. Supporting the inference of improved forage fish availability, we noted large foraging flocks of piscivorous seabirds, including Marbled Murrelets (*Brachyramphus marmoratus*), Black-legged Kittiwakes (*Rissa tridactyla*), and Glaucous-winged Gulls (*Larus glaucescens*), along the shoreline of the Naked Island Group in 2008, as well as foraging humpback whales (*Megaptera novaeangliae*), minke whales (*Balaenoptera acutorostrata*), harbor seals (*Phoca vitulina*), and Steller sea lions (*Eumetopias jubatus*) (KSB, pers. obs.). These aggregations of piscivorous marine birds and mammals near the Naked Island Group suggest that forage fish were abundant and readily available.

We demonstrated that two factors contributed to the failure of guillemots to recover from EVOS and the continued dramatic decline in nesting guillemots at the Naked Island Group nearly 20 years after EVOS: predation by introduced mink and food supply. The introduction of mink to the Naked Island Group in the 1970s and the apparent rapid increase in size of the mink population on the Naked Island Group post-EVOS led to a well-documented increase in predation rates on nesting guillemots and their chicks and eggs, such that predation became the primary cause of nest failure during the 1990s and in 2008. The abundance of lipid-rich schooling forage fish that formerly were key prey resources for guillemots at the Naked Island Group increased during the 2000s, but the recovery of prey populations was not sufficient to overcome the impact of mink predation. The risk of extirpation of a formerly large local guillemot breeding population by the introduction of mink to the Naked Island Group may have been enhanced because the guillemot population was already in decline due to a catastrophic disturbance (EVOS) and poor ocean conditions driven by climate change, as seen in other systems (Brook *et al.* 2008, Dias *et al.* 2019). Nevertheless, recovery of the remnant guillemot population at the Naked Island Group is highly unlikely as long as mink have access to their nesting areas. Because at least one quarter of the Sound-wide population of guillemots formerly nested at the Naked Island Group, even partial recovery of the historical nesting population at the Naked Island Group has the potential to influence the population trajectory of the species throughout PWS.

Postscript: The results of the present study led to the implementation of management to remove introduced mink from guillemot nesting habitat at the Naked Island Group starting in 2014. The results of that management effort and its impact on the guillemot breeding population at the Naked Island Group is the subject of a separate manuscript (Stark *et al.*, In review.).

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