



Lingering impacts of the 2014–2016 northeast Pacific marine heatwave on seabird demography in Cook Inlet, Alaska (USA)

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ABSTRACT: A protracted period (2014–2016) of anomalously warm water in the northeast Pacific Ocean precipitated an extensive die-off of common murres *Uria aalge* (hereafter 'murre') during 2015–2016, accompanied by reduced colony attendance and reproductive success of murre and black-legged kittiwakes *Rissa tridactyla* ('kittiwakes') starting in 2015. Most murre died of starvation following a large-scale reduction in abundance and quality of forage fish. To assess murre and kittiwake recovery following the marine heatwave, we monitored their demographics at 2 colonies (Chisik and Gull Islands) in Cook Inlet, Alaska (USA), from 2016 to 2019. Compared to historic data (1995–1999), we observed declines and increased variability in colony attendance and productivity across species and colonies, and predation was widespread. At Chisik, where food limitations were common during historic studies, both species experienced substantial population declines and reproductive failures in all 4 years (2016–2019) following the heatwave. At Gull, a typically productive colony during historic studies, murre failed to fledge chicks for 3 years (2016–2018) following the heatwave. By 2019, murre productivity recovered to about half that observed during historic studies (0.28 vs. 0.54 chicks per pair), but populations had declined by half. Kittiwake population size at Gull declined a quarter from historic counts, and reproduction alternated between complete breeding failures (2016/2018) and high productivity (2017/2019). These multi-year demographic impacts indicate lingering effects of the heatwave on kittiwakes and murre through forage fish depletion and increased predator disturbance, and possibly other stressors. It remains unknown whether populations can rebound to historic levels. If so, recovery would likely take decades.

KEY WORDS: Marine heatwave · 'The Blob' · Common murre · *Uria aalge* · Black-legged kittiwake · *Rissa tridactyla* · Die-off · Gulf of Alaska

1. INTRODUCTION

Marine heatwaves, which have recently been defined as prolonged periods of anomalously warm ocean temperatures characterized by specific thresholds in duration, intensity, and spatial extent (Hobday et al. 2016), have increased around the world in recent decades (Hobday et al. 2018). From 2014 to 2016, two water temperature warming events in the

northeast Pacific, 'The Blob' in 2014–2016 and a strong El Niño in 2015–2016, created marine heatwave events in the northeast Pacific that persisted longer and covered a larger area than any previous event on record (Bond et al. 2015, Di Lorenzo & Mantua 2016, Hobday et al. 2018, Oliver et al. 2021). In the northern Gulf of Alaska, marine heatwave event intensity averaged 1.4 to 2.1°C above normal and lasted for more than 750 d in some areas of lower

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Cook Inlet (Arimitsu et al. 2021a). These persistent warm-water anomalies elicited dramatic responses from the Gulf of Alaska marine ecosystem, including large changes in primary productivity, the largest harmful algal bloom on record, marked changes in plankton community composition and abundance, and massive declines in the abundance of forage fish species and many of their higher predators (McCabe et al. 2016, Barbeaux et al. 2020, Arimitsu et al. 2021a, Suryan et al. 2021, Gabriele et al. 2022).

During this prolonged marine heatwave, the availability and quality of forage fish and other forage nekton were drastically reduced in the system throughout the Gulf of Alaska. An abrupt decline in capelin *Mallotus catervarius* and cool-water euphausiid species occurred at the onset of the heatwave (Arimitsu et al. 2021a). The energy content of Pacific sand lance *Ammodytes personatus* declined as much as 89% during the heatwave years compared to previous cooler years (von Biela et al. 2019). Spawning capelin were younger and smaller during the heatwave, and Pacific herring *Clupea pallasii* spawning biomass was historically low (Arimitsu et al. 2021a, Trochta & Branch 2021). A notable truncation of older, larger size classes of forage fish from research fishery samples suggested top-down removals, which may have resulted from increased predation pressure by ectothermic predatory fish that responded to warmer waters with higher metabolic rates and food demands (Barbeaux et al. 2020, Piatt et al. 2020). Holsman & Aydin (2015) demonstrated through a modeling approach that a 2°C increase in temperature has the potential to increase metabolism of ectothermic predators by 34–70%. During this nearly continuous heatwave, these increased feeding rates would have lasted through multiple winters, when metabolic rates of groundfish are typically low. However, this analysis does not account for potential changes in groundfish predator distribution (e.g. shifts to cooler waters) or abundance (declines due to unusually high mortality).

Negative effects on higher predators were likely amplified by a collapse in the forage fish portfolio (i.e. simultaneous decline in multiple key forage fish populations), thereby reducing their resilience in the trophic system (Arimitsu et al. 2021a). Pacific cod stock biomass, comprised largely of older adult age classes, declined by 83% (Barbeaux et al. 2020). Additionally, this led to changes in the distribution, mass mortality, reproductive failures, and reduced body condition of pelagic predators such as marine birds (e.g. common murres *Uria aalge*, hereafter 'murres') and mammals (e.g. humpback whales *Megaptera novaeangliae*) (Savage 2017, Piatt et al.

2020, Arimitsu et al. 2021a, Gabriele et al. 2022). In southeast Alaska (USA), non-calf humpback whale abundance decreased by 56% between 2013 and 2018, survival declined after the heatwave, calf production was much lower during and after the heatwave than before, and calf survival dropped tenfold starting in 2013 (Gabriele et al. 2022).

Massive die-offs of multiple marine bird species were among the more conspicuous effects of the heatwave, with an estimated 0.5–1.2 million murres dying along the US west coast from California to Alaska during this persistent, multi-year event (Jones et al. 2018, 2019, Piatt et al. 2020). Die-offs of murres have occurred periodically in Alaska (e.g. 1970, 1993, 1998, and 2004); however, the 2015/2016 murre die-off was distinguished from others by its extremes in duration, magnitude, and geographic extent (Piatt et al. 2020). Alongside the die-off, murres exhibited complete reproductive failure at one colony in the Gulf of Alaska and poor productivity at another colony in the Bering Sea during 2015, and by 2016, those breeding failures became common (Dragoo et al. 2016, 2017, Piatt et al. 2020). Reproductive failures also plagued black-legged kittiwakes *Rissa tridactyla* (hereafter 'kittiwakes') across the Gulf of Alaska and the Bering Sea in 2015 and 2016 (Dragoo et al. 2016, 2018).

Murres and kittiwakes are two of the most long-lived, wide-spread, and numerous seabird species, with circumpolar distributions across the northern hemisphere (Ainley et al. 2020, Hatch et al. 2020). Both species share similar diets, consuming forage fish and marine invertebrates, but they differ in their foraging niches: murres capture prey by diving, typically to depths of 20–50 m, whereas kittiwakes are surface-feeders (Ainley et al. 2020, Hatch et al. 2020). These colonial nesters often breed at the same colonies and have high nest-site fidelity (Ainley et al. 2020, Hatch et al. 2020). Murres typically nest on flat ledges adjacent to cliff walls, or on flat terrain when in high concentrations, and lay eggs directly on the bare ground (Ainley et al. 2020). Kittiwakes, on the other hand, build nests out of mud and vegetation and nest on narrower cliff ledges than other cliff-nesters (Hatch et al. 2020). The breeding site characteristics of both species are shaped by predator avoidance, and avian predators are a common cause of mortality to both adult birds, chicks, and eggs (Ainley et al. 2020, Hatch et al. 2020). The main causes of mortality for both species, however, are winter die-offs related to starvation from inadequate forage (Ainley et al. 2020, Hatch et al. 2020).

To better understand the recovery of seabirds following the 2014–2016 marine heatwave, we con-

ducted a study from 2016 to 2019 of murre and kittiwakes at 2 colonies in lower Cook Inlet, in the northern Gulf of Alaska, near the geographic center of the 2015–2016 murre die-off in Alaska. In 2019, the last year of this study, a second marine heatwave emerged, which extended into 2020 (Chen et al. 2021). We chose to study colonies in lower Cook Inlet because intensive studies of seabirds and factors influencing their distribution, abundance, and reproductive success were conducted there during the mid- to late 1990s (Piatt 2002, Harding et al. 2007, Shultz et al. 2009). In this paper, we characterize the intensity and duration of marine heatwaves in our study region, examine seabird demographics in lower Cook Inlet in the aftermath of the 2014–2016 heatwave and during the 2019 heatwave, and compare recent findings to historic studies conducted in the 1990s to better understand the mechanisms by which heatwaves can impact seabird demography.

2. MATERIALS AND METHODS

2.1. Study site

Our study area was lower Cook Inlet (58.7°–60.4° N, 154.2°–151.1° W), in southcentral Alaska, where we focused on 2 seabird colonies: Chisik Island (and adjacent Duck Island, hereafter combined as ‘Chisik’) on the west side of the inlet, and Gull Island on the east side (Fig. 1). Despite being relatively close to each other, the waters around the colonies have distinctly different oceanographic regimes. Waters around Chisik are shallow (<60 m), well-mixed, relatively warm, highly turbid, and support low levels of primary production (Speckman et al. 2005). Conversely, Gull is situated inside Kachemak Bay, a fjord with shallow shelves on both sides and a deep (~100–200 m) trough running through it. Waters are cold and mixed by upwelling at the entrance of the bay, but glacial runoff promotes stratification and high productivity within the bay (Speckman et al. 2005, Harding et al. 2007). Forage fish communities in lower Cook Inlet include sand lance and herring in shallow, nearshore habitats, and walleye pollock *Gadus chalcogrammus*, Pacific cod *G. macrocephalus*, and capelin in deeper, offshore habitats (Abookire & Piatt 2005).

2.2. Marine heatwaves

To document local changes in marine temperatures likely to be relevant to breeding seabirds in our study

area, we quantified the monthly duration (number of days) and mean intensity (magnitude of the anomaly, °C) of marine heatwave events between 1982 and 2021. Marine heatwave events were defined to occur when local sea surface temperatures (SSTs) exceeded the 90th percentile threshold for at least 5 d (Hobday et al. 2016). Daily ¼ degree optimum interpolation SST data (OISST v2.1, Huang et al. 2020) from the study area region (Fig. 1) were averaged and compared to the 30 yr climatological period between 1983 and 2012 (inclusive) as the baseline to estimate percentile thresholds and mean climatological SST, based on recommendations from recent global analyses (Hobday et al. 2018, Sen Gupta et al. 2020). OISST data are satellite derived, so are not as accurate as directly measured SST. Analyses were conducted in R version 4.1.2 (R Core Team 2020) using the R package ‘heatwaveR’ (Schlegel & Smit 2018, Schlegel et al. 2019).

2.3. Population monitoring

We based our 2016–2019 monitoring protocols on historical studies of seabirds in Cook Inlet (Piatt 2002) and US Fish and Wildlife Service (USFWS) pro-

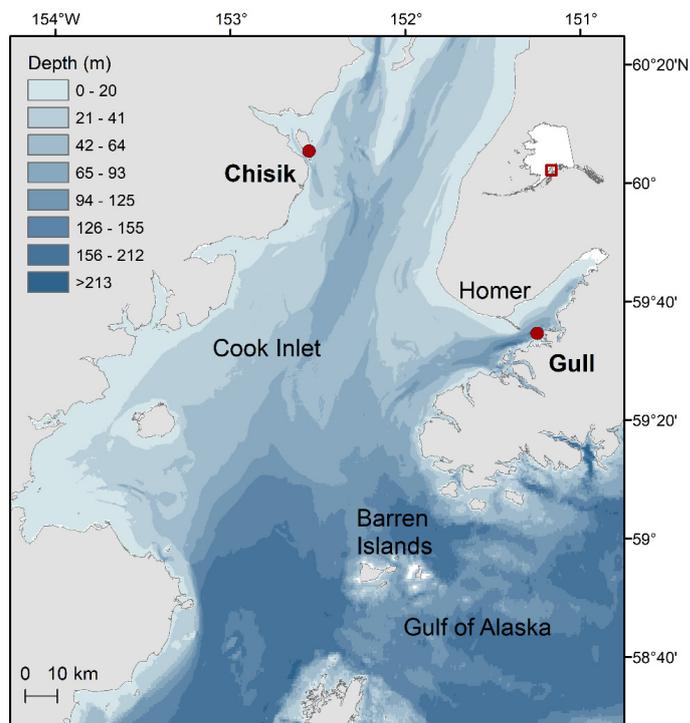


Fig. 1. Two seabird colonies (red circles) studied in 1995–1999 and 2016–2019 in lower Cook Inlet, Alaska, USA. Bathymetry data are shown in blue, with darker shades indicating deeper seafloor depths (Zimmermann & Prescott 2014)

protocols (Alaska Maritime National Wildlife Refuge 2019), with some modifications as outlined below. The associated data release (Arimitsu et al. 2021b) includes population monitoring data, productivity data, and predation data.

2.3.1. Census counts

We conducted colony-wide censuses to monitor possible growth or contractions of seabird populations (Piatt 2002). These were usually conducted only once a year (2016–2019) at Chisik and Gull during the mid-incubation period for each species. Census counts generally occurred between 10:00 and 16:00 h, when attendance is most stable during daylight hours (Piatt & McLagan 1987). Censuses were conducted by circumnavigating islands in a small skiff and counting (with aid of binoculars) all murres and kittiwakes observed on land. For areas that were difficult to observe from the water (e.g. high cliffs or island tops), we took photographs using Nikon digital SLR cameras with telephoto lenses and counted individuals from photographs using ArcGIS (10.3, ESRI). After importing the images, we marked points at the location of each bird by species, and the program summed the number of each bird species within each point shapefile.

2.3.2. Population plots

Population plots were established in the 1990s for monitoring population trends (Piatt 2002). We counted birds between 10:00 and 16:00 h on established population plots at Chisik ($n = 8$ plots) and Gull ($n = 10$) several times throughout the breeding seasons of 2016–2019 (see Table 1). At both colonies, we photographed individual population plots from an inflatable skiff on the water. We imported plot photos, digitized the plot boundaries, and counted kittiwakes and murres within the plots using ArcGIS.

For each survey day, we summed the total number of birds counted in all plots for a colony-wide total. We then calculated a mean and standard deviation of the number of kittiwakes and murres at each colony across all survey days in each year, and across all survey days within each time period (historic and recent). Historical counts were conducted by eye, using binoculars, also from small skiffs. To compare the accuracy of the different methods, we counted plots using both methods once per year during 2016–2018. Counts of kittiwakes and murres were within 1 and

6% of each other, respectively, for the different methods. This was better than the precision ($<10\%$ difference) deemed acceptable by the USFWS in protocols for conducting replicate binocular counts of ledge-nesting seabirds on plots from skiffs (Alaska Maritime National Wildlife Refuge 2019), so we treated the photo counts as comparable to the historical counts using binoculars.

In accordance with recommended protocols, historic population plot data were gathered during a time window between mid-incubation and start of fledging for both kittiwakes and murres, when stable, peak numbers of birds are generally observed (Piatt 2002). During this study, breeding phenology was difficult to assess due to multiple years of breeding failure. Mid-incubation appeared to occur at dates similar to those in the past, but initiation of fledging was often relatively late, if any chicks were fledged at all. Birds that fledged may have been from replacement clutches, and they fledged so late in the season that most adults had already abandoned the colony. To compensate for this protracted time window which would have created a bias in our analysis, we used population plot count dates (Table S1 in the Supplement, www.int-res.com/articles/suppl/m14177_supp.pdf) that were 5 d before or after the range of historic mid-incubation to start-of-fledge dates for kittiwakes (Chisik: 19 June–28 July; Gull: 22 June–28 July) and murres (Chisik: 21 July–25 August; Gull: 24 July–24 August), a slightly different subset of dates than those reported by Arimitsu et al. (2021c). Phenology can be variable year to year, as seen at other colonies across Alaska in post-heatwave years (Dragoo et al. 2017, 2018, 2019, 2020). Nonetheless, we believe that the historic timeframe from mid-incubation to start of fledging provided the most accurate window for measuring peak, stable populations of both species at these colonies for reasons described above.

2.3.3. Population index

Population plots typically provide a more precise metric for tracking population change over time than colony-wide census counts, but either method can be used as an index of change. Population plots usually comprise a small but representative subset of the colony population, making them easier to count repeatedly and to establish estimates of variability. Colony-wide census counts, on the other hand, take longer to conduct than plot counts, so are not feasible to conduct repeatedly, but they encompass the entire colony, so sometimes capture different trends than

what occur on population plots (e.g. murres on Chisik in 2017). For these reasons, replicated population plot counts are most often used as an index of population change for cliff-nesting species, and we used population plot data to assess change for kittiwakes at both colonies and for murres at Chisik. However, we used colony-wide census data to assess change in murre populations at Gull because a large portion of murres occur on the flat tops of the colony, and those birds were counted during censuses but not on the cliff-side population plots. To summarize changes in population size over time, we calculated standardized anomalies by species and colony by subtracting the mean of all years pooled from the annual value and dividing by the standard deviation of all years. We assessed interannual variability in colony attendance by calculating the coefficient of variation (CV) of the annual population index values in each study period.

2.4. Productivity

We obtained an index of reproductive success for kittiwakes based on the proportion of nests within population plots during mid-incubation that contained chicks later in the season. This index is reasonably accurate, and well correlated ($r^2 > 0.90$) with indices of productivity measured by frequent (every 3 d) nest monitoring, although it may overestimate production by 5% or more (depending on fledging success rates) because this method assumes that every chick observed will survive to fledge (Piatt 2002). We counted kittiwake nests during incubation that were well developed and apparently active, with new nesting material and a well-formed nest cup. For our index of productivity in each year, we divided the maximum number of chicks by the maximum number of well-developed nests. We use the ratio of the chicks per nest as a proxy for the number of chicks fledged per active nest of a breeding pair of adults to indicate breeding success in kittiwakes.

We estimated murre productivity using time-lapse videos and photographs taken from cameras mounted near island tops. The number of pairs attempting to nest on these plots was highly variable, owing largely to failed breeding attempts. We monitored 2 plots on Chisik (~22 eggs observed across all years) and 3 plots on Gull (~189 eggs). We were unable to determine nest fate from footage at primary observation plots at Gull in 2017 and at Chisik in 2019, so we calculated productivity using suboptimal plots (areas where fewer murres were attempting to nest),

which may have underestimated productivity in those years. Game cameras recorded videos (Brinno and Plotwatcher Pro) or time-lapse photographs (Reconyx HyperFire 2[®]; recorded every 15, 20, or 30 s) across the entire breeding season for murres, from late June to early October, in most years. We calculated productivity by dividing the number of chicks estimated to be at least 15 d old by the number of eggs laid. We did not distinguish between initial or replacement eggs, which murres will sometimes lay if the first egg is lost (Ainley et al. 2020), as we were unable to reliably distinguish replacement eggs due to a large field of view including many nest sites. We calculated chick age using the date the chick was first seen to the last day it was seen, and used 15 d as the threshold age to be considered a likely fledgling because that is generally the youngest age of departure, and mortality of chicks is usually very low after reaching that age (Gaston & Jones 1998, Piatt 2002). If the chick was hidden from view when it hatched and was medium/large when first seen (i.e. large enough that the chick could not be obscured beneath a brooding adult), then the estimated hatch date was calculated from the date the egg was first laid and the average length of incubation (32 d; Ainley et al. 2020). We use the common term of chick per pair as a proxy for the number of chicks fledged per egg laid by a pair of breeding adults.

2.5. Predation

We reviewed nest camera footage to assess avian disturbance of nesting birds and predation on eggs or chicks. Video of kittiwake nest plots on Gull was recorded for 5 min twice daily throughout the breeding season by the Pratt Museum (Homer, AK) from 2016 to 2018. These remote 'live' transmission cameras were installed for the benefit of museum visitors and were positioned to view large numbers of seabirds. Footage of kittiwake nests was unavailable for Gull in 2019 or for Chisik in any year. We used our own time-lapse videos and photographs (as described in Section 2.4) to assess predation on murre eggs at Chisik and Gull from 2016 to 2019. Eggs were considered predated if they were observed being taken from the nest by a predator or if the egg disappeared from the nest in one frame and a predator was seen with an egg in subsequent frames. The number of nests we could observe varied among years owing to low numbers of nesting attempts in some years, camera malfunctions, or obstruction of the camera view by vegetation.

3. RESULTS

3.1. Marine heatwaves

Marine heatwave events had low frequency, short duration, and low intensity from 1982 through the early 1990s (Fig. 2; Fig. S1). More modest marine heatwave events occurred between summer 1997 and spring 1998, and in the early 2000s, with peaks in intensity during winter 1998 and summer 2005. A cooler period occurred in lower Cook Inlet from 2007 through 2013, when no marine heatwave events were detected. In contrast, persistent marine heatwave events were detected in most months between July 2014 and December 2016 (Fig. 2; Table S2). Heatwave conditions were nearly continuous throughout all of 2016, with high intensities detected especially during late spring (April–June), and mean intensities peaking at 2.49°C above average in May that year. Following the extended period of heatwave events in our study area throughout most of 2014–2016, there were relatively few events during 2017 through summer 2018. Heatwave event intensity and duration increased again starting in fall 2018 and continued through the summer of 2019, with events peaking during summer months (June–August), and peak mean intensities of 2.18°C above average in July.

3.2. Population monitoring

3.2.1. Census counts

Colony-wide census counts for kittiwakes at Chisik were on average 80% lower in the recent study period (2016–2019) than in the historic period (1995–1999), although only one census from 1995 was available for comparison (Table 1). Kittiwake attendance at Chisik was extremely low in 2016, and kittiwakes had completely abandoned the colony by the time of the census (Table 1). Excluding the outlier year of 2016 results in a 73% decline in population between study periods. Average census counts for kittiwakes at Gull in recent years declined by only 8% from the mean of past surveys and exhibited low variability among recent years (Table 1).

Murre populations declined at both colonies from historic census counts (Table 1). Recent census counts for murre were on average 72% lower than historic counts on Chisik. The recent murre census counts on Gull were on average 46% lower than historic censuses.

3.2.2. Population plots

The mean number of birds counted on population plots during the recent study period was lower than during the historic period for kittiwakes at both Chisik (–92%) and Gull (–25%; Table 1). Counts at both colonies were lowest in 2018. Similarly, the mean number of murre on population plots was 71% lower at Chisik and 22% lower on Gull than they were in historic surveys (Table 1).

3.2.3. Population index

Using a mixture of colony-wide census counts and population plots (see Section 2.3.3), we observed mostly negative population anomalies for kittiwakes and murre at both colonies during recent post-heatwave years compared to mostly positive anomalies during the historic period (Fig. 3). Kittiwake attendance was higher and relatively stable (CV < 20%) at both colonies during historic years, followed by much lower and moderately variable (CV = 44%) attendance at Chisik, and slightly lower but stable (CV = 10%) attendance at Gull during the recent study period. Similarly, murre attendance was much higher at both colonies in historic years, with moderate variability at Chisik (CV = 42%) and Gull (CV = 24%). Variability in murre attendance increased markedly during the recent post-heatwave years at both Chisik (CV = 116%) and Gull (CV = 41%). The lowest murre population anomalies were observed in 2016 and 2017 at Chisik, and in 2018 and 2019 at Gull.

3.3. Productivity

Kittiwakes failed to successfully reproduce (<0.02 chicks per nest, henceforth 'chicks' in this paragraph) at Chisik in all recent years (Table 1, Fig. 3). Average kittiwake productivity during historic years at Chisik was low (0.04 chicks), yet it was even lower (0.01 chicks) in recent years. Kittiwakes at Gull also failed to successfully reproduce in 2016 and 2018; however, they had high levels of productivity in 2017 (0.61 chicks) and 2019 (0.67 chicks). That recent high productivity was comparable to the most productive years of the historic period (i.e. 1995, 1996, 1998; Table 1), and included many multiple-chick nests. Mean productivity of kittiwakes at Gull was lower in recent years (0.32 chicks) than in historic years (0.46 chicks).

Murre failed to fledge any chicks on study plots at both Gull and Chisik during the first 3 years (2016–

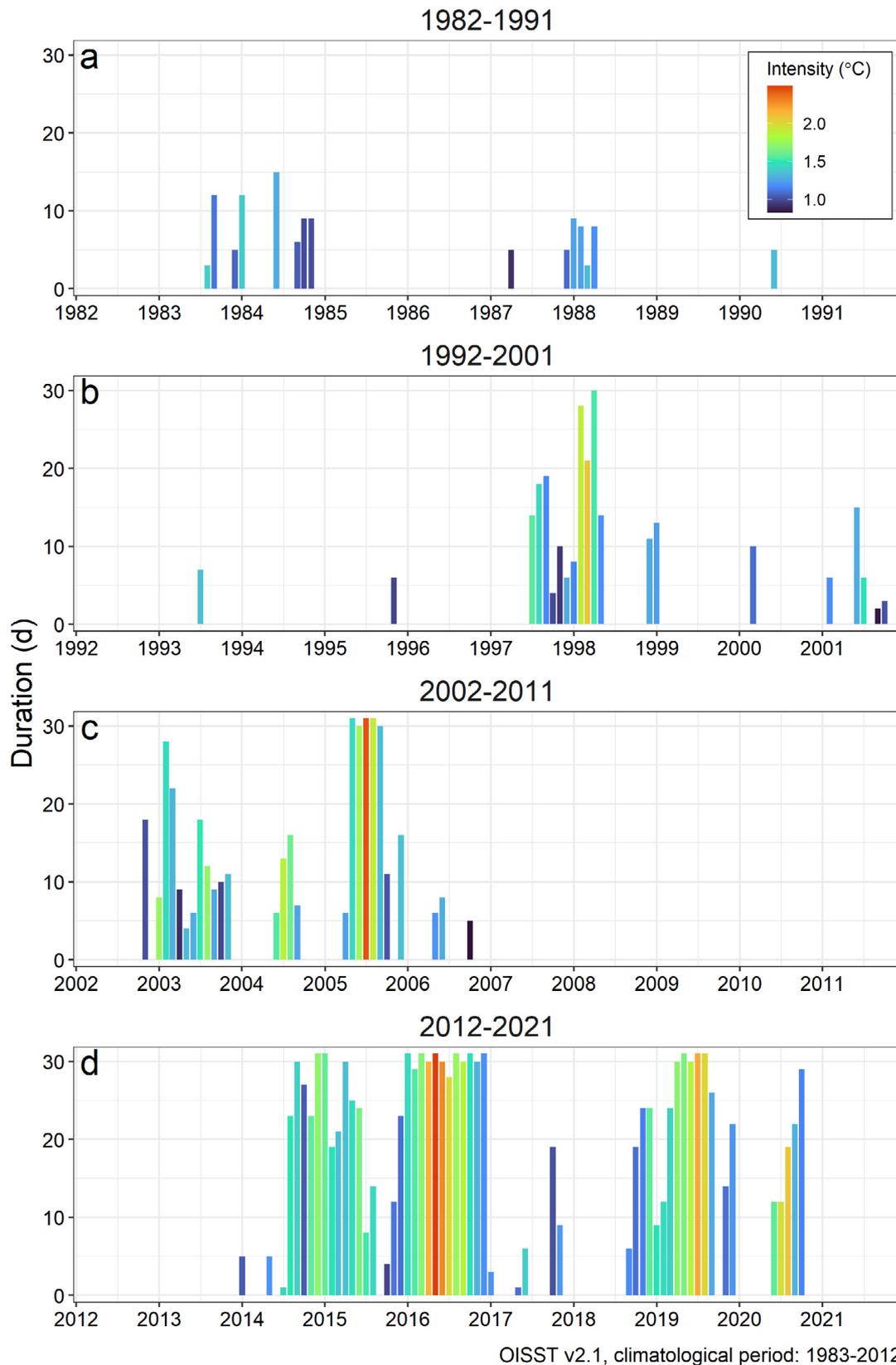


Fig. 2. Duration and mean intensity (°C above average; color scale) by month for marine heatwave events in lower Cook Inlet, Alaska, across decades between 1982 and 2021: (a) 1982–1991, (b) 1992–2001, (c) 2002–2011, (d) 2012–2021

Table 1. Demographic indices by colony (Chisik and Gull Islands) and year (1995–1999, 2016–2019) for common murre (COMU) and black-legged kittiwakes (BLKI) in lower Cook Inlet, Alaska, USA. Mean and SD were calculated for each time series and for annual population plots, and the number of surveys is shown (N). Productivity was measured as chicks per nest for BLKI and chicks fledged per pair for COMU. The ‘-’ indicates no available data

Year	Species	Colony-wide censuses		Population plots				Productivity	
		Chisik	Gull	Chisik		Gull		Chisik	Gull
				Mean (SD)	N	Mean (SD)	N		
1995	BLKI	16504	8166	857 (264)	6	1312 (85)	5	-	0.40
1996	BLKI	-	-	890 (313)	5	1109 (82)	5	0.05	0.56
1997	BLKI	-	-	591 (84)	6	1196 (69)	7	0.01	0.46
1998	BLKI	-	-	584 (173)	5	1203 (118)	7	0.00	0.28
1999	BLKI	-	5809	688 (25)	3	1094 (61)	6	0.09	0.59
1995–1999	BLKI	16504 (-)	6988 (1667)	725 (237)		1182 (110)		0.04 (0.04)	0.46 (0.13)
2016	BLKI	1	5141	42 (57)	2	927 (84)	4	0.00	0.01
2017	BLKI	4707	6369	81 (28)	2	997 (37)	3	0.00	0.61
2018	BLKI	2552	7479	27 (37)	2	790 (231)	4	0.00	0.00
2019	BLKI	5931	6719	74 (10)	3	896 (163)	4	0.02	0.67
2016–2019	BLKI	3298 (2604)	6427 (975)	58 (35)		896 (157)		0.01 (0.01)	0.32 (0.37)
1995	COMU	2246	8553	64 (12)	5	384 (8)	3	-	0.61
1996	COMU	-	-	153 (15)	4	340 (47)	5	0.74	0.64
1997	COMU	3500	6068	139 (42)	8	344 (21)	10	0.67	0.53
1998	COMU	-	10400	69 (7)	3	334 (31)	5	0.18	0.65
1999	COMU	-	10725	187 (58)	5	407 (49)	6	0.63	0.28
1995–1999	COMU	2873 (887)	8937 (2138)	127 (57)		359 (43)		0.56 (0.25)	0.54 (0.15)
2016	COMU	80	7636	0 (0)	2	297 (198)	6	0.00	0.00
2017	COMU	1285	4658	20 (-)	1	366 (46)	3	0.00	0.00
2018	COMU	971	3147	89 (-)	1	217 (93)	3	0.00	0.00
2019	COMU	854	3771	76 (-)	1	242 (64)	4	0.00	0.28
2016–2019	COMU	798 (512)	4803 (1988)	37 (43)		281 (135)		0.00 (0.00)	0.07 (0.14)

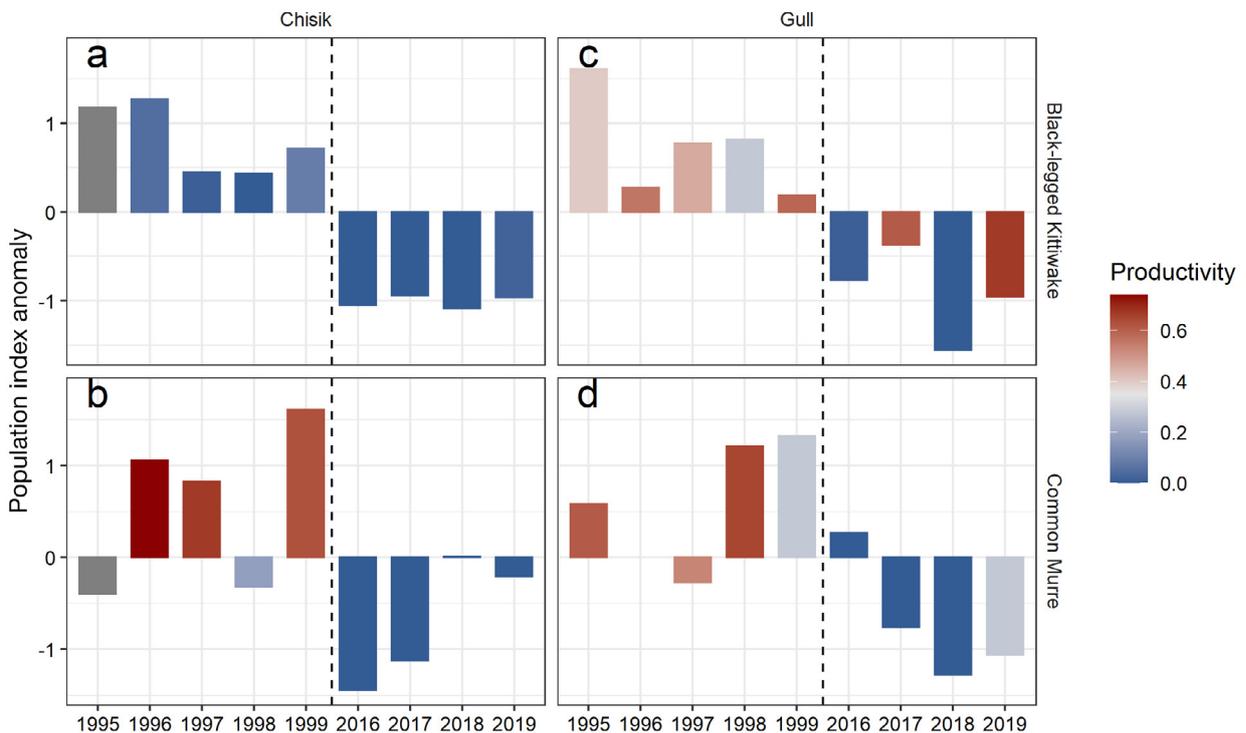


Fig. 3. (a,c) Black-legged kittiwake and (b,d) common murre population index anomalies (height of bar) and productivity (color of bar from highest value in dark red to lowest value in dark blue) at 2 colonies (Chisik: a,c; Gull: b,d) in lower Cook Inlet, Alaska, in 1995–1999 and 2016–2019. The vertical dashed line separates study periods before and after the northeast Pacific marine heatwave from 2014 to 2016

2018) of our recent study (Table 1, Fig. 3). In 2016 and 2018, no chicks were observed anywhere on the colonies, on or off study plots. One chick hatched on a plot at Gull in 2017, and 5 chicks were observed off plots, but the on-plot chick disappeared before it could have fledged (3 d post hatch). During 2019, murren again failed to produce chicks on study plots at Chisik, but fledged chicks (0.28 chicks per pair) at Gull for the first time since the heatwave. Although this was a marked improvement in breeding success, it was still just over half the average productivity observed in the past (0.54 ± 0.14 chicks per pair; Table 1). Overall productivity of murren in recent years was lower at Gull (−87%) and Chisik (−99%) than in historic years.

3.4. Predation

The vast majority of observed predation events at the colonies were of murre and kittiwake eggs, with smaller instances of predation on adults and chicks of both species. Predator species included glaucous-winged gulls *Larus glaucescens*, herring gulls *L. argentatus*, bald eagles *Haliaeetus leucocephalus*, peregrine falcons *Falco peregrinus*, and northwestern crows *Corvus caurinus*. Kittiwake eggs disappeared from monitored nests ($n = 68$ nests in 2016, 59 in 2017, and 83 in 2018) in video plots on Gull in all years, but only in 2018 was there video footage of eggs ($n = 4$ eggs) being directly taken by predators, possibly indicating increased predation pressure in 2018.

We observed high levels of predation on murre eggs throughout the study period. At Chisik, 92% of murre eggs ($n = 24$) at monitored nests were preyed upon by glaucous-winged gulls, and the remainder (8%) disappeared for unknown reasons. We did not observe any murre chicks hatch at Chisik in any year. At Gull, we also observed high levels of murre egg predation by both glaucous-winged and herring gulls. This predation was often facilitated by an appearance of bald eagles or occasionally peregrine falcons, which often resulted in murren and kittiwakes being flushed off their nest sites en masse. From 2016 to 2018, 67% of murre eggs laid at Gull ($n = 113$) were observed being preyed upon and 33% disappeared; no eggs hatched. In 2019, 51% of murre eggs laid at Gull ($n = 102$) were preyed upon, 27% disappeared, and 22% hatched.

We saw few instances of predation on adult seabirds. In 2018, our productivity plot camera captured an adult murre being preyed by a bald eagle. We directly observed a peregrine falcon taking an adult

kittiwake in 2018, and in other years we occasionally observed eagles taking adult kittiwakes and chicks, as well as adult murren.

4. DISCUSSION

4.1. Marine heatwaves

Warm ocean temperature anomalies, regardless of whether they meet current criteria of marine heatwaves, are known drivers of ecosystem change in the North Pacific (Rosenzweig et al. 2008, Wernberg et al. 2013). For example, during the late 1970s, the change from a persistent cold to persistent warm ocean state in the northeast Pacific as a result of the Pacific Decadal Oscillation radically changed the composition and abundance of zooplankton and fish communities during a multi-year transition (Hare & Mantua 2000). In turn, this impacted the diets, population size, and demographics of long-lived vertebrates, including groundfish, seabirds, and marine mammals during the decade following the transition (Anderson & Piatt 1999, Trites et al. 2007, Sydeman et al. 2009). The scale of oceanographic and biological changes was so pervasive and persistent that the term ‘regime shift’ was adopted to describe this event in marine systems (Francis et al. 1998). Since that time, regime shifts have been reported widely in the north Pacific and Atlantic Oceans, and often appear to be driven by long-term ocean temperature oscillations (Möllmann & Diekmann 2012).

Higher-frequency warming events linked to El Niño, or stochastic weather anomalies, have been responsible for relatively short-lived (1–2 yr) disruptions of the California Current ecosystem (Jacox et al. 2016), and to a lesser degree, the Gulf of Alaska ecosystem (Bailey et al. 1995). These disruptions often include negative impacts on seabird breeding success, likely mediated by reductions in the availability of preferred prey (Hatch 1987, Wilson 1991, Velarde et al. 2004, Ainley et al. 2020). One of the largest warm-water events of the 20th century, the El Niño of 1997–1998 (Chandra et al. 1998), had wide-ranging impacts throughout the Pacific, including a die-off of murren, an increase in murre and kittiwake physiological stress during the following breeding season, chick diet changes, delayed phenology, and reproduction declines and failures (Piatt et al. 1999, Miller & Sydeman 2004, Gladics et al. 2015).

In comparison to these historical warm-water events, the recent ecosystem (Arimitsu et al. 2021a, Suryan et al. 2021) and seabird community (Jones et

al. 2018, 2019, Piatt et al. 2020) responses to the 2014–2016 heatwave were more extreme. This was likely due to the high intensity, multi-year persistence, and substantial thermal impact of the heatwave over a vast area of the Gulf of Alaska (Di Lorenzo & Mantua 2016, Hobday et al. 2018, Oliver et al. 2021). The magnitude of the 2014–2016 heatwave impact on seabirds, marine mammals, and groundfish was unprecedented, causing rapid and marked declines (20–80%) in some high trophic-level animal populations as well as severe reductions in reproductive success (Barbeaux et al. 2020, Piatt et al. 2020, Arimitsu et al. 2021a, Gabriele et al. 2022).

The influence of the 2019 heatwave on seabirds was not so obvious. In 2019, numbers of birds at colonies remained reduced compared to historic levels (Fig. 3), and the number of birds foraging at sea in our study area was just slightly higher than all-time lows observed in 2018 (Arimitsu et al. 2021c), and yet we observed high kittiwake productivity and the first sign of recovery in murre reproduction at Gull Island. The warm-water anomaly in 2019 may have had limited impact on birds because it was much shorter in duration (Amaya et al. 2020) and peaked later in the summer breeding season than the 2014–2016 heatwave (Fig. 2). Thus, there were cooler temperatures preceding the breeding season, which would predict higher fish abundance and seabird breeding success in the following summer (Ainley et al. 1995, Shultz et al. 2009). In the California Current, the apparent effects of the 2019 marine heatwave on seabirds were mixed: murres and other seabirds at Yaquina Head experienced moderate reproductive success in 2019; however, farther south at Southeast Farallon Island, productivity of murres and other seabirds was low in 2019 (Thompson et al. 2019).

Perhaps the most disturbing finding was that impacts of the heatwave in lower Cook Inlet, manifested initially in the very visible die-off event during the winter of 2015–2016, continued for at least 3 more years after its peak in 2016, even after the water temperatures returned to normal for most of 2017 and 2018 (Fig. 2). We identified lingering impacts of the heatwave on seabird demography in Cook Inlet up to 2019, which we discuss below. Murre productivity showed the first signs of recovery in 2019, albeit at only half the historic rate. Kittiwakes managed to produce chicks in 2017 and 2019 at high levels, which suggests they were not constrained by food (Piatt & Harding 2007), but they had 2 years of complete reproductive failure among those years of success. Evidence from this and other studies suggests that both initial and lingering impacts of

the heatwave were driven by marked reductions in forage fish abundance and quality (von Biela et al. 2019, Arimitsu et al. 2021a), and that these and other ecosystem impacts persisted for years (Suryan et al. 2021). Our studies also suggest that predator disturbance (*C. Marsteller* unpubl. data) impacted seabird demographics directly, an effect that was likely exacerbated by the original heatwave and lingering effects on food supplies.

4.2. Population declines at colonies

Reduced attendance was observed at many other seabird colonies in Alaska for one or more years following the 2014–2016 heatwave. Lower kittiwake attendance was observed at a subset of monitored colonies across Alaska: St. Paul, Cape Peirce, Round Island, and in Prince William Sound (Dragoo et al. 2020). The dramatic reduction of kittiwake attendance we observed at Chisik was following a declining trajectory from 1978–1995 (Piatt & Harding 2007), and likely some continued declines from 1995–1999 (see population plot data in Table 1), so may reflect a combination of heatwave effects and the persistent effect of low food supply around that colony (Piatt & Harding 2007). Following the heatwave, murre attendance was depressed at Cape Lisburne, St. Paul, St. George, Cape Peirce, Round Island, Aiktak, Chowiet, and Puale Bay (Dragoo et al. 2020).

The declines we observed in murre population indices (71% at Chisik and 46% at Gull) post heatwave compared to historic counts were on the same order of magnitude as declines in attendance of murres in the Gulf of Alaska (50%) and Bering Sea (80%) in the 3 years prior to and following the 2015–2016 murre die-off (Piatt et al. 2020). Murres at Chisik had likely begun a population decline prior to the 1995–1999 surveys, whereas murres on Gull were on an increasing trajectory prior to the 1995–1999 censuses (Piatt & Harding 2007). In 2017, the decline in murre attendance at Gull (see colony-wide census count data in Table 1) occurred in concert with a spike in at-sea abundance driven by large rafts of murres near Gull Island (Arimitsu et al. 2021c). This may be explained by deferred breeding (i.e. when birds do not return to the colony to breed), which is an adaptive strategy when long-lived seabirds are faced with environmental constraints such as higher ocean temperatures (Cubaynes et al. 2011). However, deferred breeding is unlikely to explain multi-year declines at colonies (Erikstad et al. 2013), and attendance at Gull continued to drop in 2018 and remained below aver-

age in 2019 (Table 1), alongside below-average at-sea abundances in those same years (Arimitsu et al. 2021c). In addition to the known loss of adult murres during the widespread mortality event (Piatt et al. 2020), it is possible that these species experienced declines in survival during and after the heatwave. Even small changes in adult survival can result in large changes to population dynamics for long-lived species with low fecundity, and survival of other long-lived Alcidae species have been negatively correlated with summer SSTs (Hovinen et al. 2014).

4.3. Reproductive failures

Total reproductive failures are rare for murres, a species that generally produces over 0.50 chicks per pair (henceforth 'chicks' in this paragraph) (Ainley et al. 2020), but averages as high as 0.85 chicks at some colonies (Birkhead & Nettleship 1987, Bryant et al. 1999). Over a total of 138 colony-years (1995–2014), murres from the largest, most stable colonies in the Bering Sea and Gulf of Alaska had an average annual breeding success of 0.49 chicks, with complete breeding failures (<0.02 chicks) occurring at colonies only once (Round Island in 2009; Piatt et al. 2020). Thus, the sequential, 3–4 yr murre breeding failures we observed at 2 colonies in Cook Inlet were unprecedented, and stand in stark contrast to historic productivity recorded at Gull and Chisik (0.54 and 0.56 chicks, respectively) from 1995 to 1999 (Piatt 2002). At the nearby Barren Islands, murres were successful (average 0.73 chicks) during the 1995–1999 period (Piatt 2002) and during the gap years in which we did not monitor Gull and Chisik (2000–2014; average 0.64 chicks; A. Kettle unpubl. data). Like at Gull and Chisik, murres at the Barren Islands never failed reproductively in years monitored ($n = 17$) prior to the heatwave but failed completely in 2015 and 2016. Murres recovered progressively at the Barrens in 2017, 2018, and 2019 (0.15, 0.27, 0.57 chicks; Kettle et al. 2021).

Over a larger spatial scale, at least 1 year of complete reproductive failure was observed during 2015–2017 at 13 murre breeding colonies in the Gulf of Alaska and Bering Sea in association with the 2014–2016 heatwave, and multi-year failures were observed at 8 colonies (Piatt et al. 2020). Further reproductive failures and unusual levels of breeding season mortality occurred in the Bering and Chukchi Seas in 2018, attributed to record low sea-ice extent coupled with warm ocean temperatures (Romano et al. 2020). Murre reproductive failures during the

heatwave were also observed at several murre colonies in the California Current System, but breeding success recovered partially or entirely by 2018 or 2019 (Wells et al. 2017, Thompson et al. 2018, 2019, Piatt et al. 2020). Murre reproduction has not yet fully recovered in lower Cook Inlet, making it perhaps the last area to recover from the lingering effects of the heatwave throughout the full range of impacted areas.

Kittiwakes also had reproductive failures (≤ 0.02 chicks per nest, henceforth 'chicks' in this paragraph) at Chisik in all years (2016–2019), but productivity was similarly low from 1995 to 1999 (0.04 chicks), reflective of chronically low food supplies near Chisik (Speckman et al. 2005). This was low even for Alaska kittiwakes (mean annual productivity: 0.3 chicks from 1960 to 1989), and much lower than mean annual productivity in northeast Greenland (1.4 chicks) and most colonies in eastern North America (Hatch et al. 2020). In contrast, the reproductive failures of kittiwakes at Gull in 2016 and 2018 were notable when compared to the consistently ($CV = 24\%$) high (0.46 chicks) productivity observed at Gull historically (1995–1999). Kittiwakes at Gull achieved high (>0.60 chicks) productivity in 2017 and 2019, and overall annual variability ($CV = 100\%$) was higher than in historic years. At the nearby Barren Islands (Kettle et al. 2021), kittiwakes averaged 0.43 chicks ($CV = 53\%$) during 1995–1999 and maintained modest (0.27 chicks), variable ($CV = 89\%$) productivity during the gap years (2000–2014). Kittiwakes then failed completely in 2016, followed by progressively higher production (0.10–0.45 chicks) from 2017 to 2019 (overall $CV = 106\%$). Breeding failures (<0.02 chicks) were also observed at 9 of 10 other monitored kittiwake colonies throughout the Bering and Chukchi Seas and the Gulf of Alaska between 2015 and 2016 (Dragoo et al. 2020). At long-term breeding sites in the Gulf of Alaska, including Middleton Island, Prince William Sound, and Chowiet Island, breeding success recovered progressively from 2017 to 2019, and no total reproductive failures were recorded after 2016 (Dragoo et al. 2020). In the Bering Sea, however, complete reproductive failures were reported at multiple colonies from 2015 through 2018 (Dragoo et al. 2016, 2017, 2018, 2019).

During historic years in Cook Inlet, when food supply was measured independently, breeding failure (<0.02 chicks per nest) in kittiwakes reflected extreme food scarcity (Piatt & Harding 2007), whereas breeding success in kittiwakes was associated in a non-linear fashion to food supply and fluctuated over a wide range of prey densities (Piatt et al. 2007). Further, food supply has been shown to influence kittiwake

fledgling success, breeding phenology, and non-breeding season movements (Whelan et al. 2020). In contrast, murres can behaviorally buffer against changes in prey abundance, allowing them to maintain constant and high breeding success over a wide range of moderate to high prey densities, although they can still fail at very low prey densities (Zador & Piatt 1999, Piatt & Harding 2007, Piatt et al. 2007).

Despite their ability to behaviorally buffer against the effects of low prey abundance, murres failed to successfully produce chicks or did poorly reproductively in 2017 and 2019 (respectively), whereas kittiwakes had high productivity at Gull in those years. This may have been related to differences in availability of prey to surface-feeding kittiwakes versus deep-diving murres, as schools of lipid-rich forage fish such as sand lance were relatively more abundant in surface layers (<20 m) than deep waters (>20 m) during 2017 and 2019 (Arimitsu et al. 2021a). In addition, kittiwakes have some life history traits that allow them to subsist and raise chicks at lower prey densities than murres. These include a smaller body mass and lower energy demands, requiring a fraction (37%) of the daily food requirements of murres by mass (Piatt et al. 2007). Kittiwakes also have substantially lower (21%) wing loading than murres, which reduces the cost of foraging considerably (Piatt et al. 2007). Furthermore, kittiwakes provision chicks by ingesting multiple prey items during foraging bouts, which are stored in their crop, then regurgitating the partially digested forage to chicks once back at the colony (Hatch et al. 2020). Murres, in contrast, provision chicks with single fish from several foraging bouts a day (Ainley et al. 2020), thus requiring more

energetically costly commuting between the colony and foraging locations. These high energetic costs of chick rearing likely explain why murre chicks fledge at earlier ages than kittiwake chicks, although murre chicks subsequently remain dependent on parental care for feeding and protection for at least 1–2 mo (Ainley et al. 2020, Hatch et al. 2020).

These differences in foraging and chick provisioning favor kittiwakes when prey items are small or are of lower quality, which were the conditions observed during the heatwave (von Biela et al. 2019, Arimitsu et al. 2021a). Furthermore, once prey availability drops below a certain threshold (Schrimpf et al. 2012), adult murres prioritize their own body condition above breeding success, which requires consuming roughly half of their body mass in prey per day (Burger & Piatt 1990, Piatt et al. 2007). Thus, the reproductive failures in murres suggest that the foraging conditions around these 2 breeding colonies were insufficient to support average energy demands for breeding murres from 2016–2019. A reduced abundance of prey or shift of preferred prey was also implicated in reproductive failures observed in murres in Oregon (2014–2017) and California (2015–2017, 2019) in relationship to the marine heatwave (Wells et al. 2017, Thompson et al. 2019).

Finally, support for our food deprivation hypothesis also comes from our observations of murres with abnormally concave breast profiles and visible keels attending Gull, which were especially prevalent in 2018 (Fig. 4). We can find no reports in the literature of such abnormal body conditions at colonies of breeding murres, nor from correspondence with long-time murre researchers. These observations suggest con-

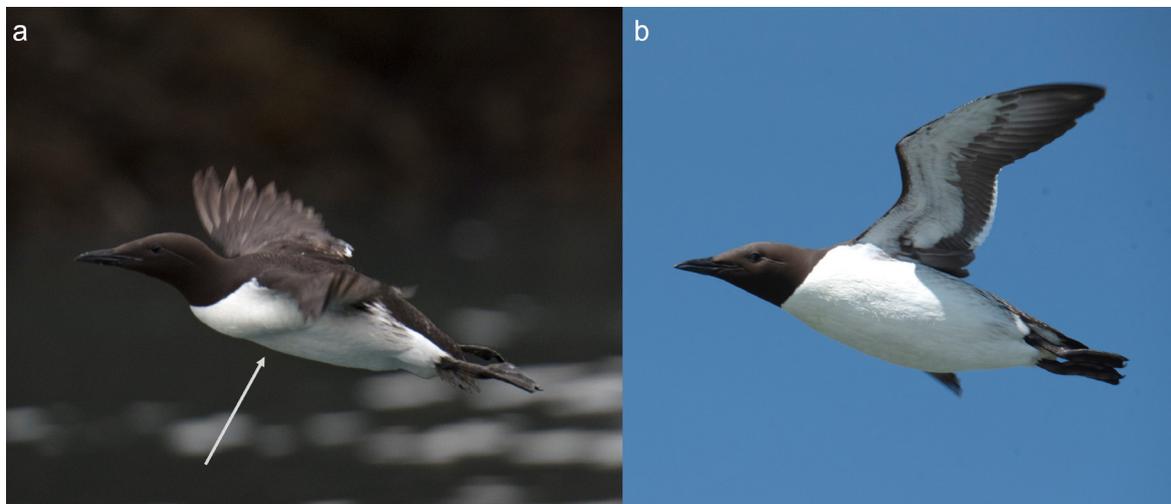


Fig. 4. (a) A common murre with a concave breast profile (arrow) and protruding keel, contrasted by (b) a murre in apparently normal body condition in lower Cook Inlet, Alaska. Credit: S. Schoen, US Geological Survey, public domain

ditions of extreme prey scarcity, as evidenced by the lowest acoustic biomass of fish measured throughout lower Cook Inlet in 2018 compared to 2016–2019 (Arimitsu et al. 2021c). In 2016 and 2017, the forage community was dominated by juvenile fish (Arimitsu et al. 2021c), which were of low nutritional value to seabirds following the heatwave (von Biela et al. 2019, Arimitsu et al. 2021a). It appears that foraging conditions had improved slightly by 2019, when aggregations of pre-spawning capelin and large sand lance and herring were observed near Gull (Arimitsu et al. 2021c), but conditions were likely still marginal for reproduction, as murres fledged chicks at just over half the rate of the historical average (Piatt 2002).

4.4. Other factors affecting seabird demography

Predation also played a role in the breeding failures we observed. The secondary (facilitated) predation of eggs by gulls after murres are flushed by bald eagles was also commonly observed at Yaquina Head, Oregon (Horton 2014). Flyovers of avian predators caused large-scale disturbances at our breeding colonies, and were most extreme at Gull in 2018, when eruptions of thousands of kittiwakes and murres from the colony were a common occurrence. Avian predation influences the reproductive performance of murres more when food supplies are diminished (Parrish et al. 2001, Schrimpf et al. 2012, Horton 2014, Suryan et al. 2017). Thus, the low fish biomass in Cook Inlet recorded in 2018 (Arimitsu et al. 2021c) may have exacerbated predator disturbances, likely contributing to the worst year for reproduction for both kittiwakes and murres at both colonies. Similarly, the rate of egg and chick depredation increased at Yaquina Head during the 3 years (2015–2017) of reproductive failures associated with the marine heatwave, and decreased in the following 2 productive years (2018–2019) (Wells et al. 2017, Thompson et al. 2018, 2019). Predation pressure could also be partially responsible for differences in reproductive success between species, due to differences in nesting habitat. Although predation of adults, chicks, and eggs of both kittiwakes and murres was observed, predation of murre eggs from the flat, open tops of the colony was more common than that of kittiwakes nesting on rocky cliffs.

Biotoxins associated with harmful algal blooms could have been an additional stressor to breeding seabirds at the colonies we monitored. Harmful algal blooms have been increasing in frequency and

severity alongside rising ocean temperatures, and there was a large bloom of *Alexandrium*, the dominant paralytic shellfish toxin-producing species, in Cook Inlet in 2016 in association with the 2014–2016 heatwave (Vandersea et al. 2018). Saxitoxin, a neurotoxin involved in paralytic shellfish poisoning, was found in tissues of murres that had died in the 2015–2016 mass mortality event in higher concentrations than it was found in the tissues of breeding murres and kittiwakes, and their forage, collected near Gull and Chisik in summer 2016 (Van Hemert et al. 2020). Although saxitoxin was not implicated as the primary cause of mortality during the murre die-off (Piatt et al. 2020, Van Hemert et al. 2020), the sensitivity of seabirds to threshold concentrations or chronic exposure to saxitoxin is still under investigation. In saxitoxin dosing experiments, mallard ducks *Anas platyrhynchos* that survived saxitoxin dosing lost between 1.8 and 6.3% of their body mass within 24 h of dosing (Dusek et al. 2021). A similar reduction in body mass would be detrimental to seabirds like murres with high metabolic demands (Piatt et al. 2007), and may help explain the observed reductions in body condition and reproductive failures.

5. CONCLUSIONS

The response of the marine ecosystem to the 2014–2016 heatwave is complex and still unfolding in the Gulf of Alaska. In addition to seabirds, strong multi-year demographic impacts have been documented for other higher-level predators and long-lived vertebrates that declined dramatically during and after the heatwave (Barbeaux et al. 2020, Gabriele et al. 2022). Most biological time-series in the Gulf of Alaska ($n = 187$) exhibited anomalies following the heatwave that lasted until 2018 (Suryan et al. 2021). Some forage fish species appeared to rebound towards pre-heatwave states during 2018 (Arimitsu et al. 2021a). Since the impacts of reduced forage fish abundance and quality were particularly challenging for larger piscivorous vertebrates (adult groundfish, seabirds, seals, whales; Suryan et al. 2021), this more recent rebound is a promising sign.

Nonetheless, evidence suggests that severe disruptions in the food web have substantially changed equilibrium populations of kittiwakes and murres in our study area, which will have lingering effects into the future. The impact on population size is particularly notable, as murres declined by approximately half, and kittiwakes by one-quarter, at the historically most successful colony (Gull Island) in Cook

Inlet (Piatt & Harding 2007). It appears that similar, and even larger declines may have occurred at other colonies in the Gulf of Alaska and Bering Sea (Dragoo et al. 2020, Piatt et al. 2020). Although hints of recovery of breeding success are encouraging, the ongoing impact of the heatwave will have long-term demographic consequences for populations, particularly given the absence of multiple cohorts of birds following sequential breeding failures.

Recovery of seabird populations would require a return of forage fish quantity and quality to pre-heatwave levels capable of supporting moderate, sustained growth (e.g. 3 and 5% per annum for kittiwakes [Coulson 2017] and murrens [Ainley et al. 2020], respectively). However, that growth is reliant upon normal levels of recruitment, which has been impacted by the low production of chicks at Gull and Chisik Islands during our study following the loss of subadult and breeding-aged adult murrens during the heatwave (11–25 and 64–68% of carcasses recovered in Alaska, respectively; Piatt et al. 2020). Thus, assuming emigration and immigration are balanced, populations will likely continue to decline due to normal adult mortality until reproductive success recovers and those fledglings recruit back into the population, 3 yr later at the earliest (Ainley et al. 2020). Given all of these factors, we believe it would likely take decades for populations to rebound to historic levels. This estimate falls in line with the 17 yr recovery of murre populations in Norway following a mortality event associated with the collapse of multiple key forage species (Erikstad et al. 2013). Alternatively, the heatwave may have precipitated a 'shifting baseline,' and current population sizes may become the new normal (Suryan et al. 2021). Either way, the impacts of the heatwave are ongoing, and continued monitoring of the trajectory of change during the coming decade will be informative.

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