

PREDATOR DISTURBANCE CONTRIBUTED TO COMMON MURRE *URIA AALGE* BREEDING FAILURES IN COOK INLET, ALASKA, FOLLOWING THE 2014–2016 PACIFIC MARINE HEATWAVE

CAITLIN E. MARSTELLER^{1*}, MAYUMI L. ARIMITSU², SARAH K. SCHOEN¹, SAMUEL B. STARK¹ & JOHN F. PIATT¹

¹*U.S. Geological Survey, Alaska Science Center, Anchorage, Alaska, 99508, United States*

²*U.S. Geological Survey, Alaska Science Center, Juneau, Alaska, 99801, United States* *(cmarsteller@usgs.gov)

Received 17 May 2023, accepted 20 December 2023

ABSTRACT

MARSTELLER, C.E., ARIMITSU, M.L., SCHOEN, S.K., STARK, S.B. & PIATT, J.F. 2024. Predator disturbance contributed to Common Murre *Uria aalge* breeding failures in Cook Inlet, Alaska following the 2014–2016 Pacific marine heatwave. *Marine Ornithology* 52: 129–139.

The 2014–2016 Pacific marine heatwave caused unprecedented die-offs and multi-year reproductive failures for Common Murres *Uria aalge* along the west coast of North America. Lingering impacts, such as declines in colony attendance and productivity, have persisted at some colonies following the heatwave and are attributed largely to changes in prey availability and quality. Here, we present evidence of an additional, top-down mechanism contributing to Common Murre breeding failures on Gull Island (Alaska): disturbance of nesting birds by aerial predators and associated egg depredation. We collected time-lapse images over five murre breeding seasons (2016–2020) on Gull Island to document the frequency, duration, and intensity of disturbances caused by aerial predators, as well as to quantify disturbance-associated egg depredation. To identify seasonal and inter-annual variability of disturbances, we calculated a daily disturbance index and compared years using generalized additive models. In all years, Bald Eagles *Haliaeetus leucocephalus* were the primary cause of disturbance, which led to periods of prolonged colony abandonment by murrens and facilitated high levels of murre egg depredation by Glaucous-winged Gulls *Larus glaucescens* and Herring Gulls *L. argentatus*. We found that the seasonality of disturbance was an important factor in determining egg depredation rates. In years when disturbance levels were high and persisted later in the season, the colony experienced complete breeding failures due to disturbance-associated egg depredation. Our study revealed that the response of nesting murrens to a strong environmental perturbation, such as the Pacific marine heatwave, can be complex and involve multiple stressors from both bottom-up and top-down factors.

Key words: Common Murres, *Uria aalge*, depredation, Bald Eagle, *Haliaeetus leucocephalus*, breeding failures, marine heatwave

INTRODUCTION

Aerial predators, such as Bald Eagles *Haliaeetus leucocephalus* and Peregrine Falcons *Falco peregrinus*, can cause large-scale disturbances to colonial seabirds, often leading to declines in breeding success and other negative impacts (Verbeek 1982, Paine *et al.* 1990, Parrish 1995). Disturbances caused by Bald Eagles have also been blamed for changes in seabird breeding habitat, colony abandonment, and population declines along the North American west coast (Parrish *et al.* 2001, Hayward *et al.* 2010, Hipfner *et al.* 2011, Thomas & Lyons 2017). Further, the prevalence of impacts from aerial predators may be increasing as their populations have recovered from historical declines caused by pesticide use and habitat destruction in recent decades (Paine *et al.* 1990, Hipfner *et al.* 2012).

The effects of aerial predators on seabird colonies go beyond direct depredation of adults, chicks, and eggs. There may also be a direct effect on adult seabird time-energy budgets and behavior, as adults must increase vigilance and flee from predators in order to avoid direct depredation (White *et al.* 2006, Hipfner *et al.* 2012). Further, indirect effects of aerial predators include the depredation of unprotected eggs by gulls or other scavengers during disturbance events, which can have the greatest impact on breeding success (Hipfner *et al.* 2012, Horton 2014, Henson *et al.* 2019). The magnitude of depredation effects on breeding success is greatest in colonies where birds are less protected, either by

habitat characteristics, such as vegetation, narrow ledges, or rock crevices (Parrish & Paine 1996, Gaston & Elliot 1996, Barrett *et al.* 2006), or by having few close neighbors associated with lower nesting density (Birkhead 1977, Hernández-Matías *et al.* 2003). Thus, predator impacts may be magnified in cliff-top colonies or in colonies with declining populations, as nesting birds are more accessible to predators (Parrish 1995, Gilchrist 1999).

Changes in food supply can also make seabirds more susceptible to disturbance and nest depredation (Suryan *et al.* 2006, Veitch *et al.* 2016, Bårdsen & Ove Bustnes 2022). Environmental conditions that influence prey availability can secondarily affect the timing and synchrony of egg laying (Shultz *et al.* 2009, Schroeder *et al.* 2009). Additionally, as prey resources decline, nesting birds can require more time away from the colony to forage (Zador & Piatt 1999, Harding *et al.* 2007), leaving eggs more vulnerable to depredation (Irvine *et al.* 2021). Depredation pressure on adults, chicks, and eggs may also increase as alternate food sources become less available for predators (Spear 1993, Massaro *et al.* 2000, Elliott *et al.* 2011).

Common Murres *Uria aalge* (hereafter, murrens) are one of the most abundant breeding seabirds in the Northern Hemisphere (Ainley *et al.* 2021). Adults are long-lived and nest in dense colonies, mostly on remote islands offshore in sub-Arctic regions and within areas of cold, temperate waters (Ainley *et al.* 2021). Murrens do not make nests, but instead lay a single egg on island cliffs with level ledges

or platforms. Mates take turns incubating their egg and completing foraging trips. Like many colonial breeders, murre egg-laying, incubation, and fledging are synchronized, and nesting birds rely on close neighbors for protection from predators (Hatchwell 1991, Ainley *et al.* 2021, Irvine *et al.* 2021). If eggs are lost to depredation, adults may attempt to relay, with a higher probability of relaying if eggs are lost early in the season (Hatchwell 1991, Schauer & Murphy 1996). Murres maintain high levels of reproductive success, largely due to their k-selected life history strategy (e.g., only one egg/chick at a time) as well as their ability to buffer breeding success by reallocating time budgets in times of limited prey resources (Ainley & Boekelheide 1990, Piatt *et al.* 2007, Piatt & Harding 2007).

Historically, murre breeding failures have occurred only rarely along the North American west coast, such as during intense El Niño events (Ainley & Boekelheide 1990, Warzybok *et al.* 2017). However, during and following the 2014–2016 Pacific marine heatwave (hereafter, heatwave), multi-year breeding failures were recorded at multiple murre colonies along the West Coast of North America (Piatt *et al.* 2020, Romano *et al.* 2020, Schoen *et al.* 2022). During this period, anomalous warm water persisted (e.g., di Lorenzo & Mantua 2016) and had far-reaching effects on all levels of the ecosystem, including the largest murre die-off ever recorded (von Biela *et al.* 2019, Piatt *et al.* 2020, Arimitsu *et al.* 2021a, Suryan *et al.* 2021). Breeding failures and below-average productivity during and following this time have been largely attributed to heatwave-related declines in food availability and quality that did not meet the foraging threshold for murres (Wells *et al.* 2017, Piatt *et al.* 2020, Arimitsu *et al.* 2021a). A second strong marine heatwave occurred in 2019, but the timing of peak impact made it less likely to produce the same damage to ecosystems observed in the 2014–2016 heatwave (Amaya *et al.* 2020).

One colony that experienced multi-year breeding failures during and following the heatwave was Gull Island in Kachemak Bay, Alaska. Historically this colony exhibited stable productivity of 0.54 ± 0.15 chicks/pair and an increasing population trend, totaling 20%, from 1995 to 1999 (Zador & Piatt 1999, Piatt 2002, Schoen *et al.* 2022). However, following the heatwave, the murre population attending Gull Island has declined (> 64% decrease from 2016 to 2020) and experienced multiple years of breeding failures (Schoen *et al.* 2022). While heatwave-related declines in food availability and quality (e.g., Arimitsu *et al.* 2021a) likely contributed to these population and productivity declines, aerial predator disturbances and disturbance-associated egg depredation events were also observed during this time and could have exacerbated the impact of poor conditions for murres (Schoen *et al.* 2022).

The goal of this paper was to quantify seasonal and inter-annual variability in disturbances caused by aerial predators during the 2016–2020 breeding seasons to better understand how disturbances impacted murre behavior and facilitated egg depredation leading to breeding failures following the heatwave. We used time-lapse photographs of the murre breeding colony on Gull Island to assess levels of disturbance and associated egg depredation. To evaluate overall impacts, we (1) calculated the frequency, duration, and intensity of disturbances to create a disturbance index during the incubation phase of each year; (2) modeled how disturbance changed over time, both within and among years; and (3) characterized the effect of variable disturbance levels on murre behavior and egg depredation rates.

METHODS

Study site

This study took place on a murre breeding colony at Gull Island (59.59°N, 151.33°W) in Kachemak Bay, a glacially influenced fjord located on the lower east end of Cook Inlet in southcentral Alaska (Fig. 1). Gull Island is part of a three-island cluster, which also includes Murre Rock and Gorilla Rock, all of which are nearshore and ~5 km across the bay from the town of Homer (Fig. 1). Most murres nest on the flat, exposed clifftops of Gull Island, Murre Rock, and Gorilla Rock, which have little vegetation, and to a lesser degree on the steep, rocky cliff walls (Fig. 1). During this study, the estimated number of breeding murres attending Gull Island declined from ~7600 in 2016 to 2700 in 2020 (Schoen *et al.* 2022). Additionally, an estimated 6667 (± 1001 , 2016–2020) Black-legged Kittiwakes *Rissa tridactyla* also nested in close proximity to murres along the rocky cliff walls of the colony, with no significant population decline observed during the time of this study (Schoen *et al.* 2022).

Data collection

To monitor disturbance of murres by aerial predators and associated egg depredation, we deployed time-lapse cameras at a single plot viewing the main murre nesting area on top of Gull Island during the 2016–2020 breeding seasons (Figs. 1, 2). Declines in attendance at this colony over time (Schoen *et al.* 2022) have reduced the areas where murres breed on the island. As a result, this main nesting area is used for monitoring productivity (number of chicks fledged/breeding pair; Schoen *et al.* 2022) and provided the best option for viewing disturbances to the colony. We used Day 6 PlotWatcher Pro (2016–2017) and Reconyx HyperFire 2 (2018–2020) cameras, which collected images every 15–30 sec during daylight hours. We aimed to collect images throughout the egg laying and incubation period (approximately late June to late August) in each year, though for logistical reasons cameras were not deployed until late July in 2016 (Table 1). These dates were selected because recent reproductive failures at this colony have been due to egg loss, and 97% of recorded eggs were laid during this time period.

We kept the placement and view of the camera as consistent as possible between years, with approximately 50–100 nest sites in view each year. There were slight variations among years in distance from the nesting area and angle of the camera, which affected the view of the surrounding colony where aerial predators are often observed. However, the camera captured the majority of the main nesting area on Gull Island in every year (Figs. 1, 2). Nests on Gorilla Rock, Murre Rock, and along the cliff walls (Fig. 1) could not be monitored for logistical reasons.

Predator disturbances

Upon camera retrieval, time-lapse photos were stitched together into a video file using Time-lapse Tool Version 2.4 (03 May 2022) and reviewed by trained observers to evaluate murre disturbance and associated egg depredation (for the associated data release see Arimitsu *et al.* 2021b). Disturbances were defined as any event in which > 1% of visible murres flushed (evacuated) from the colony. When possible, species identification of aerial predators causing disturbance events were recorded. We treated each sighting, when an aerial predator entered the view, as a new observation. We assumed that all disturbances were caused by aerial predators, aside from three events

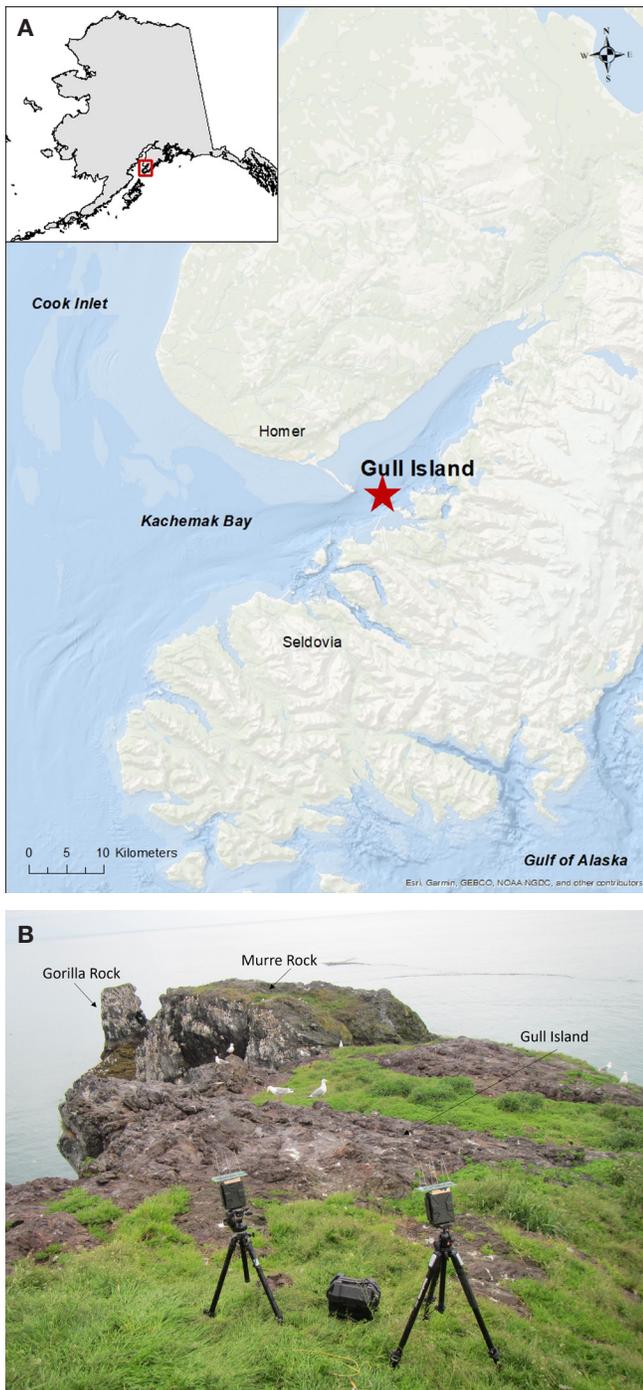


Fig. 1. (A) Map of the Common Murre *Uria aalge* breeding colony on Gull Island (red star) in Kachemak Bay, Alaska. (B) Location of the time-lapse cameras used to document disturbance to breeding Common Murres on Gull Island, Kachemak Bay, Alaska in proximity to other neighboring islands. Though we used data from just one camera, a second camera provided a backup in the event that one camera failed.

in 2016 and 2017, when camera maintenance visits caused disturbance. We ceased in-person camera maintenance in subsequent years by using a mixture of external 12-volt marine batteries and solar panels, in addition to the camera's internal lithium batteries. Other sources of disturbance are assumed to be rare, as Gull Island is closed to the

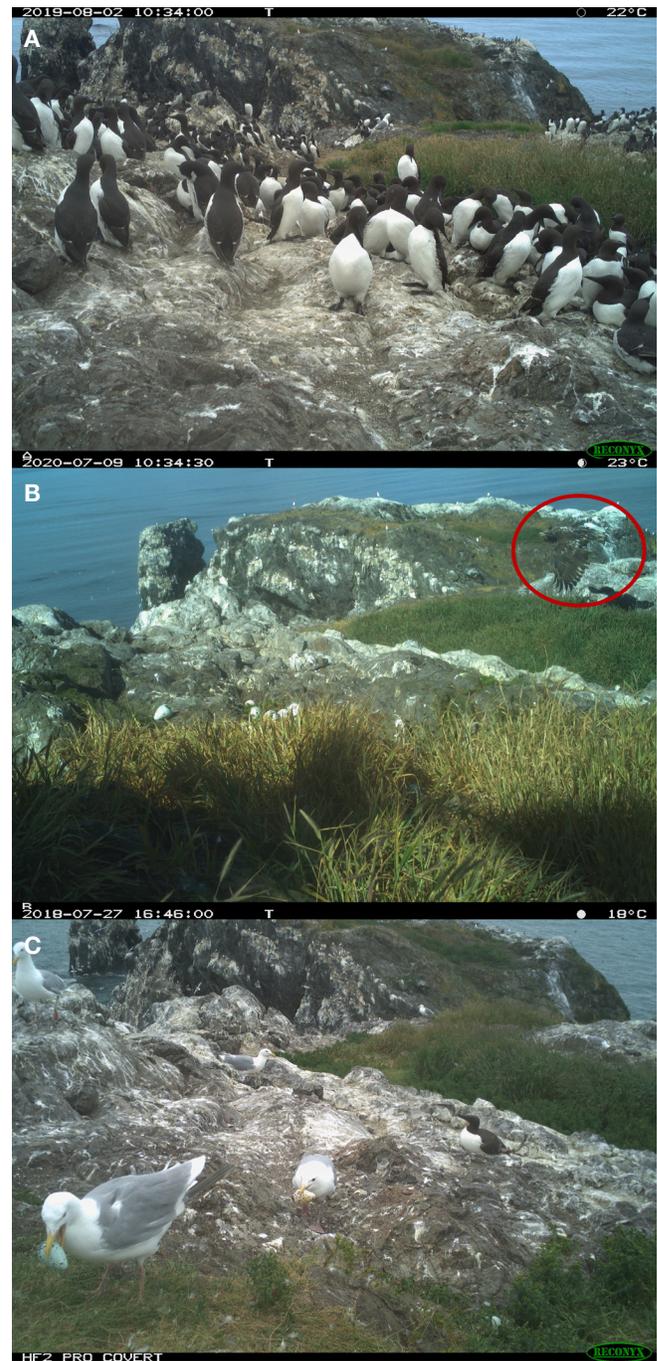


Fig. 2. Example time-lapse camera images of the Common Murre *Uria aalge* breeding colony on Gull Island, Kachemak Bay, Alaska including (A) Common Murres attending nest sites, (B) a Bald Eagle *Haliaeetus leucocephalus* flying over Common Murre nest sites with a Black-legged Kittiwake *Rissa tridactyla* in its talons (red circle), and (C) murre egg predation by Glaucous-winged Gulls *Larus glaucescens* during a disturbance event.

public, the top of the colony is far removed from marine vessels, and there have been no documented mammalian predators on the colony.

To measure variability in disturbance levels throughout the breeding season and among years, we quantified the frequency of events

(count per day), as well as the duration (minutes) and intensity (percent of birds flushed) of each disturbance event. The frequency of events was calculated as the number of disturbances per calendar day. Duration of each event was recorded in minutes, beginning when murres flushed and ending when > 75% of the flushed murres returned. If disturbances extended into non-daylight hours, the event record was conservatively ended at sundown and started as a new event at sunrise, because return of birds could not be documented after dark. Disturbance intensity was recorded as the maximum percent (0–100%) of the visible colony (hereafter, ‘colony’) that was flushed during each event.

To measure egg depredation rates and the response of murre behavior to disturbance levels, we counted the number of eggs eaten during each disturbance event, identified the egg predators, and counted the number of murres actively nesting at the time of the disturbance. We defined birds actively nesting as the number of murres that remained in incubation posture or did not move from their nest site during disturbance events, which we used as an indicator of reproductive investment. The number of birds actively nesting during each disturbance event was quantified to provide an indication of resilience to disturbance because their behavior suggested they were more invested in their reproductive effort than birds that were not attending a nest site. This metric included all birds in incubation posture, regardless of whether we were able to positively confirm an egg or chick underneath them. Additionally, it included birds that remained at their nest sites during disturbances even if we were not able to discern whether their posture changed during a disturbance (e.g., when they were too densely aggregated).

Statistical analyses

We multiplied disturbance duration by intensity for each event, then summed the result for each day to create a daily disturbance index. This index allowed us to weight the duration of each disturbance by the percent of birds that flushed from the colony. This metric has units of minutes per day, and it weights longer disturbance events that affected a larger portion of the colony more heavily than events that were brief and affected fewer birds.

To model seasonal variability in disturbance for each year, we used a generalized additive model (GAM) with the “mcgvm” package v. 1.9-0 (Wood 2011) in R v. 4.1.3 (R Core Team 2022). We modeled the disturbance index (rounded to the nearest minute) as

the response variable, and we included year as a factor and a smooth term for day of year by year as the predictor variables. We specified a negative binomial error distribution with a log-link function to account for overdispersion. We examined the model residuals for signs of serial autocorrelation using autocorrelation function (ACF) plots and evaluated final model fit based on residual plots. We chose to run separate models for each year because (1) of the lack of early season data in 2016, and (2) during the exploratory phase, we found differences in the degree of serial autocorrelation present in the residuals of year models. For the 2016 data, we used the “gamm” routine to include a smooth term for day of the year, as well as an AR1 correlation structure, to account for temporal autocorrelation across days.

RESULTS

Data overview

During the period from 2016 to 2020, we recorded 850 disturbance events that lasted 1432 h, with 376 associated egg depredation events (Table 1). Disturbances during 2016, 2018, and 2020 were longer and affected a greater portion of the colony compared to 2017 and 2019 (Fig. 3). Multiple disturbance events still occurred on most days in 2017 and 2019, but the duration and intensity of those disturbances were comparatively lower than other years (Fig. 3).

Bald Eagles were the only aerial predator observed causing disturbance events in camera images ($n = 573$ observations during 169 disturbance events; Fig. 2) but were rarely observed directly depredating adults ($n = 1$ in 2018) and were never observed depredating eggs or chicks on the plot. Most Bald Eagles were observed on the cliff edges, depredating or perching on Black-legged Kittiwake nests ($n = 331$). Bald Eagles were also observed flying over and landing directly on murre nesting areas ($n = 39$ and $n = 203$, respectively; Fig. 2). While Peregrine Falcons were not directly observed in camera images, they were occasionally observed causing mass disturbances and depredating kittiwakes during in-person visits to the colony in 2018. Their presence at the colony and depredation of other species, such as kittiwakes, likely contributed to colony disturbances, but to a lesser degree.

The only confirmed secondary predators seen directly taking murre eggs during disturbance events were Glaucous-winged and Herring Gulls, which were present during all disturbance events (Fig. 2).

TABLE 1
Summary of Common Murre *Uria aalge* colony monitoring effort and Bald Eagle *Haliaeetus leucocephalus* disturbance metrics by year on Gull Island, Kachemak Bay, Alaska

Year	Dates	Number of days	Number of disturbance events	Total disturbance duration (hrs)	Number of eggs depredated (% eggs laid) ^a
2016	23 July–20 Aug	29	92	156	36 (100%)
2017	28 Jun–20 Aug	54	177	176	103 (not available ^b)
2018	28 Jun–20 Aug	54	242	519	104 (100%)
2019	28 Jun–20 Aug	54	199	223	78 (72%)
2020	28 Jun–20 Aug	54	140	358	55 (64%)

^a Eggs with unknown fate were excluded in the count of total number of eggs laid.

^b The total number of eggs laid was not available for 2017 (see Methods).

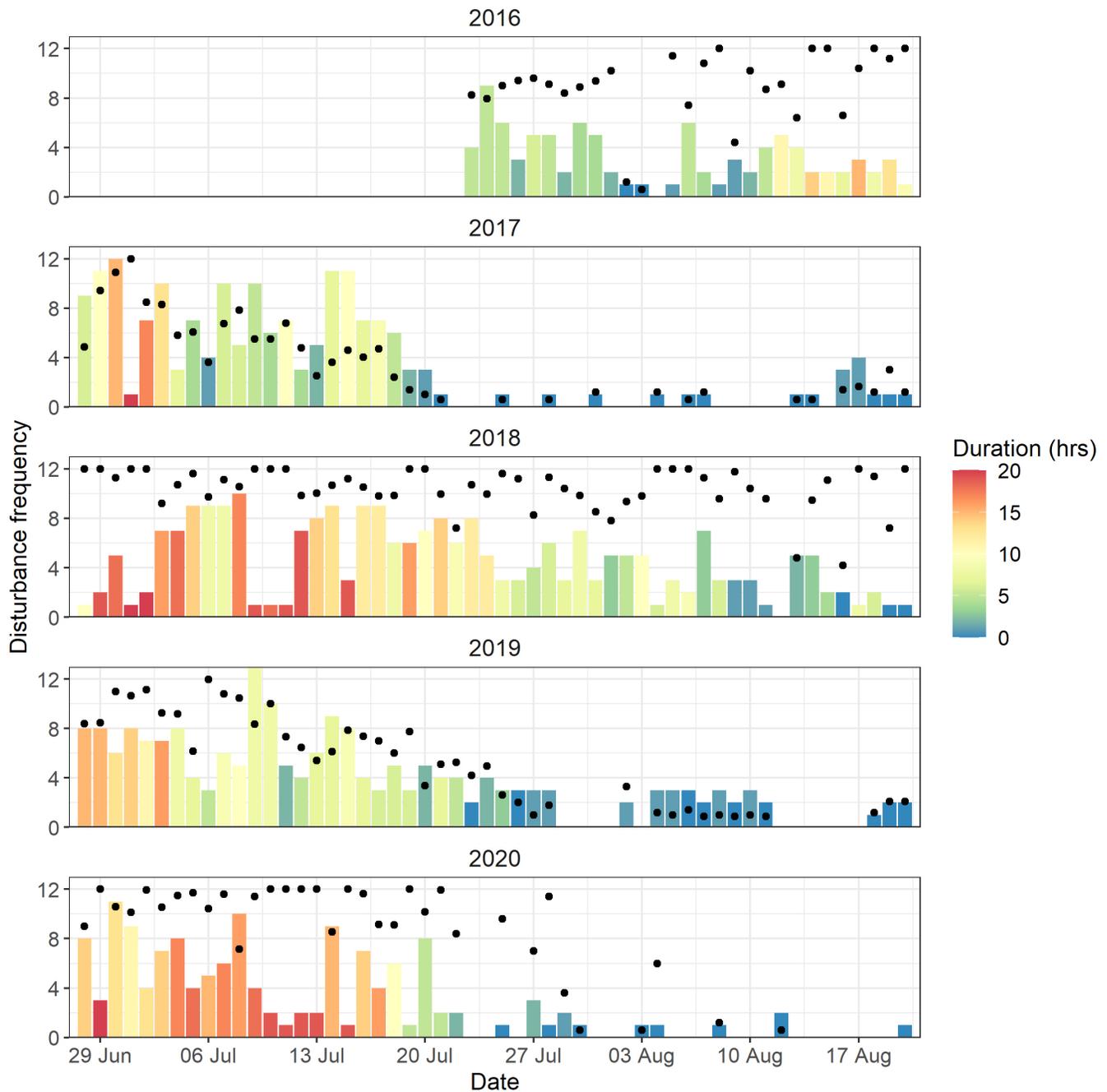


Fig. 3. Common Murre *Uria aalge* colony disturbance frequency (y-axis, total number of disturbance events per day) and duration (color, sum of disturbance duration per day) at Gull Island, Kachemak Bay, Alaska from 2016–2020. Black points indicate average disturbance intensity (proportionally scaled to maximum frequency to facilitate plotting). There were no early season data available in 2016.

Predator disturbance

The model fits to disturbance index over time for each year produced residuals with no evidence of significant autocorrelation at lags less than four in 2017 and 2019, and only minimal evidence (i.e., < 0.03 above the 95% confidence interval [CI] autocorrelation function estimate) of significant autocorrelation at lag one in 2018 and 2020. However, we detected moderate autocorrelation at lag 1 in the model fit to disturbance data from 2016, which was greatly reduced (i.e., from autocorrelation function estimates of 0.60 to 0.39) by accounting for an AR1

correlation structure using the “gamm” routine. QQ plots generally indicated that residuals produced by a negative binomial fit were reasonably normally distributed, aside from a few instances of days of zero disturbance. Annual models explained 56% to 93% of the variance (Table 2).

We observed significantly different levels of disturbance among years, as well as seasonal variation within years (Table 2, Fig. 4). Within years, disturbance levels were usually highest at the beginning of the season and decreased over time. This was most apparent in 2017, 2019, and 2020, which all had early peaks in

TABLE 2
Results of generalized additive models of disturbance index by day of the year^{a, b}

Year	n	edf	Intercept	R ²	Deviance explained
2016	29	2.146*	5.496***	0.56	
2017	54	7.216***	2.082***	0.75	0.89
2018	54	1.465***	6.155***	0.65	0.39
2019	54	4.287***	3.5949***	0.89	0.77
2020	54	3.722***	2.5699***	0.93	0.86

^a Included are number of days monitored per year (n), estimated degrees of freedom (edf) of the smoothed terms, intercept coefficient of the fixed parameters, variance explained (R^2), and deviance explained compared to the null model. Significance: $P < 0.001$ *** and $P < 0.05$ *.

^b The 2016 model differed in that no early season data were available, and an AR1 correlation structure was required to account for serial autocorrelation in the residuals.

disturbance followed by a steep decline and multiple disturbance-free days (Figs. 3, 4). However, in 2017, after the initial decline in disturbance until ~19 July, the disturbance level remained consistent with a slight increase at the end of the season (Figs. 3, 4). Additionally, the peak and decline in disturbance levels occurred later in 2020 compared to 2017 and 2019 (Figs. 3, 4), and this was associated with the observation of Bald Eagles later in the year at the colony.

We observed consistently higher levels of disturbance throughout the season in 2018 compared to other years ($P < 0.001$; Table 2, Figs. 3, 4). In 2018, there was a slight decrease in disturbance levels later in the season, but intensity remained high throughout the sampling period (Figs. 3, 4). Unlike other years, disturbance levels during 2016 increased toward the end of the breeding season (Figs. 3, 4) and were also associated with persistent late season Bald Eagle observations.

Egg depredation

In 2016 and 2018, the colony experienced complete breeding failures because 100% of observed eggs were depredated by Glaucous-winged and Herring Gulls during disturbance events

(Table 1). In these years, egg depredation continued late into the season when there were fewer than 10 birds actively nesting at any time (Fig. 5).

In 2019 and 2020, 72% and 64% of eggs observed were depredated, respectively (Table 1). Relative egg depredation rates could not be calculated in 2017, as eggs being incubated were not reliably visible due to the camera being placed further from nest sites than in other years. In 2017 and 2019, although disturbance events were frequent in the early season, the amount of the colony they affected decreased over time, which coincided with higher numbers of birds actively nesting and decreased rates of egg depredation (Figs. 3, 5). In 2020, the number of birds actively nesting increased comparatively later in the season, during the last week of July (Fig. 5), following an observed decrease in disturbance (Fig. 3). Chicks were observed on the colony in 2017, 2019, and 2020, and while chicks were not tracked to fledging, no chick depredation was observed on camera images during the study period.

DISCUSSION

We documented seasonal and inter-annual variability in the disturbance of Common Murres by aerial predators across five breeding seasons on Gull Island. This disturbance led to high rates of egg depredation, and murres experienced complete breeding failures, or below average productivity, across these same years (Schoen *et al.* 2022). We found that when disturbance increased or was sustained later in the breeding season, murres experienced complete breeding failures. In some years, greater numbers of actively nesting birds coincided with decreased levels of disturbance and egg depredation, but the murres still experienced lower than average reproductive success compared to baseline studies (Schoen *et al.* 2022). Evidence from other studies has shown that limitation in murre productivity at most colonies following the heatwave was due to heatwave-induced food web collapse (Piatt *et al.* 2020, Arimitsu *et al.* 2021). However, the data presented here show that widespread and persistent disturbance by aerial predators and associated depredation of murre eggs also contributed directly to ongoing breeding failures and reduced productivity at this colony. It seems likely that the effects of the heatwave, low food supply, and predator disturbance are interactive but cannot be disentangled with existing data.

This study is the first to identify disturbance by aerial predators as a mechanism for Common Murre breeding failures in Alaska. These findings help explain why breeding success has not recovered at this

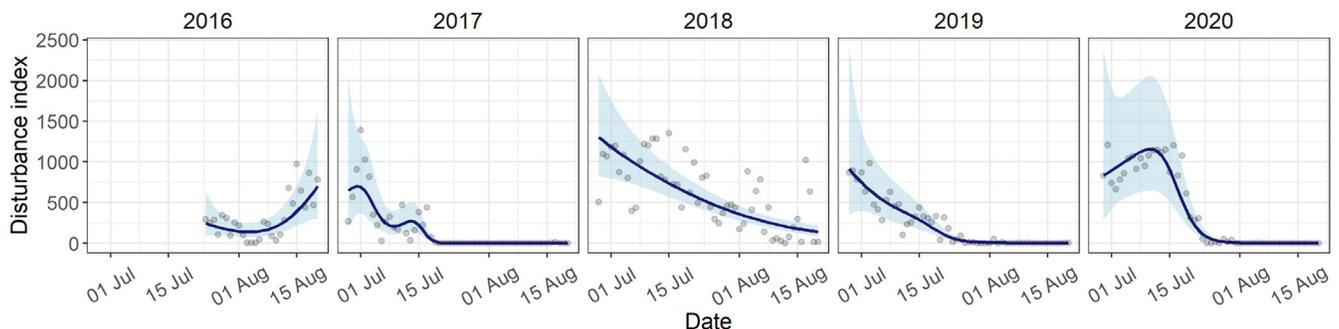


Fig. 4. Modeled seasonal variability (blue line, \pm 95% confidence interval) of predicted disturbance index (grey circles, minutes) by date (x-axis) and year (panels). Model predictions were made on a log-scale and back-transformed for plotting.

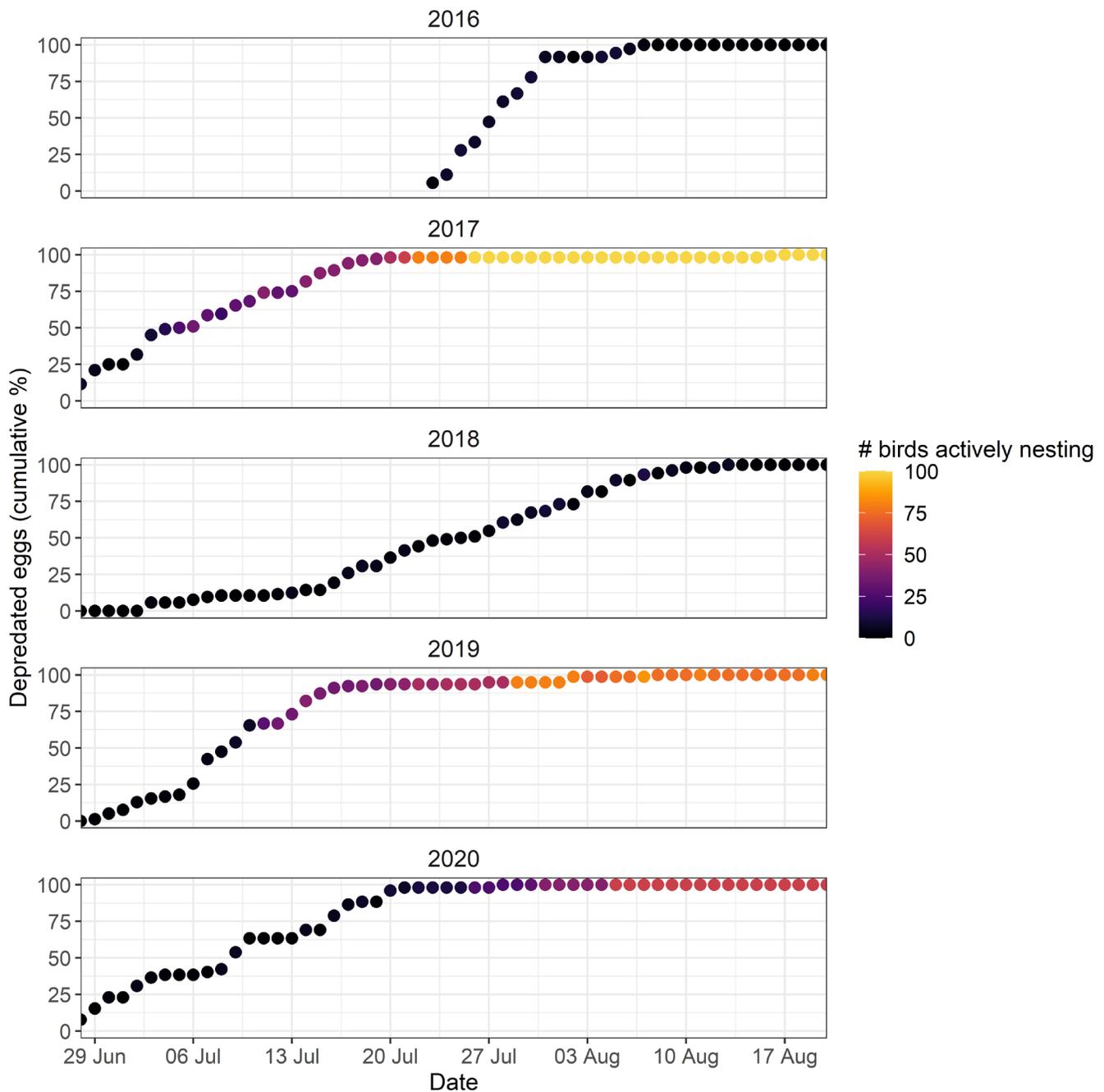


Fig. 5. The cumulative percent of Common Murre *Uria aalge* eggs depredated by date for each breeding season from 2016 to 2020 at Gull Island, Kachemak Bay, Alaska. All confirmed egg predators were Glaucous-winged *Larus glaucescens* and Herring Gulls *L. argentatus*. Color indicates the maximum number of murres actively nesting each day. There were no early season data available in 2016.

colony compared to other larger colonies where prey resources were the only documented cause of declines in productivity and where breeding success rebounded within one to three years following the heatwave (Piatt *et al.* 2020, Dragoo *et al.* 2020). This study is also the first to use a combined index to evaluate the collective impact of disturbance characteristics, as well as to use a fine time scale to describe seasonal variation of disturbance within and among years. These parameters are important when considering the timing and impacts of varying disturbance levels on breeding murres and, when combined, may provide a better metric for measuring the magnitude of disturbances than the frequency of events alone.

The effects of disturbance by aerial predators in this study were mediated by adult murre behavior, specifically their propensity to abandon the colony *en mass*. Doing so left eggs unattended and vulnerable to depredate by gulls. Bald Eagles were the only identified source of disturbance in images from our study site. Similar responses to Bald Eagles have been observed at other murre colonies such as Tatoosh Island in Washington (Parrish 1995), Triangle Island in British Columbia (Hipfner *et al.* 2011), and Yaquina Head in Oregon (Porquez *et al.* 2021), as well as to White-tailed Eagles *Haliaeetus albicilla* in the Baltic Sea and along the Norwegian coast (Barrett *et al.* 2006, Hentati-Sundberg *et al.* 2021).

While Peregrine Falcons can also be a source of disturbance, and occasionally prey on murres (Paine *et al.* 1990, Sydeman 1993), we personally observed Bald Eagles frequently on-site at the colony, whereas sightings of Peregrine Falcons were rare (Schoen *et al.* 2022) and were never detected on camera images.

We detected seasonal and inter-annual differences in disturbance, which appear to be important factors in murre egg survival. In most years, we recorded the highest levels of disturbance and Bald Eagle presence in the early breeding season. Disturbance early in breeding phenology facilitates high rates of egg depredation, as eggs laid early are more asynchronous (Murphy & Schauer 1994, Schauer & Murphy 1996, Gilchrist & Gaston 1997, Wilhelm & Storey 2002) and birds without an egg or chick are more likely to flush from the colony when predators are present (Gaston & Elliot 1996, Irvine *et al.* 2021), which leaves fewer neighbors to provide protection to breeders. However, early season depredation may be less consequential for overall productivity, as murres are more likely to relay if eggs are lost early in the season (Murphy & Schauer 1994). In contrast, in years when we observed frequent disturbance events and associated egg depredation persisting later in the breeding season (2016, 2018), murres experienced complete reproductive failures. These years were also associated with higher rates of Bald Eagle observations, which persisted later into the breeding season. In 2020, despite high early season disturbance and Bald Eagle observations, murres were still able to produce chicks (Arimitsu *et al.* 2021b) because disturbance levels declined to nearly zero during the last week of July and subsequently remained low.

In cliff-top colonies where birds are unprotected by habitat, such as vegetation cover, narrow ledges or rock crevices, protection from other breeding neighbors becomes even more important (Parrish 1995). This conspecific protection can be scarce in times of high disturbance, when increased egg depredation can cause breeding phenology to become protracted and less synchronous as birds attempt to relay depredated eggs (Parrish 1995). Declining populations can have a similar effect, as birds become less dense within nesting areas, making eggs more accessible to predators (Gilchrist 1999). During an extensive examination of factors affecting colony attendance and breeding success of murres at Gull Island in the 1990s, disturbances by aerial predators were not a prominent feature of the system (Piatt *et al.* 2002). At that time, murre population size, nesting density, and productivity were much higher than at any time since the heatwave, and colony abandonment during critical later periods of the breeding cycle were rare, suggesting that the relative importance of top-down factors has increased over time. This change could be due to increases in the Bald Eagle population, although evidence suggests that coastal Alaska populations likely increased through the 1980s and remained relatively stable thereafter (Hodges 2011, Hipfner *et al.* 2012).

In addition to depredation, murre breeding success is also affected by forage fish abundance, timing, and body condition (Piatt *et al.* 2007, Shultz *et al.* 2009, Regular *et al.* 2014). While we know forage fish abundance and quality declined during and after the marine heatwave in this region (Arimitsu *et al.* 2021a, Suryan *et al.* 2021), we detected the return of high-quality prey (e.g., larger size classes of Pacific Sand Lance *Ammodytes personatus* and spawning Capelin *Mallotus catervarius*) to the area in 2019 (Arimitsu *et al.* 2021b), a year with some

reproductive success. However, productivity was still roughly half the historical rate in that year (Schoen *et al.* 2022), likely due to the high rates of disturbance-associated egg depredation early in the breeding season.

Therefore, it is likely that inter-annual differences in murre productivity at Gull Island are being driven by both top-down and bottom-up factors which are difficult to untangle (Suryan *et al.* 2006, Votier *et al.* 2008, Piatt *et al.* 2020) and, when occurring simultaneously, can amplify negative effects on breeding birds (Bårdsen & Ove Bustnes 2022). As we observed at Gull Island, murres at Yaquina Head, Oregon, experienced reproductive failures during and after the heatwave, as well as increased disturbance by Bald Eagles, which have been increasing since 2011 (Horton 2014, McClatchie *et al.* 2016, Suryan *et al.* 2017, Wells *et al.* 2017). The reproductive failures at Yaquina Head were also caused by Bald Eagle disturbance facilitating high rates of egg depredation, which were coupled with reduced prey availability and lack of parental investment (McClatchie *et al.* 2016, Suryan *et al.* 2017).

Although we rarely ($n = 1$) observed Bald Eagles directly depredating murres during disturbance events, Bald Eagles that flushed the murre colony were most commonly seen on and around Black-legged Kittiwake nests. The latter are in close proximity to the murre nesting area and could have influenced the susceptibility of murres to disturbance (Labansen *et al.* 2021). In-person observations during this study confirmed Bald Eagle depredation on Black-legged Kittiwake adults, chicks, and eggs, especially during 2016, 2018, and 2020, when Black-legged Kittiwakes at this colony also experienced complete reproductive failures and high rates of depredation (Arimitsu *et al.* 2021b, Schoen *et al.* 2022). The seasonal timing of elevated disturbance to murres coincides with late incubation and start of hatch for kittiwakes, which predators could be targeting to maximize energy content, as observed in other studies (e.g., White *et al.* 2006).

The level to which Bald Eagles rely upon seabirds as prey can be affected by changes in alternate prey availability and timing (Grubb & Hensel 1978, Anthony *et al.* 2008, Elliott *et al.* 2011), which has the potential for multi-trophic level cascade dynamics (Harvey *et al.* 2012). In Prince William Sound, Alaska, researchers found a positive relationship between Black-legged Kittiwake productivity and Pink Salmon *Oncorhynchus gorbuscha* returns, attributed to decreased depredation by Bald Eagles on kittiwakes during times of increased salmon availability (Ruggerone *et al.* 2023). Therefore, investigation of the availability of food sources for eagles in Kachemak Bay should be explored to help explain varying degrees of disturbance to seabirds, such as the timing and availability of Pink Salmon, which spawn in close proximity to this colony (Hollowell *et al.* 2017). This should also be considered for secondary predators, like gulls, that may increase their reliance on murre eggs when other prey, such as forage fish, are less available (Massaro *et al.* 2000, Spear 1993).

CONCLUSIONS

Seasonality of disturbance by aerial predators is an important factor determining egg depredation rates on murre colonies. Though disturbance during the early breeding season was also pervasive during this study, heightened depredation pressure during the late-breeding season occurred in years when murres experienced

complete reproductive failure. Compared to baseline monitoring in the 1990s, it appears that disturbance by aerial predators has become a more prominent stressor affecting population dynamics at this colony following the Pacific marine heatwave. We predict that murres at Gull Island will continue to experience heightened depredation pressure until sufficient food resources are available to both murres and their predators.

ACKNOWLEDGEMENTS

This work was funded by the U.S. Geological Survey (USGS) Alaska Science Center, the USGS Outer Continental Shelf Program, and the Bureau of Ocean Energy Management. We thank the Seldovia Native Association and the U.S. Fish and Wildlife Service for permitting land access to the colony. Field crews were essential to this work, and we appreciate the contributions from Brielle Heflin, Jonathan Felis, Brian Robinson, Abby Blackstone, Nate Anderson, and Scott Jelich. We also thank Brian Robinson and two anonymous reviewers for their helpful comments on earlier drafts. Any use of trade, firm, or product names is for descriptive purposes and does not imply endorsement by the U.S. Government.

REFERENCES

- AINLEY, D.G., NETTLESHIP, D.N. & STOREY, A.E. 2021. Common Murre (*Uria aalge*). In: BILLERMAN, S.M., RODEWALD, P.G. & KEENEY, B.K. (Eds.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology. doi:10.2173/bow.commur.02
- AINLEY, D.G. & BOEKELHEIDE R.J. 1990. *Seabirds of the Farallon Islands: Ecology, Dynamics, and Structure of an Upwelling-System Community*. Stanford, USA: Stanford University Press.
- AMAYA, D.J., MILLER, A.J., XIE, S. & KOSAKA, Y. 2020. Physical drivers of the summer 2019 North Pacific marine heatwave. *Nature Communications* 11: 1903.
- ANTHONY, R.G., ESTES, J.A., RICCA, M.A., MILES, A.K. & FORSMAN, E.D. 2008. Bald Eagles and Sea Otters in the Aleutian Archipelago: indirect effects of trophic cascades. *Ecology* 89: 2725–2735.
- ARIMITSU, M.L., PIATT, J.F., HATCH, S. ET AL. 2021a. Heatwave-induced synchrony within forage fish portfolio disrupts energy flow to top pelagic predators. *Global Change Biology* 27: 1859–1878. doi:10.1111/gcb.15556
- ARIMITSU, M.L., SCHOEN, S.K., PIATT, J.F. & MARSTELLER, C.E. 2021b. *Assessing the Status and Trends of Seabirds and Forage Fish in Lower Cook Inlet, Alaska, ver. 3.0, January 2024*. U.S. Geological Survey data release. Anchorage, USA: Alaska Science Center.
- BÅRDSSEN, B.J. & OVE BUSTNES, J. 2022. Multiple stressors: negative effects of nest predation on the viability of a threatened gull in different environmental conditions. *Journal of Avian Biology* 2022: e02953. doi:10.1111/jav.02953
- BARRETT, R., LORENTSEN, S.-H. & ANKER-NILSEEN, T. 2006. The status of breeding seabirds in mainland Norway. *Atlantic Seabirds* 8: 97–126.
- BIRKHEAD, T.R. 1977. The effect of habitat and density on breeding success in the Common Guillemot (*Uria aalge*). *Journal of Animal Ecology* 46: 751–764.
- DI LORENZO, E. & MANTUA, N. 2016. Multi-year persistence of the 2014/15 North Pacific marine heatwave. *Nature Climate Change* 6: 1042–1047. doi:10.1038/nclimate3082
- DRAGOO, D. E., H. M. RENNER, and R. S. A. KALER. 2020. *Breeding Status and Population Trends of Seabirds in Alaska, 2019*. U.S. Fish and Wildlife Service Report AMNWR 2020/01. Homer, USA: US Fish and Wildlife Service.
- ELLIOTT, K.H., ELLIOTT, J.E., WILSON, L.K., JONES, I. & STENERSON, K. 2011. Density-dependence in the survival and reproduction of Bald Eagles: Linkages to Chum Salmon. *Journal of Wildlife Management* 75: 1688–1699. doi:10.1002/jwmg.233
- GASTON, A.J. & ELLIOT, R.D. 1996. Predation by Ravens *Corvus corax* on Brunnich's Guillemot *Uria lomvia* eggs and chicks and its possible impact on breeding site selection. *Ibis* 138: 742–748.
- GILCHRIST, H. 1999. Effect of declining population size on predation in murre colonies. *Biological Conservation* 87: 21–19.
- GILCHRIST, I.H.G. & GASTON, A.J. 1997. Effects of murre nest site characteristics and wind conditions on predation by Glaucous Gulls. *Canadian Journal of Zoology* 75: 518–524.
- GRUBB, T.G. & HENSEL, R.J. 1978. Food habits of nesting Bald Eagles on Kodiak Island, Alaska. *Source: The Murrelet, Summer* 59: 70–72.
- HARDING, A.M.A., PIATT, J.F., SCHMUTZ, J.A. ET AL. 2007. Prey density and the behavioral flexibility of a marine predator: the Common Murre (*Uria aalge*). *Ecology* 88: 2024–2033.
- HARDING, A.M.A., PIATT, J.F. & SCHMUTZ, J.A. 2007. Seabird behavior as an indicator of food supplies: sensitivity across the breeding season. *Marine Ecology Progress Series* 352: 269–274. doi:10.3354/meps07072
- HARVEY, C.J., GOOD, T.P. & PEARSON, S.F. 2012. Top-down influence of resident and overwintering Bald Eagles (*Haliaeetus leucocephalus*) in a model marine ecosystem. *Canadian Journal of Zoology* 90: 903–914. doi:10.1139/Z2012-059
- HATCHWELL, B.J. 1991. An experimental study of the effects of timing of breeding on the reproductive success of Common Guillemots (*Uria aalge*). *Journal of Animal Ecology* 60: 721–736.
- HAYWARD, J.L., GALUSHA, J.G. & HENSON, S.M. 2010. Foraging-related activity of Bald Eagles at a Washington seabird colony and seal rookery. *Journal of Raptor Research* 44: 19–29. doi:10.3356/JRR-08-107.1
- HENSON, S.M., DESHARNAIS, R.A., FUNASAKI, E.T., GALUSHA, J.G., WATSON, J.W. & HAYWARD, J.L. 2019. Predator–prey dynamics of Bald Eagles and Glaucous-winged Gulls at Protection Island, Washington, USA. *Ecology and Evolution* 9: 3850–3867. doi:10.1002/ece3.5011
- HENTATI-SUNDBERG, J., BERGLUND, P.A., HEJDSTRÖM, A. & OLSSON, O. 2021. COVID-19 lockdown reveals tourists as seabird guardians. *Biological Conservation* 254: 108950. doi:10.1016/j.biocon.2021.108950
- HERNÁNDEZ-MATÍAS, A., JOVER, L. & RUIZ, X. 2003. Predation on Common Tern eggs in relation to sub-colony size, nest aggregation and breeding synchrony. *Waterbirds* 26: 280–289. doi:10.1675/1524
- HIPFNER, J.M., MORRISON, K.W. & DARVILL, R. 2011. Peregrine Falcons enable two species of colonial seabirds to breed successfully by excluding other aerial predators. *Waterbirds* 34: 82–88. doi:10.1675/063.034.0110
- HIPFNER, M., BLIGHT, L., LOWE, R. ET AL. 2012. Unintended consequences: how the recovery of Sea Eagle *Haliaeetus* spp. populations in the northern hemisphere is affecting seabirds. *Marine Ornithology* 40: 39–52.
- HODGES, J.I. 2011. Bald Eagle population surveys of the north Pacific Ocean, 1967–2010. *Northwestern Naturalist* 92: 7–12.

- HOLLOWELL, G., OTIS, E.O. & FORD, E. 2017. *2016 Lower Cook Inlet Area Finfish Management Report*. Homer, USA: Alaska Department of Fish and Game, Divisions of Sport Fish and Commercial Fisheries.
- HORTON, C.A. 2014. *Top-down Influences of Bald Eagles on Common Murre Populations in Oregon*. MSc thesis. Corvallis, USA: Oregon State University.
- IRVINE, A.L., GULKA, J.E. & DAVOREN, G. 2021. Hatching success of Common Murres *Uria aalge* is linked to the number of neighbours and resource availability. *Marine Ornithology* 49: 229–240.
- LABANSEN, A.L., MERKEL, F. & MOSBECH, A. 2021. Reactions of a colonial seabird species to controlled gunshot disturbance experiments. *Wildlife Biology* 2021: 1–13 doi:10.2981/wlb.00752
- MASSARO, M., CHARDINE, J.W., JONES, I.L. & ROBERTSON, G.J. 2000. Delayed Capelin (*Mallotus villosus*) availability influences predatory behaviour of large gulls on Black-legged Kittiwakes (*Rissa tridactyla*), causing a reduction in kittiwake breeding success. *Canadian Journal of Zoology* 78: 1588–1596.
- MCCLATCHIE, S., GOERICKE, R., LEISING, A. ET AL. 2016. State of the California current 2015–16: Comparisons with the 1997–98 El Niño. *California Cooperative Oceanic Fisheries Investigations Reports* 57: 5–61.
- MURPHY, E.C. & SCHAUER, J.H. 1994. Numbers, breeding chronology, and breeding success of Common Murres at Bluff, Alaska, in 1975–1991. *Canadian Journal of Zoology* 72: 2105–2118.
- PAINE, R.T., WOOTTON, J.T. & BOERSMA, P.D. 1990. Direct and indirect effects of Peregrine Falcon predation on seabird abundance. *The Auk* 107: 1–9.
- PARRISH, J.K. 1995. Influence of group size and habitat type on reproductive success in Common Murres (*Uria aalge*). *The Auk* 112: 390–401.
- PARRISH, J.K., MARVIER, M. & PAINE, R.T. 2001. Direct and indirect effects: interactions between Bald Eagles and Common Murres. *Ecological Applications* 11: 1858–1869. doi:10.1002/9781118445112.stat06589
- PARRISH, J.K. & PAINE, R.T. 1996. Ecological interactions and habitat modification in nesting Common Murres, *Uria aalge*. *Bird Conservation International* 6: 261–269. doi:10.1017/S0959270900003154
- PIATT, J.F. 2002. *Response of Seabirds to Fluctuations in Forage Fish Density*. USGS Final Report to Exxon Valdez Oil Spill Trustee Council and Minerals Management Service. Anchorage, USA: Exxon Valdez Oil Spill Trustee Council.
- PIATT, J.F., HARDING, A., SHULTZ, M. ET AL. 2007. Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology Progress Series* 352: 221–234. doi:10.3354/meps07078
- PIATT, J.F. & HARDING, A.M.A. 2007. Population ecology of seabirds in Cook Inlet. In: SPIES, R. (Ed.) *Long-Term Ecological Change in the Northern Gulf of Alaska*. Amsterdam, Netherlands: Elsevier.
- PIATT, J.F., PARRISH, J.K., RENNER, H.M. ET AL. 2020. Extreme mortality and reproductive failure of Common Murres resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One* 15: 1–32. doi:10.1371/journal.pone.0226087
- PORQUEZ, J., KLUNIS, L., KIM, E., COX, A., DOLINAJEC, N. & ORBER, R. 2021. *Yaquina Head Seabird Colony 2021 Season Summary*. Newport, USA: Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center.
- REGULAR, P.M., HEDD, A., MONTEVECCHI, W.A., ROBERTSON, G.J., STOREY, A.E. & WALSH, C.J. 2014. Why timing is everything: energetic costs and reproductive consequences of resource mismatch for a chick-rearing seabird. *Ecosphere* 5: 1–13. doi:10.1890/ES14-00182.1
- ROMANO, M.D., RENNER, H.M., KULETZ, K.J. ET AL. 2020. Die-offs, reproductive failure, and changing at-sea abundance of murres in the Bering and Chukchi seas in 2018. *Deep-Sea Research Part II* 181–182: 104877.
- RUGGERONE, G.T., SPRINGER, A.M., VAN VLIET, G.B. ET AL. 2023. From diatoms to Killer Whales: impacts of Pink Salmon on North Pacific ecosystems. *Marine Ecology Progress Series* 719: 1–40. doi:10.3354/meps14402
- SCHAUER, J.H. & MURPHY, E.C. 1996. Predation on eggs and nestlings of Common Murres (*Uria aalge*) at Bluff, Alaska. *Colonial Waterbirds* 19: 186–198.
- SCHOEN, S., ARIMITSU, M., MARSTELLER, C. & PIATT, J. 2022. Lingering impacts of the 2014–2016 northeast Pacific marine heatwave on seabird demography in Cook Inlet, Alaska (USA). *Marine Ecology Progress Series*: HEATav1. doi:10.3354/meps14177
- SCHROEDER, I.D., SYDEMAN, W.J., SARKAR, N., THOMPSON, S.A., BOGRAD, S.J., SCHWING, F.B. 2009. Winter pre-conditioning of seabird phenology in the California current. *Marine Ecology Progress Series* 393: 211–223. doi:10.3354/meps08103
- SHULTZ, M.T., PIATT, J.F., HARDING, A.M.A., KETTLE, A.B. & VAN PELT, T.I. 2009. Timing of breeding and reproductive performance in murres and kittiwakes reflect mismatched seasonal prey dynamics. *Marine Ecology Progress Series* 393: 247–258. doi:10.3354/meps08136
- SPEAR, L.B. 1993. Dynamics and effect of Western Gulls feeding in a colony of Guillemots and Brandt's Cormorants. *Journal of Animal Ecology* 62: 399–414.
- SURYAN, R., LOREDO, S., DOLLIVER, J., MEDINA DE ROMAN, A., PORQUEZ, J. & ORBEN, R. 2017. *Yaquina Head Seabird Colony Monitoring 2017 Season Summary*. Newport, USA: Department of Fisheries and Wildlife, Oregon State University, Hatfield Marine Science Center.
- SURYAN, R.M., ARIMITSU, M.L., COLETTI, H.A. ET AL. 2021. Ecosystem response persists after a prolonged marine heatwave. *Scientific Reports* 11: 1–17. doi:10.1038/s41598-021-83818-5
- SURYAN, R.M., IRONS, D.B., BROWN, E.D., JODICE, P.G.R. & ROBY, D.D. 2006. Site-specific effects on productivity of an upper trophic-level marine predator: Bottom-up, top-down, and mismatch effects on reproduction in a colonial seabird. *Progress in Oceanography* 68: 303–328. doi:10.1016/j.pocean.2006.02.006
- SYDEMAN, W.J. 1993. Survivorship of Common Murres on Southeast Farallon Island, California. *Scandinavian Journal of Ornithology* 24: 135–141
- THOMAS, S.M. & LYONS, J.E. 2017. Population trends and distribution of Common Murre *Uria aalge* colonies in Washington, 1996–2015. *Marine Ornithology* 45: 95–102.
- VEITCH, B.G., ROBERTSON, G.J., JONES, I.L. & BOND, A.L. 2016. Great Black-Backed Gull (*Larus marinus*) predation on seabird populations at two colonies in eastern Canada. *Waterbirds* 39: 235–245. doi:10.1675/063.039.sp121
- VERBEEK, N.A.M., Egg predation by Northwestern Crows: its association with human and Bald Eagle activity. *The Auk* 99: 347–352

- VON BIELA, V.R., ARIMITSU, M.L., PIATT, J.F. ET AL. 2019. Extreme reduction in nutritional value of a key forage fish during the Pacific marine heatwave of 2014-2016. *Marine Ecology Progress Series* 613: 171–182. doi:10.3354/meps12891
- VOTIER, S.C., HEUBECK, M. & FURNESS, R.W. 2008. Using inter-colony variation in demographic parameters to assess the impact of Skua predation on seabird populations. *Ibis* 150: 45–53. doi:10.1111/j.1474-919X.2008.00804.x
- WARZYBOK, P.M., JOHNS, M., & BRADLEY, R.W. 2017. Population Size and Reproductive Performance of Seabirds on Southeast Farallon Island, 2017. Unpublished report to the U.S. Fish and Wildlife Service. Point Blue Conservation Science Contribution Number 2158. Petaluma, USA: Point Blue Conservation Science.
- WELLS, B.K., SCHROEDER, I.D., BOGRAD, S.J. ET AL. 2017. State of the California Current 2016–17: still anything but “normal” in the north. *California Cooperative Oceanic Fisheries Investigations Reports* 58: 1–55
- WHITE, A.F., HEATH, J.P. & GISBORNE, B. 2006. Seasonal timing of Bald Eagle attendance and influence on activity budgets of Glaucous-winged Gulls in Barkley Sound, British Columbia. *Waterbirds* 29: 497–500. doi:10.1675/1524
- WILHELM, S.I. & STOREY, A.E. 2002. Influence of cyclic pre-lay attendance on synchronous breeding in Common Murres. *Colonial Waterbirds* 25: 156–163.
- WOOD, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. *Journal of the Royal Statistical Society Series B: Statistical Methodology* 73: 3–36.
- ZADOR, S.G., PARRISH, J.K. & PUNT, A.E. 2009. Factors influencing subcolony colonization and persistence in a colonial seabird, the Common Murre *Uria aalge*. *Marine Ecology Progress Series* 376: 283–293. doi:10.3354/meps07797
- ZADOR, S.G. & PIATT, J.F. 1999. Time-Budgets of Common Murres at a declining and increasing colony in Alaska. *The Condor* 101: 149–152
-