OCS Study
BOEM 2021-031

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ABOUT THE COVER

Common Murres around Gull Island in Kachemak Bay, Alaska (2019). Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

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List of Abbreviations and Acronyms

BLKI/kittiwake	Black-legged Kittiwake
BOEM	Bureau of Ocean Energy Management
CFE	Chicks Fledged per Eggs Laid
CFN	Chicks Fledged per Nest
COMU/murre	Common Murre
CPUE	Catch per unit effort
CSE	Council of Science Editors
DOI	US Department of the Interior
ESP	Environmental Studies Program
ESPIS	Environmental Studies Program Information System
GWGU	Glaucous-winged Gull
GOA	Gulf of Alaska
HOPU	Horned Puffin
PDO	Pacific Decadal Oscillation
PIGU	Pigeon Guillemot
PPC	Population Plot Count
TS	Target strength
TUPU	Tufted Puffin
USGS	U.S. Geological Survey
WCC	Whole Colony Census

1 Abstract

Following the North Pacific marine heatwave of 2014-2016 and associated extreme die-off of seabirds in the winter of 2015-2016, we repeated historical marine bird and forage fish surveys around two seabird colonies (Gull Island, Chisik Island) in lower Cook Inlet during 2016-2019 in order to document immediate and lingering impacts of the heatwave on resident fish and seabird populations. At sea, we conducted acoustic/trawl surveys for fish in near-colony areas, while simultaneously counting seabirds on survey transects. At colonies, we monitored bird numbers on whole colony censuses and population plot counts and assessed annual reproductive success of Black-legged Kittiwakes (*Rissa tridactyla*) and Common Murres (*Uria aalge*). Our studies suggest that impacts of the heatwave on seabirds and their forage base were severe and extended for several years beyond the heatwave itself. Although fish biomass

indices were greatest in 2016-2017, the forage community was largely dominated by juvenile fish with low nutritional value following a collapse of key species of forage fish during the marine heatwave. Lowest fish biomass was observed in 2018, coincident with a marked decline in the at-sea abundance of many seabirds around colonies. By 2019 there were signs of improvement in prey abundance and quality, and significant aggregations of pre-spawning capelin and large sand lance were observed in and around Kachemak Bay. In comparison with historical (1996-1999) bird colony surveys, kittiwake population counts decreased by more than 73% at Chisik Island, and by 8-26% at Gull Island. Similarly, murre counts decreased at Chisik Island by 72% and by more than 20% at Gull Island. Kittiwakes had complete reproductive failure at Chisik Island from 2016-2018, with minimal success in 2019. At Gull Island, kittiwakes also failed in 2016 and 2018 but had unusually high productivity in 2017 and 2019. Murres also had complete reproductive failures at Chisik Island in all four years and at Gull Island during 2016, 2017 and 2018. Murres finally fledged chicks in 2019, albeit at about half the normal rate. Finally, we also observed unusually high levels of predator disturbance (egg predation, flushing adults from plots) and unprecedented numbers of adult birds in poor body condition (“skinny murres”), particularly in 2018. Together, these results indicate that an extreme disruption of marine food webs occurred during and after the heatwave. Given the prolonged reproductive failures, continued monitoring is required to assess continuing impacts and recovery from the 2014-2016 heatwave. For example, murre chicks that would have been produced in 2016 should, after 4-5 years away, start recruiting to the colony in 2021, and thereby replace aged adults that would have died naturally in the past year(s). Without such natal recruitment for at least the next 3-4 years, we should document a continuing decline in bird numbers at the colonies.

2 Background

Seabird densities in lower Cook Inlet are among the highest in Alaska – one reason why this location suffered the greatest damage to marine bird populations following the *Exxon Valdez* oil spill (Piatt et al. 1990). Large resident and migratory seabird populations are sustained by locally abundant stocks of key forage fish species such as sand lance, capelin, herring, and juvenile walleye pollock (Abookire and Piatt 2005, Piatt et al. 2007). Monitoring seabird populations and forage fish stocks in lower Cook Inlet – an oil and gas lease area – has been a Bureau of Ocean Energy Management (BOEM) priority for decades. Past BOEM studies have collected monitoring data in Cook Inlet that can be used to mitigate impacts of future development on fish and wildlife populations, and to assess the impact of potential oil spills.

Seabird populations in the Gulf of Alaska (GOA) have fluctuated markedly during the past few decades (Dragoo et al. 2020). Whereas human impacts from oil spills and drilling operations, colony disturbance, bycatch in fishing gear, etc., can account for some proportion of these fluctuations (Piatt et al. 1990, Ainley et al. 1994, Hatch and Piatt 1995), natural changes in the marine environment have resulted in larger, sustained impacts on seabird populations (Piatt and Anderson 1996, Anderson and Piatt 1999, Piatt et al. 2020, Arimitsu et al. 2021).

Factors that regulate seabird populations in Alaska are complex and not fully understood, but food supply is clearly important (Piatt et al. 2007, Hatch 2013). Coincident with warming of sea-water temperatures, the abundance of small forage fish species such as capelin declined precipitously in the late 1970's while populations of large predatory fish such as walleye pollock and Pacific cod (*G. macrocephalus*) increased (Anderson and Piatt 1999). Correspondingly, capelin virtually disappeared from seabird diets in the late 1970's, and were replaced by juvenile pollock and other species in the 1980's (Piatt and Anderson 1996). All these changes occurred as part of the so-called “1976 Regime Shift”, which appeared to impact the oceanography, productivity and food web structure of the entire Gulf of Alaska during the late 1970s and beyond (Francis et al. 1998, Anderson and Piatt 1999). In response, seabirds and marine mammals exhibited several signs of food stress (population declines, reduced productivity, die-offs) throughout the 1980's and 1990's (Robert C Francis et al. 1998). During the 2000’s, water temperatures in the GOA cooled again as the Pacific Decadal Oscillation index (Mantua and Hare 2002) entered a negative phase after about 2007. Capelin began to appear again in seabird diets at Middleton Island, and in catches elsewhere in the GOA, and Black-legged Kittiwakes began to breed successfully again after nearly 30 years of decline and breeding failure (Hatch 2013).

Shortly thereafter, surface water temperatures returned to much warmer than average in 2014-2016, coincident with two warming events in the NE Pacific, “the Blob” in 2014-2015 and a strong El Nino in 2015-2016, collectively causing a North Pacific marine heatwave (Bond et al. 2015, Di Lorenzo and Mantua 2016, Hobday et al. 2018). In the northern Gulf of Alaska temperatures were 1.4 to 2.1 °C above normal (Arimitsu et al. 2021). During this multi-year persistent marine heatwave, unusually large numbers of Common Murres (hereafter “murres” unless otherwise noted) washed up dead on beaches along the US west coast from California to Alaska in pulses from spring of 2015 to spring of 2016, and we estimate between 500 thousand to 1.2 million birds died in this event (Piatt et al. 2020). Die-offs of murres have occurred periodically in Alaska (e.g. 1993, 1997/1998, and 2004); however, the 2015/2016 die-off was distinguished from others by its duration, magnitude, and geographic extent (Piatt et al. 2020). At the same time, murres exhibited an unprecedented number of total reproductive failures at multiple colonies in the Gulf of Alaska and Bering Sea (Piatt et al., 2020). This large-scale murre die-off and breeding failure, along with unusual mortality of cetaceans (Savage 2017) and the collapse of the Pacific cod fishery in the Gulf of Alaska (Barbeaux et al. 2018) were all alarming indications of a major disruption to the marine food web.

Underlying mass mortality, breeding failures, and malnutrition of marine predators was a synchronous collapse of the forage fish community and reduced quality of key forage fish (von Biela et al. 2019, Arimitsu et al. 2021). Capelin had disappeared from the system abruptly, while sand lance and herring were at historically low levels of abundance for several years prior to and during the heatwave. In addition to bottom up stressors that affected the nutritional quality of forage fish during the heatwave, changes in the age- and length-structure of capelin and sand lance identified size truncation typical of top-down stressors (i.e., predation) to these populations. Unlike the late 1970’s regime shift, which was driven by decadal scale ocean climate patterns and played out over many decades (Anderson and Piatt 1999), the response of the marine food web to the multi-year marine heatwave was abrupt and short-lived. Still, the response of the marine ecosystem to the heatwave persisted for years (Suryan et al. 2021).

In this study, we set out to assess the status and trends of marine birds and forage fish around two seabird colonies in lower Cook Inlet in order to document immediate and long-term impacts of the heatwave on the marine ecosystem. From 2016 to 2019, we conducted at-sea surveys for marine birds concurrently with acoustic-trawl surveys for forage fish. We also gathered demographic information on Common Murres and Black-legged Kittiwakes at the colonies. We compared our findings to USGS-led studies that were conducted in lower Cook Inlet during 1995-1999 to assess the recovery of seabird populations following the 1989 *Exxon Valdez* oil spill (Piatt 2002).

3 Objectives

The main objectives for this work were to:

1. Assess the abundance, distribution and species composition of forage fish in marine waters of lower Cook Inlet adjacent to seabird colonies on Chisik and Gull islands.

2. Assess at-sea distribution and abundance of marine birds in lower Cook Inlet and Kachemak Bay.
3. Census breeding populations and obtain an index of reproductive success for Common Murres and Black-legged Kittiwakes at Chisik and Gull island colonies in lower Cook Inlet.
4. Compare our findings from 2016-2019 with those obtained from historical studies conducted in 1995-1999.

4 Methods

Our primary research platform was the 16 m USGS R/V *Alaskan Gyre* (https://alaska.usgs.gov/science/tools/Gyre.php). Work requiring a smaller vessel was conducted from a 4.8 m rigid hull inflatable skiff. All field work was conducted between June and October of 2016-2019 (Table 1), which was planned to coincide with the seabird breeding season and the timing of previous work (Piatt 2002, Piatt et al. 2004). All data and metadata presented here are publicly available in Arimitsu et al. (2021*b*).

Table 1. Dates of surveys

Dates of sampling completed by survey type from 2016-2019.

Project component	Survey Type	2016	2017	2018	2019
At Sea Surveys	Hydroacoustic-trawl	7/14-7/29	7/15-8/3	7/8-7/31	7/16-7/27
	Marine predator	7/14-7/29	7/15-8/3	7/8-7/31	7/16-7/27
Colony Surveys: Chisik Island	Kittiwake Census	7/14-7/15	7/2	6/27	7/5
	Murre Census	7/14-7/15	7/2	7/16	7/20
	Population Plots	7/14-7/18	7/2-7/25	6/27-7/16	6/29-7/20
	Kittiwake Productivity	7/14-7/18	7/2-7/25	6/27-7/16	6/29-7/20
	Murre Productivity	7/15-8/28	6/5-9/13	6/27-10/4	6/29-9/21
Colony Surveys: Gull Island	Kittiwake Census	7/23	7/3	6/28	6/19
	Murre Census	7/23	7/29	7/26	7/25
	Population Plots	7/20-8/28	7/3-8/18	6/28-8/21	6/19-8/19
	Kittiwake Productivity	7/20-8/28	7/3-8/18	6/28-8/21	6/19-8/19
	Murre Productivity	7/15-8/28	6/5-9/13	6/28-10/5	6/19-9/12

4.1 At-Sea Surveys

4.1.1 Acoustic-trawl Surveys

We conducted acoustic-trawl surveys for forage fish in lower Cook Inlet between July and August from 2016-2019 using transects established during the 1990s study (Piatt 2002). Effort was focused around two seabird colony sites: Gull and Chisik islands (Figure 1). Gull Island is owned by the Seldovia Native Association and Chisik Island is part of the Alaska Maritime National Wildlife Refuge. Transects were established in both “nearshore” and “offshore” habitats. Nearshore transects followed the contours of mainland or island shorelines in a zig-zag pattern of 1.8 km legs, where waters were generally deeper than 10 m. Offshore transects cut across open water from one shore towards the other, over depths ranging from 10 m to >100 m. Offshore transects were parallel to latitude lines, and separated by 5 minutes of latitude (ca. 9.5 km).

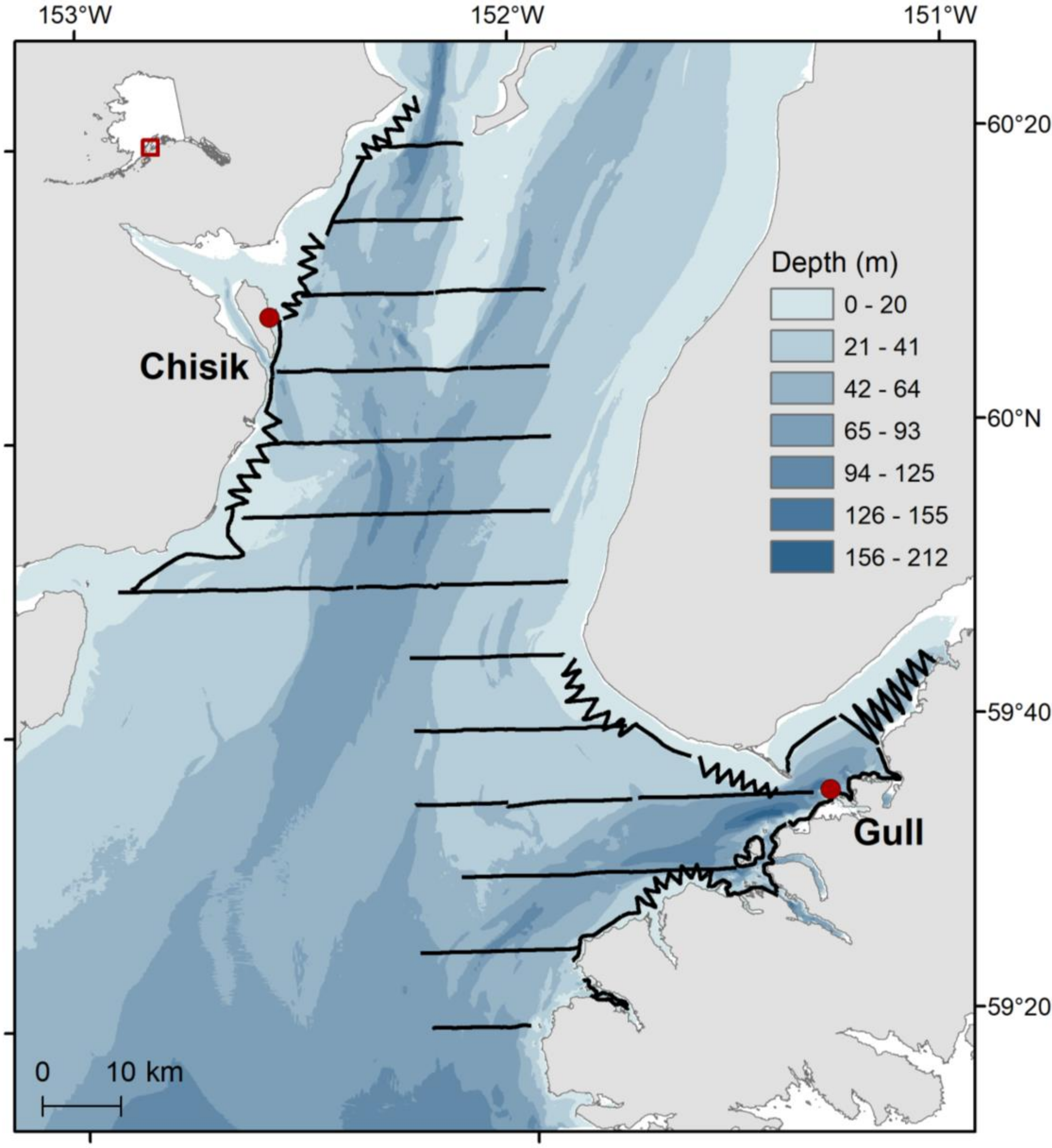

Figure 1. Study area
Map of marine bird and acoustic transects (lines) near seabird colonies (red circles) on Chisik and Gull islands in lower Cook Inlet, Alaska. Bathymetry data are shown in color (Zimmermann and Prescott 2014).

We measured hydroacoustic backscatter in the water column using a hull-mounted Simrad EK60 (Kongsberg Maritime) echosounder system operating at 38 kHz (12° beam width) and 120 kHz (7° beam width). The echosounder system was calibrated during each survey by suspending a 38.1 mm tungsten carbide sphere under each transducer following standard practices (Foote et al. 1987).

When we encountered significant acoustic sign on transects, a modified-herring trawl was deployed to confirm species and length frequency of ensonified targets, to collect samples for measures of body condition, and to detect changes in overall community structure relative to habitat (Abookire and Piatt 2005). The net was 37.2 m^2 in area at the mouth, and 30 m in length. Mesh size diminished from 5 cm at the mouth to 6 mm in the cod end and 3 mm cod end liner. Trawl catches were weighed by taxa (total catch, fish, gelatinous zooplankton, macrozooplankton). Fish were sorted by species and 25 to 50 individuals from each species were measured for total length (± 1 mm), and weight (± 0.03 grams). Large catches were subsampled by volume. For each species catch per unit effort (CPUE) was calculated by dividing the total number of fish by the distance towed (in meters).

Acoustic backscatter in the water column were classified for depths between 4 m below the surface to 1 m above the bottom using frequency response methods for inshore waters (De Robertis and Ormseth 2019). The difference in mean volume backscattering strength (S_v, dB re 1 m^{-1}, hereafter dB) between 120 and 38 kHz data ($\Delta S_{v_{120kHz - 38\ kHz}}$) in each 5 ping by 5 m acoustic sample was computed in the log domain using a minimum threshold of -67 dB to exclude jellyfish (Parker-Stetter et al. 2016). For 120 kHz data, samples with $\Delta S_{v_{120kHz - 38\ kHz}}$ values between -16 to 8 dB were classified as fish based on known acoustic scattering characteristics (De Robertis et al. 2010). Echointegration was conducted with Echoview (ver. 11, Echoview Software Ltd., Hobart, Tasmania, Australia). Area backscattering coefficient (ABC, s_a, m^2m^{-2}) data were aggregated by 500 m transect segments and summed across two depth strata: shallow (4 – 20 m), and deep (21 m – 1 m above bottom).

To identify changes in distribution and area-weighted acoustic fish indices by depth strata, we used vector autoregressive spatio-temporal models (VAST, Thorson 2019) (see section 4.1.3). We also converted backscatter consistent with fish (as above) within shallow (< 20m) and deep (≥ 20m) depth strata to species-specific densities following methods for multispecies apportionment from trawl data (Simmonds and MacLennan 2005, Parker-Stetter et al. 2013). For this analysis we summed s_a by depth strata for each 500 m long transect segment, then multiplied the mean s_a for each transect by the proportion of each species group in the nearest trawl. Target strength (TS) was estimated for each species group using fish lengths (L, cm) obtained from trawl samples by applying the following theoretical TS equations: walleye pollock: TS = 20Log(L) – 68.9 (Gauthier and Horne 2004); herring: TS = 20Log(L) = 67.6 (Gauthier and Horne 2004); sand lance: TS = 20Log(L) – 80 (Thomas et al. 2002); capelin: TS = 20Log(L) – 72.2 (Gauthier and Horne 2004). For each species the backscattering cross section (σ_{bs}) was calculated as $10^{(TS/10)}$. Fish density by species and transect was then calculated by dividing s_a by σ_{bs} (Simmonds and MacLennan 2005). Similar analyses of acoustic data from 1997-1999 were not available at the time of this report, therefore a comparative analysis across time periods was not possible.

4.1.2 Marine Predator Surveys

To measure marine predator densities, we concurrently counted marine birds and mammals along hydro-acoustic trawl surveys, following strip transect protocols (Gould and Forsell 1989) which were modified for working in coastal areas (Agler et al. 1999, Piatt et al. 2007). Two observers and one data recorder counted and identified all birds and mammals within 150 m on either side, and 300 m forward of the research vessel. Distances were frequently calibrated throughout the surveys by using a hand-held range finder. Marine predators on the water within the survey area were counted continuously, and flying birds were recorded every 90 seconds using a snapshot count (Gould and Forsell 1989). A real time data entry program (DLOG; Glenn Ford, ECI, Portland OR) was used to record entries, in addition to the behavior and GPS coordinates of the organism.

Marine bird survey data were binned into 3 km transect segments following standard protocols used for at-sea survey data (Drew and Piatt 2015). On each transect segment counts of live birds within the survey window (sample area = transect length x strip width, in km^2) during boat-based pelagic surveys were summed across behaviors at each sample location. For this analysis we included data collected during the breeding season (May-August) in 1996-1999, and 2016-2019. We used count data with sample area as an offset for a subset of 10 species groups including Marbled Murrelet, (MAMU, *B. marmoratus*), Kittlitz's Murrelet (KIMU, *B. brevirostris), Brachyramphus* spp. (ALLBRMU, the sum of MAMU, KIMU and unidentified *Brachyramphus* spp.), Common Murres (COMU), Black-legged Kittiwakes (BLKI), Shearwaters (ALLSH, *Ardenna* spp.), Horned Puffins (HOPU, *Fratercula corniculata*), Tufted Puffin (TUPU, *F. cirrhata*), Glaucous-winged Gull (GWGU, *Larus glaucescens*), and Pigeon Guillemot (PIGU, *Cepphus columba*).

4.1.3 Spatio-Temporal Models

To identify trends in at-sea distribution and abundance of forage fish and seabirds in Lower Cook Inlet, we used vector autoregressive spatio-temporal models (VAST, Thorson 2019). A similar approach was used previously for acoustic indices of forage fish (McGowan et al. 2019) and seabirds (Thorson et al. 2021). To estimate density across the study region while also accounting for spatial and spatio-temporal correlation within the survey data, we used a conventional delta model (for fish) or Poisson-link delta model (for birds, Thorson 2018). This approach separately models encounter rates using presence/absence data and positive density using non-zero density data. For sample i, species *c*, location *s*, and time *t*, linear predictors representing encounter probability $p_1(i)$:

$$p_1(i) = \beta_1(c_i) + \sum_{f=1}^{n_{\beta_1}} L_{\beta_1}(c_i, f)\beta_1(t_i, f) + \sum_{f=1}^{n_{\omega_1}} L_{\omega_1}(c_i, f)\omega_1(s_i, f) + \sum_{f=1}^{n_{\varepsilon_1}} L_{\varepsilon_1}(c_i, f)\varepsilon_1(s_i, f, t_i)$$

and positive density $p_2(i)$:

$$p_2(i) = \beta_2(c_i) + \sum_{f=1}^{n_{\beta_2}} L_{\beta_2}(c_i, f)\beta_2(t_i, f) + \sum_{f=1}^{n_{\omega_2}} L_{\omega_2}(c_i, f)\omega_2(s_i, f) + \sum_{f=1}^{n_{\varepsilon_2}} L_{\varepsilon_2}(c_i, f)\varepsilon_2(s_i, f, t_i)$$

Link functions r_1 and r_2 for conventional delta model (i.e. fish)

$$r_1(i) = logit^{-1}\big(p_1(i)\big) \text{ and } r_2(i) = a_i \times log^{-1}\big(p_1(i)\big)$$

or Poisson-link delta model (i.e., birds):

$$r_1(i) = 1 - exp\left(-a_i \times \exp\left(p_1(i)\right)\right) \text{ and } r_2(i) = \frac{a_i \times \exp\left(p_1(i)\right)}{r_1(i)} \times exp\big(p_2(i)\big)$$

are combined to predict variation in density *d*:

$$d(s, c, t) = r_1(s, c, t) \times r_2(s, c, t)$$

Where subscripts $_1$ and $_2$ refer to the first or second linear predictors, β represents temporal variability, η is the number of factors *f*, L is the loadings matrix, ω is spatial variation, ε is spatio-temporal variation, and *a* is the sample area. Samples of fish acoustic backscatter (s_a) and seabird density (counts/sample area) were modeled with a lognormal and gamma error distribution, respectively. Parameters associated with spatial variability (ω_1 and ω_2) and spatio-temporal variability (ε_1 and ε_2) were modeled as random effects, while all others were treated as fixed effects. Parameters were estimated using maximum likelihood while integrating the joint likelihood with respect to random effects as implemented in VAST (www.github.com/James-Thorson-NOAA/VAST) with R version 3.5.3 (R Core Team 2020). Model fit was evaluated for convergence and validated using QQ-plots and AIC. Density predictions were extrapolated to a 3x3 km grid over the survey area and plotted on log scale by taxa or species for each year. To identify interannual variability in seabird abundance, area-weighted predicted densities were summed across the survey area to provide an abundance index for each species. Standard errors were calculated using a generalization of the delta method.

4.2 Seabird Colony Monitoring

Protocols for monitoring murre and kittiwake populations, and breeding biology for specific colonies in lower Cook Inlet, were developed during the 1995-2001 years of colony work for BOEM. Details for that work can be found in the final report (Piatt 2002) and subsequent publications (Piatt et al. 2004, 2007, Harding et al. 2007, Shultz et al. 2009). We based our monitoring efforts on the previous work, with some adaptions (specified below), from 2016-2019.

4.2.1 Population

We conducted two full island censuses of Chisik and nearby Duck islands (hereafter combined as "Chisik") and Gull Island each year from 2016-2019. Earlier censuses targeted kittiwakes and later surveys targeted murres during mid-incubation. The census of Chisik Island was conducted by circumnavigating both Chisik and Duck islands by small skiff and counting all murres and kittiwakes observed on land with binoculars. On areas of Chisik with tall cliffs and/or where some birds were difficult to observe due to their distance from observers, we took photographs of the cliffs using a telephoto lens 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. Likewise, we counted all murres and kittiwakes observed on land with binoculars while circumnavigating Gull Island, and nearby Murre Rock and Gorilla Rock, (hereafter combined as "Gull") by small skiff. Additionally, because there were large numbers of murres on the top of the islands at Gull that were only visible from the water at a distance (such that it was impractical to count the birds with binoculars) we took photographs of the tops of the islands using telephoto lenses and counted individual birds using ArcGIS (as above).

We also surveyed historical (1996-1999) murre and kittiwake population monitoring plots at Chisik ($N_{\text{Chisik}} = 7$, $N_{\text{Duck}} = 1$) and Gull islands ($N_{\text{Gull}} = 10$) throughout the breeding season of each year (2016-2019). Historical plots were delineated by natural features (Piatt 2002), which we relocated using archived digital plot photos with hand drawn boundaries. Counts were conducted between approximately 1000 and 1600 hours at Gull and Chisik, times during daylight hours when attendance is most stable (Piatt and McLagan 1987). Using inflatable boats for access, we photographed historical population plots at both colonies using a Nikon SLR digital camera. On each day, we too photos at every plot. We imported plot photos, digitized plot boundaries, and counted kittiwakes and murres within the plots using ArcGIS (as above). For each count day, we summed the total number of birds in all the plots for a colony-wide total. We then calculated a mean and standard error of the number of kittiwakes and murres at each colony across all count days in each year and compared the mean counts across years. Because historical counts were done using binoculars rather than using photographs, we counted plots using binoculars on at least one count day each year for the first three years of the study to compare methods. Counts of kittiwakes and murres were within 1 and 6% of each other, respectively, for the two different methods, so we treated the photo counts as comparable to the past counts.

Following previously established procedures (Piatt 2002, Piatt et al. 2004), we analyzed population plot data during the general window between mid-incubation and start-of-fledging for both kittiwakes and murres, a time window during which peak numbers of birds were generally observed in recent years as well. However, there were multiple years of breeding failures during this study, making it difficult to calculate accurate phenology ranges. In years with low to no productivity, phenology was protracted, with low numbers of birds attempting to lay much later in the season, creating a bias towards using later count windows. To compensate for this bias, we used dates that were within five days of either historic or recent estimations of mid-incubation to start-of-fledge windows for population plot counts (see Table A-1). Phenology was estimated using primarily video (kittiwakes) or time-lapse camera footage (murres), as described below. Events not captured on camera were calculated using the average lengths of incubation (murres: 32 days (Ainley et al. 2020); kittiwakes: 27 days (Hatch et al. 2020) and fledging (murres: minimum nest departure age=15 days (Gaston and Jones 1998); kittiwakes: 32 days (Piatt 2002). Additionally, at Gull in 2019, when we did not have video available for analysis, we approximated kittiwake phenology based on estimates of chick hatch detected in photos. We estimated the earliest hatch date, and extrapolated start of fledge, by aging the youngest looking chicks in photos using feather stages (Maunder and Threlfall 1972). We estimated mid-chick hatch, and extrapolated mid-incubation, by approximating when 50% of total chicks observed on plots would have hatched (assuming linear hatch rates). We did not have footage to estimate phenology at Chisik for kittiwakes in any year or for murres in 2019, so we estimated the mid-incubation and start-of-fledge windows using dates within five days of historic mid-incubation to start-of-fledge dates.

4.2.2 Productivity and Predation

In our past (1995-1999) study, biologists and field camps were placed on Chisik and Gull islands throughout the breeding season. This enabled us to conduct intensive studies on the reproductive biology of seabirds. In the current study, we were only able to visit colonies periodically using our research vessel *R/V Alaskan Gyre*, and smaller skiffs launched from the *Alaskan Gyre;* or for work at Gull Island, skiffs based out of Homer Harbor. From these brief visits, we obtained an index of production for kittiwakes on plots based on the proportion of nests occupied by adult birds during mid-incubation that contained chicks later in the season. This index is reasonably accurate, and it can be well correlated ($r^2 > 0.90$) with estimates from intensive studies, although the index may overestimate production by 5% or more (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. We summed the maximum number of chicks observed on each population plot (above) late in the season and divided that by the sum of all well-developed nests counted on each population plot during incubation. The unit of this index of production is chicks fledged per nest monitored (CFN).

Measuring productivity in murres usually requires intensive visual observations every 2-3 days during the incubation and fledgling periods (Piatt and McLagan 1980, Piatt et al. 2004). Since we could not support that level of effort, we used time-lapse photography to collect data at breeding plots on both colonies. We monitored two plots on Chisik (22 total nests/eggs observed) and three plots on Gull (189 total nests/eggs observed); all plots were on the tops of islands and were separate from population plots (on cliff faces). The number of pairs attempting to nest on these plots was highly variable due to failed breeding attempts in many years, and plots in recent years included a much larger area than plots in the past, enabling the monitoring of more nests per plot simultaneously. Reconyx HyperFire 2® cameras recorded photographs (e.g., Figure 2) every 15-30 seconds 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 over 15 days old by the number of eggs laid. We calculated chick age using the date the chick was first seen to the last day it was seen, or in a few instances when hatching wasn’t observed we estimated the hatch date as 32 days after the lay date. We used 15 days as the threshold age to be considered as 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 and Jones 1998, Piatt 2002). The unit of this index of production is chicks fledged per egg monitored (CFE).

We also reviewed nest camera recordings to assess avian (e.g., gull or eagle) disturbance of nesting birds and predation on eggs or chicks. Video of kittiwake nest plots on Gull Island was recorded twice daily throughout the breeding season by the Pratt Museum (Homer, AK) from 2016-2018. No footage of kittiwake nests was available for Gull in 2019 or for Chisik in any year. We used time-lapse photography (as described above) to assess predation on murre eggs at both colonies. Eggs were considered “predated” if the video showed a predator taking the egg, and it was “presumed to be predated” if the egg disappeared in a frame and then in subsequent frames a predator was seen with an egg. We considered the fate “unknown” if an egg disappeared but no predator was ever observed, and “hatched” if we observed a chick hatch. Sample effort (number of nests observed) was variable between years due to a variety of factors including low numbers of nesting attempts in some years, camera malfunctions, or obstruction of the camera view by vegetation. Therefore, we can only summarize our observations here because we were unable to analyze for statistical differences among years.

Figure 2. Monitoring productivity of Common Murres
Example images from colonies on Gull (top) and Chisik (bottom) Islands.

5 Results

5.1 At-sea Surveys

From 2016-2019 we completed a total of 2,933 km of acoustic transects and concurrent marine predator surveys (Table 1, Figure 1). During these surveys, we caught 97,172 fish from at least 36 species in 74 trawls (Table 2).

Table 2. Annual trawl catch composition, fish abundance, and range of fish lengths. Total catch (number of fish) and length range (in mm) of the most abundant species caught in lower Cook Inlet from 2016-2019. These eight species comprised > 98% of the total catch of fish in all years combined. Fish of unknown species were not included.

Common Name	Scientific name	2016	2017	2018	2019	Length range (mm)
Pacific sand lance	*Ammodytes personatus*	6989	38672	316	13337	50-174
Walleye pollock	*Gadus chalcogrammus*	13386	11627	5706	95	24-552
Pacific herring	*Clupea pallasii*	2288	94	7	7	26-192
Capelin	*Mallotus catervarius*	46	13	34	997	22-137
Longfin smelt	*Spirinchus thaleichthys*	43	102	206	242	50-154
Variegated snailfish	*Liparis gibbus*	0	334	75	0	26-116
Pacific cod	*Gadus macrocephalus*	0	255	33	20	30-105
Pacific tomcod	*Microgadus proximus*	28	75	0	62	30-205
Other (n= 28)		75	128	69	97	

5.1.1 Forage fish abundance, distribution, and species composition

Trawl catch and modeled fish acoustic backscatter indices revealed differences in the distribution and interannual variability of shallow (< 20 m) and deep (≥ 20 m) strata across the study area (Figures 3-4). Lowest values in the shallow depth stratum were typically observed in the northern region near Chisik island and inner Kachemak Bay. Highest predicted fish acoustic indices in the shallow depth stratum occurred east of the Homer Spit during 2016, where trawl catches indicated aggregations were composed of age-0 herring and age-0 sand lance. The shallow fish acoustic index was greatest in 2016 and lowest in 2018 (Figure 4).

The deep stratum was dominated by juvenile pollock during 2016 and 2017, which were distributed mainly in the outer Kachemak Bay area (Figure 3). In contrast, fish acoustic indices within the deep stratum during 2018 and 2019 were more patchy, and the deep fish acoustic index was lowest in these years, while shallow fish acoustic index increased in 2019 (Figure 4).

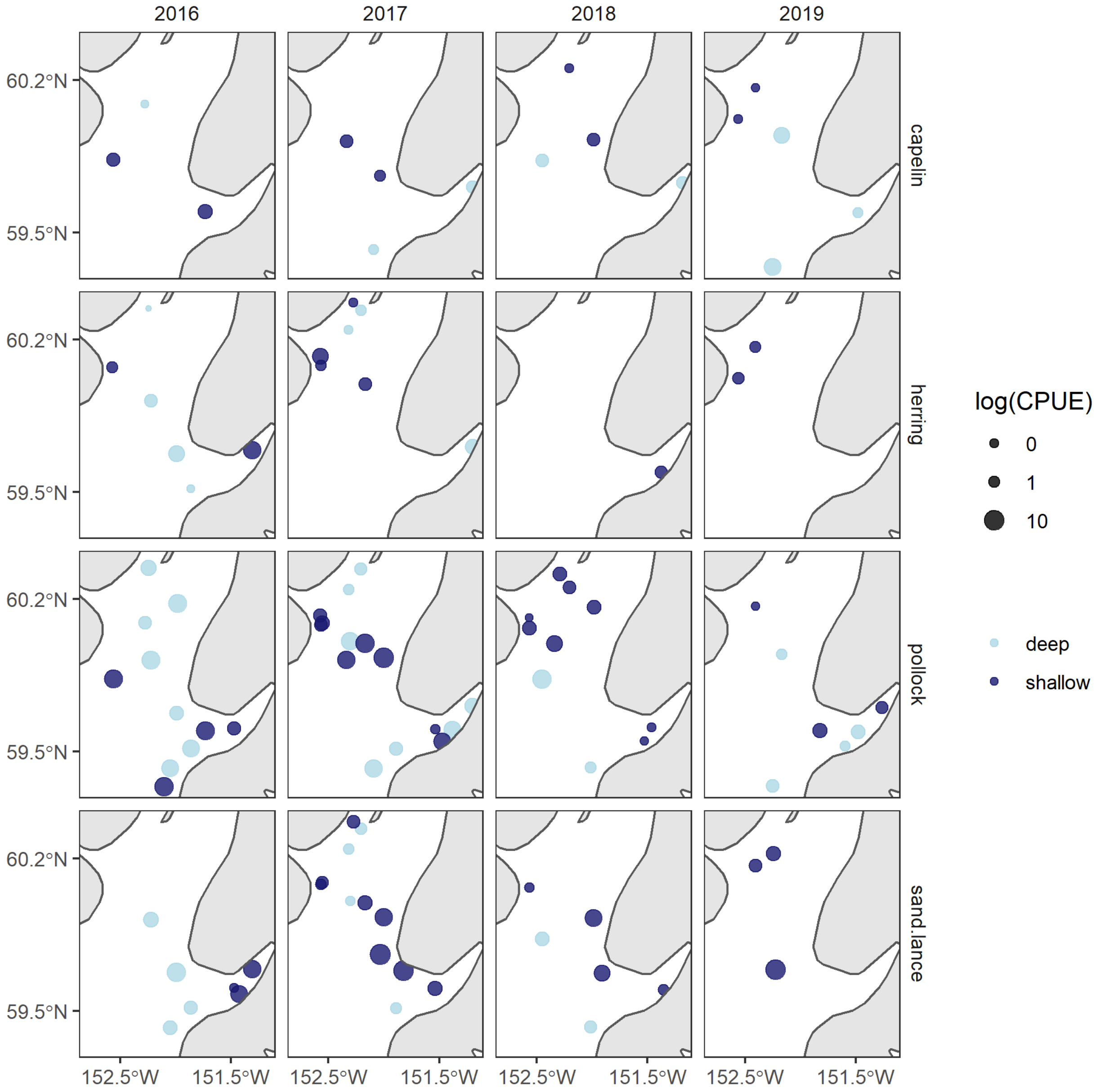

Figure 3. Distribution of key forage fish species in trawls
Log-transformed catch per unit effort (CPUE, fish km^{-1}) by depth strata (color), year (columns), and species (rows) in lower Cook Inlet, Alaska.

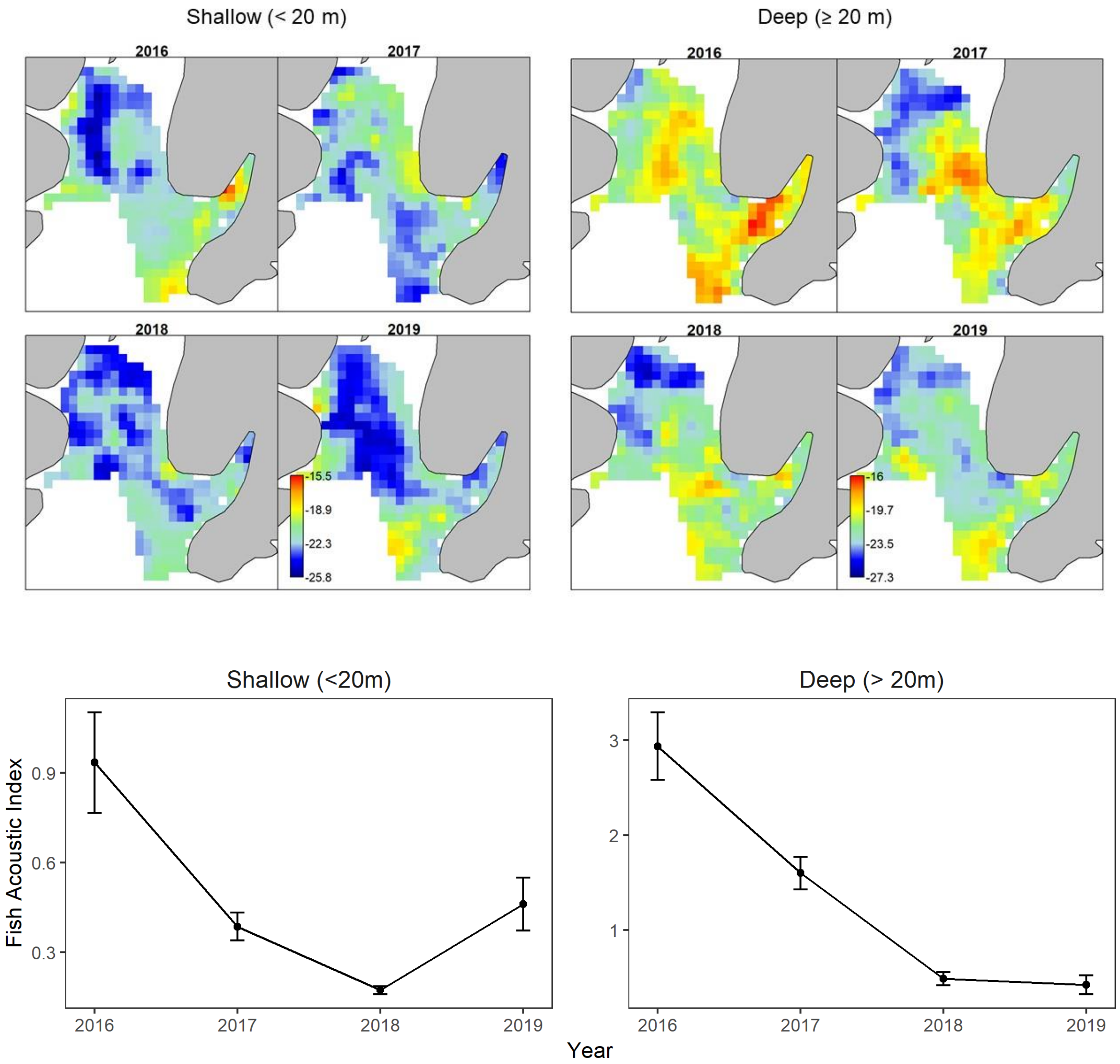

Figure 4. Distribution and trends in predicted fish acoustic indices
(Top) Log-transformed predicted fish acoustic indices (area backscattering coefficient, m^2m^{-2}) by year and depth strata in lower Cook Inlet, Alaska. (Bottom) Annual area-weighted predicted fish acoustic indices (area backscattering coefficient, $s_a \times 10^5$, m^2m^{-2}) by year in lower Cook Inlet, Alaska.

Trawl catches in all years were dominated by sand lance, age-0 walleye pollock, herring, and capelin, and smaller contributions from species such as longfin smelt and variegated snail fish near Chisik, or juvenile Pacific cod and Pacific tomcod near Kachemak Bay (Table 2). Length frequencies suggest relatively stable size of capelin and juvenile pollock across years. Sand lance exhibited multimodal size frequencies in all years but 2016, and mean size varied among years (Figure 4).

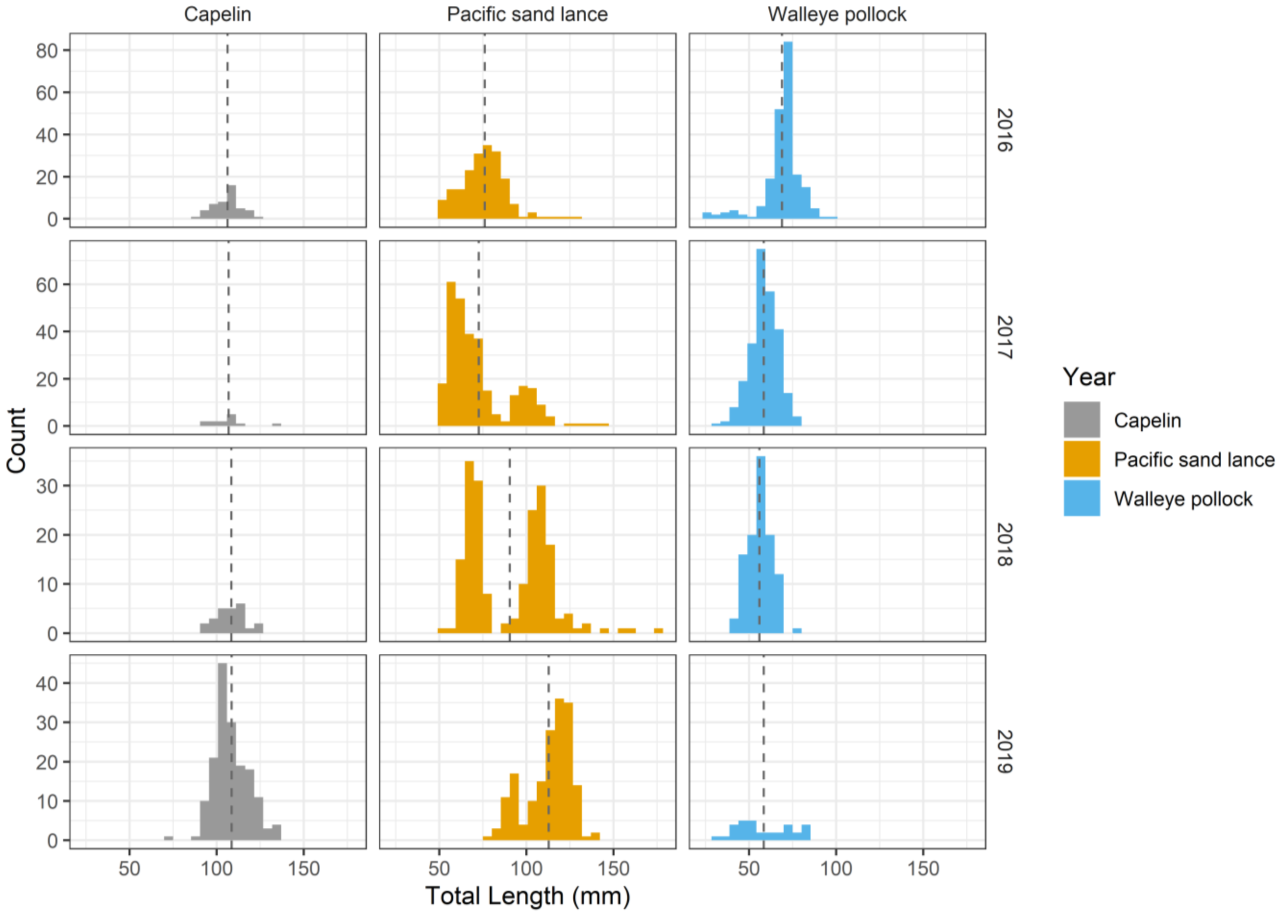

Figure 5. Forage fish size frequencies
Size frequencies for capelin (> 55 mm, to exclude larvae), Pacific sand lance and walleye pollock (< 100 mm) in lower Cook Inlet from 2016-2019. Dashed lines indicate mean lengths (mm).

Species-specific fish densities in shallow (< 20 m) and deep (≥ 20 m) depth strata identify potential prey fields for surface-feeding kittiwakes and diving murres around each colony (Figure 6). Sand lance generally dominated the shallow prey field, particularly in Kachemak Bay. Capelin densities were uniformly low in the shallow strata within both regions and increased in the deep strata in 2018 (Kachemak) and 2019 (both regions). Herring densities were highest in 2016 in both regions, with greatest densities of age-0 herring occurring near Homer Spit that year. In general, walleye pollock dominated the backscatter signal driving high acoustic backscatter indices in 2016-2017. In particular, age-0 walleye pollock densities were greatest in the deep strata in both regions in those years.

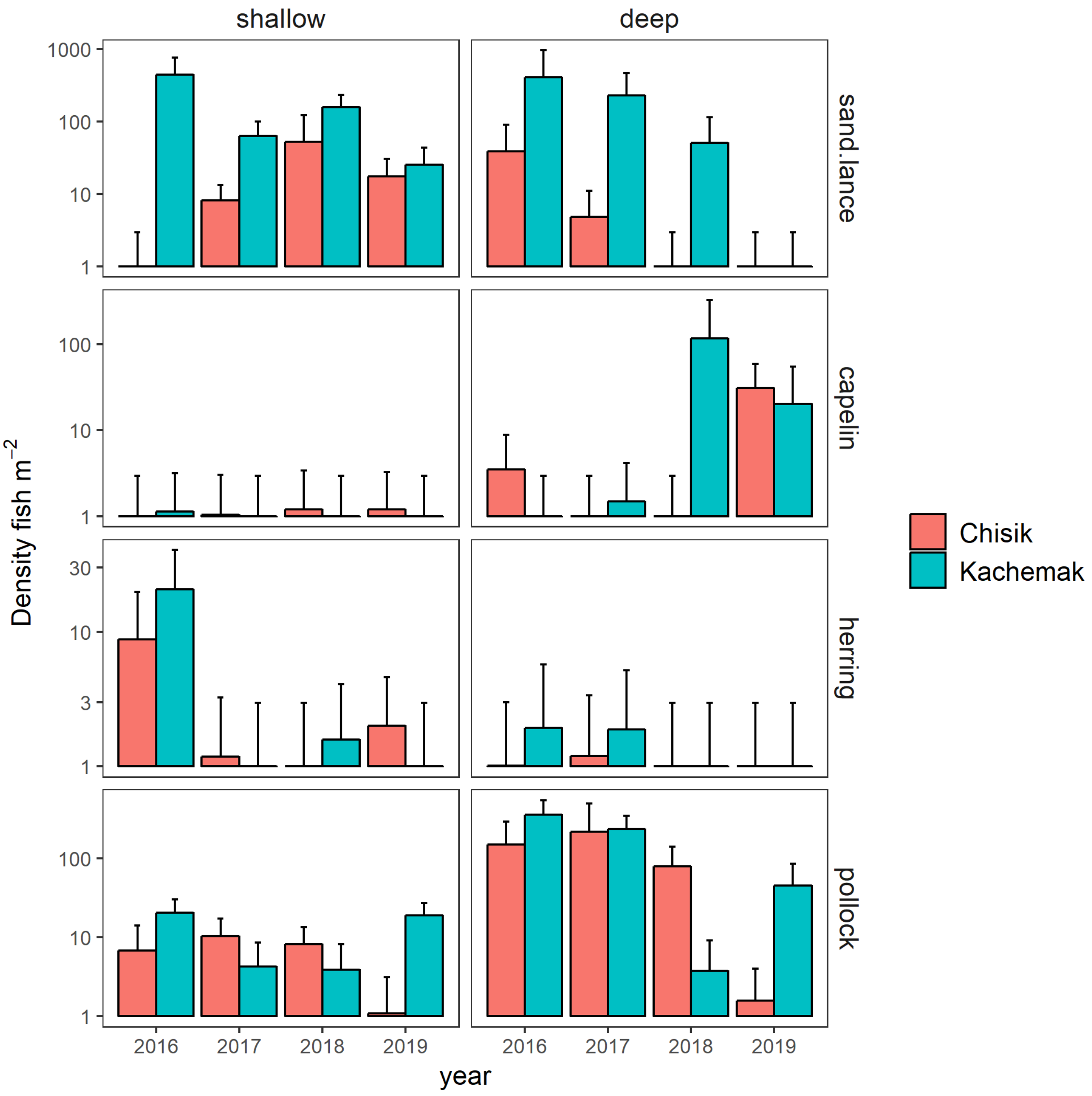

Figure 6. Species-specific fish densities
Species-specific fish density as a proportion of acoustic backscatter (mean ± 95% CI) by region on July surveys in lower Cook Inlet.

5.1.2 Marine Predator Surveys

Our main purpose in conducting marine predator surveys was to assess annual abundance of seabirds at sea, and to compare these to densities observed in the 1990s. We used VAST joint species distribution models (see Methods) to predict densities at sea for 10 focal seabird species/taxa groups shown in Figures 6 to 14 (also see Table 3 for species/taxa group names). For shearwaters (the only migrant non-breeding species group examined), high density concentrations were distributed in the outer Kachemak Bay area and extended north in some years. There was a large influx of shearwaters in 2017, when high densities were observed in outer Kachemak Bay, and the typically less-used inner bay as well (Figure 7). Kittiwake and Glaucous-winged Gull densities were patchy, mostly coastal, and generally concentrated near colonies in most years (Figure 8-9). Murres were more widely distributed in the study area, and densities were usually higher near colonies on both sides of Cook Inlet (Figure 10). Densities were highest in Kachemak bay in all years except 2018 and 2019, and murres were found in moderate densities over deeper waters of outer Kachemak Bay and off the Kenai Peninsula. Pigeon Guillemots were notably absent from the Chisik area, but they were concentrated along the entire coast of Kachemak Bay in remarkably consistent fashion during all years (Figure 11). Marbled Murrelets were widely distributed on the east side of lower Cook Inlet, with notable concentrations in the inner bay, mid-bay, on coastal shoals to the north of, and off of, Anchor Point (Figure 12). They were also found persistently on a small coastal shoal south of Chisik Island on the west side of the inlet. Kittlitz's Murrelets were concentrated in the deep inner part of Kachemak Bay near a glacial river outflow during 2016 (as in 1997-1998), but most birds were found with greatest consistency in outer Kachemak Bay and adjacent to Anchor Point or on the shallow shelf extending SW of the point (Figure 13). Horned Puffins breed almost exclusively on the west side of Cook Inlet, and mostly on Duck Island, and densities at sea were always highest in proximity to that colony (Figure 14). Moderate densities were observed along a track from Duck Island to shoals off Anchor Point in Kachemak Bay, suggesting that Horned Puffins were flying back and forth from Duck Island to this area to find forage fish. Very few Horned Puffins breed in Kachemak Bay and densities were consistently low within inner Kachemak Bay (Figure 14). Finally, only small numbers of Tufted Puffins breed in either Kachemak Bay or on the west side of Cook Inlet, whereas large numbers breed on the Barren Islands which is at the mouth of Cook Inlet and south of our study area. Hence the pattern of Tufted Puffin distribution is driven by birds flying north from the Barren Islands and feeding in mixed waters off the Kenai Peninsula and the outer edge of Kachemak Bay, often up to or beyond Anchor Point (Figure 15). The pattern of Tufted Puffin distribution is most similar to that of shearwaters (Figure 7).

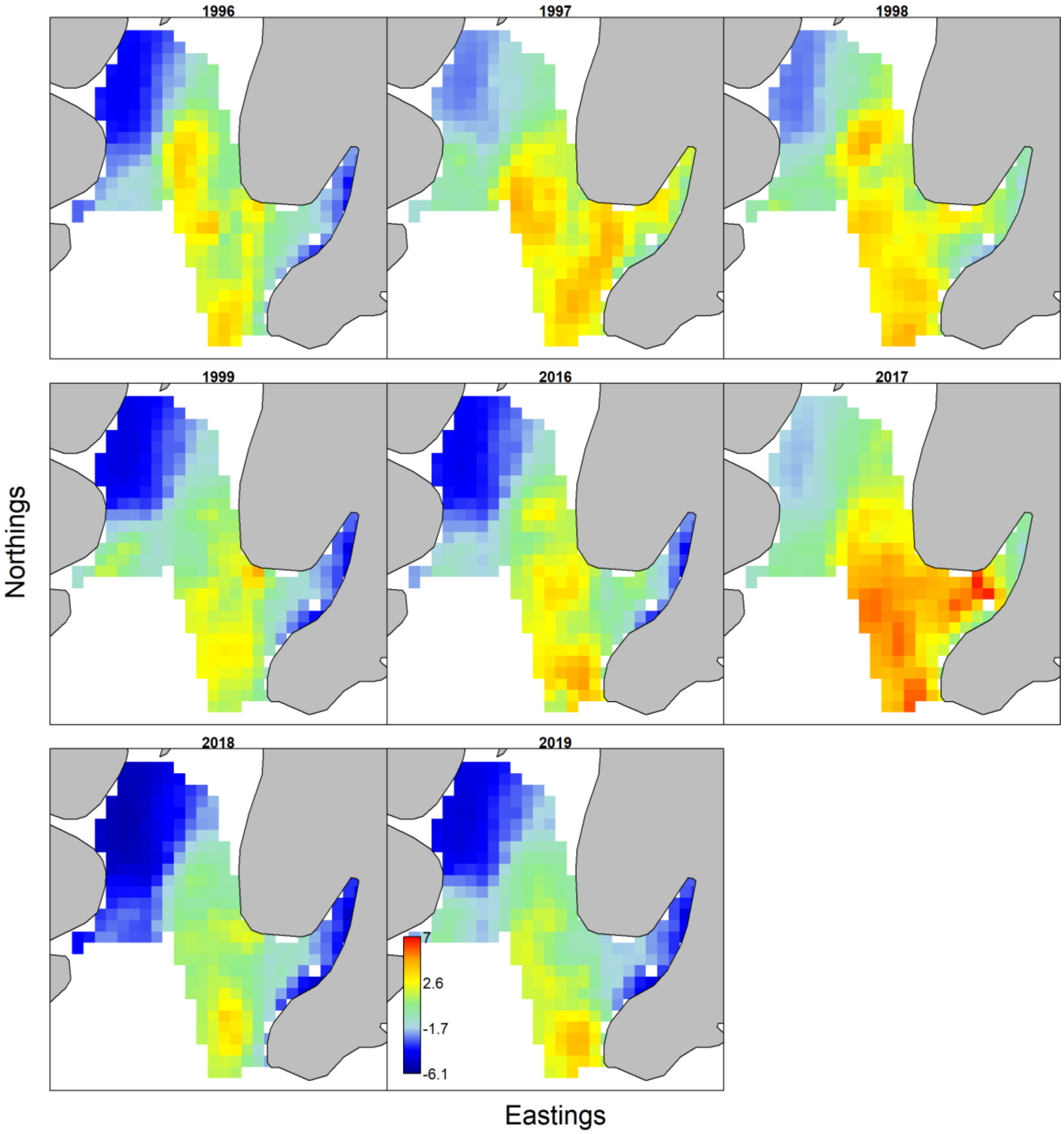

Figure 7. Predicted annual densities- Shearwater (*Ardenna* spp.)

Shearwater (*Ardenna* spp.) log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

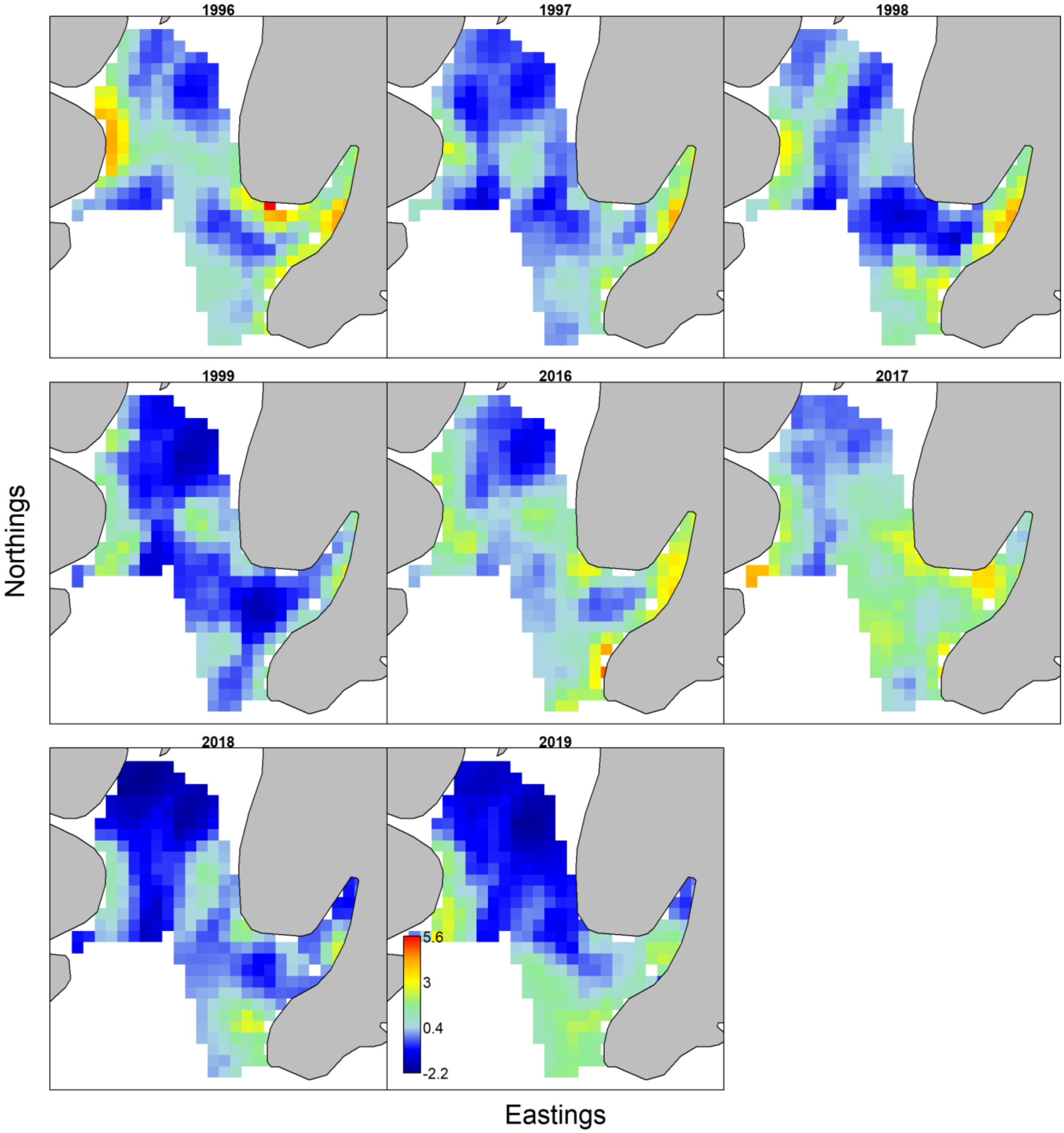

Figure 8. Predicted annual densities- Black-legged Kittiwake
Black-legged Kittiwake log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

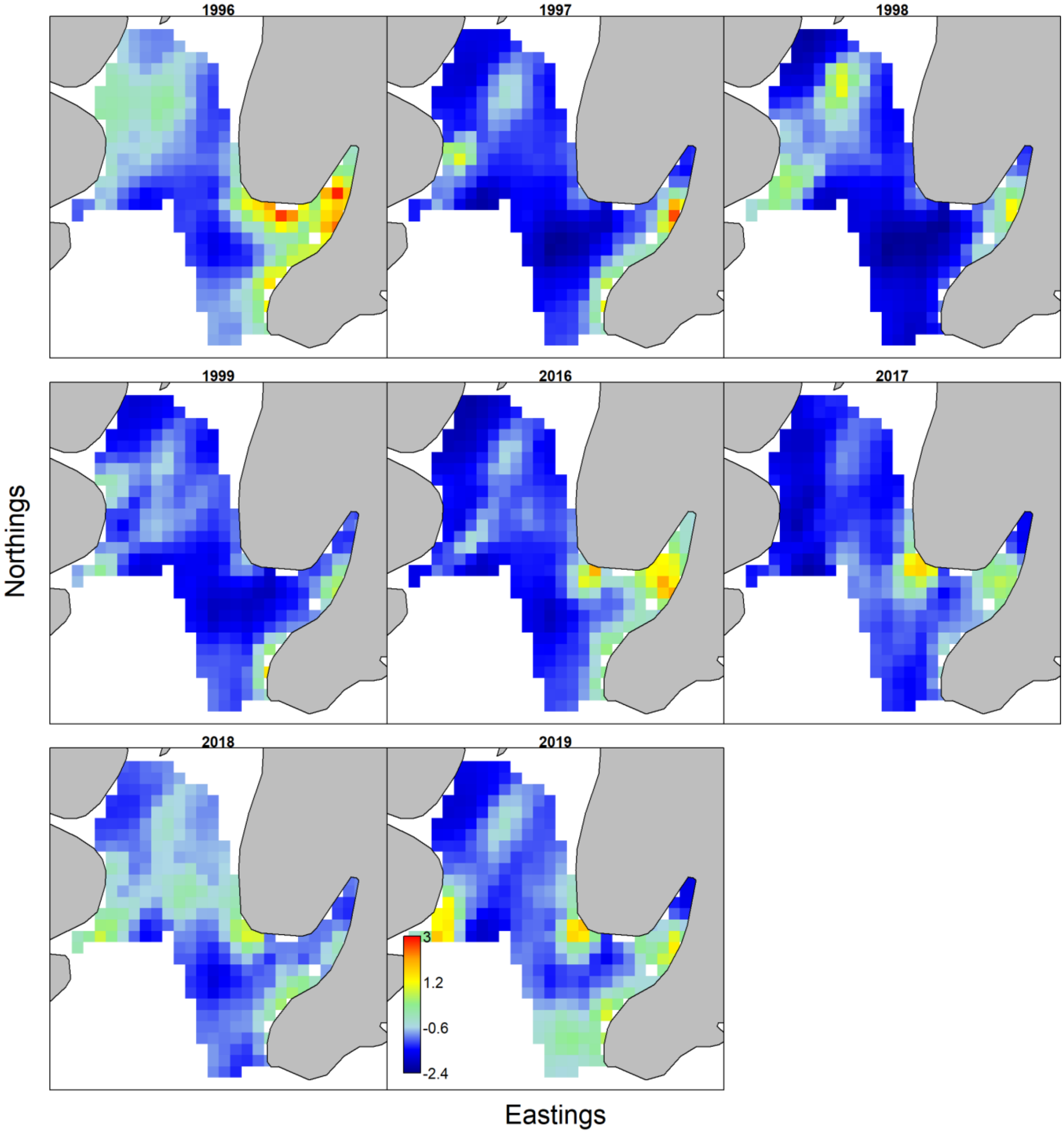

Figure 9. Predicted annual densities- Glaucous-winged Gull
Glaucous-winged Gull log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

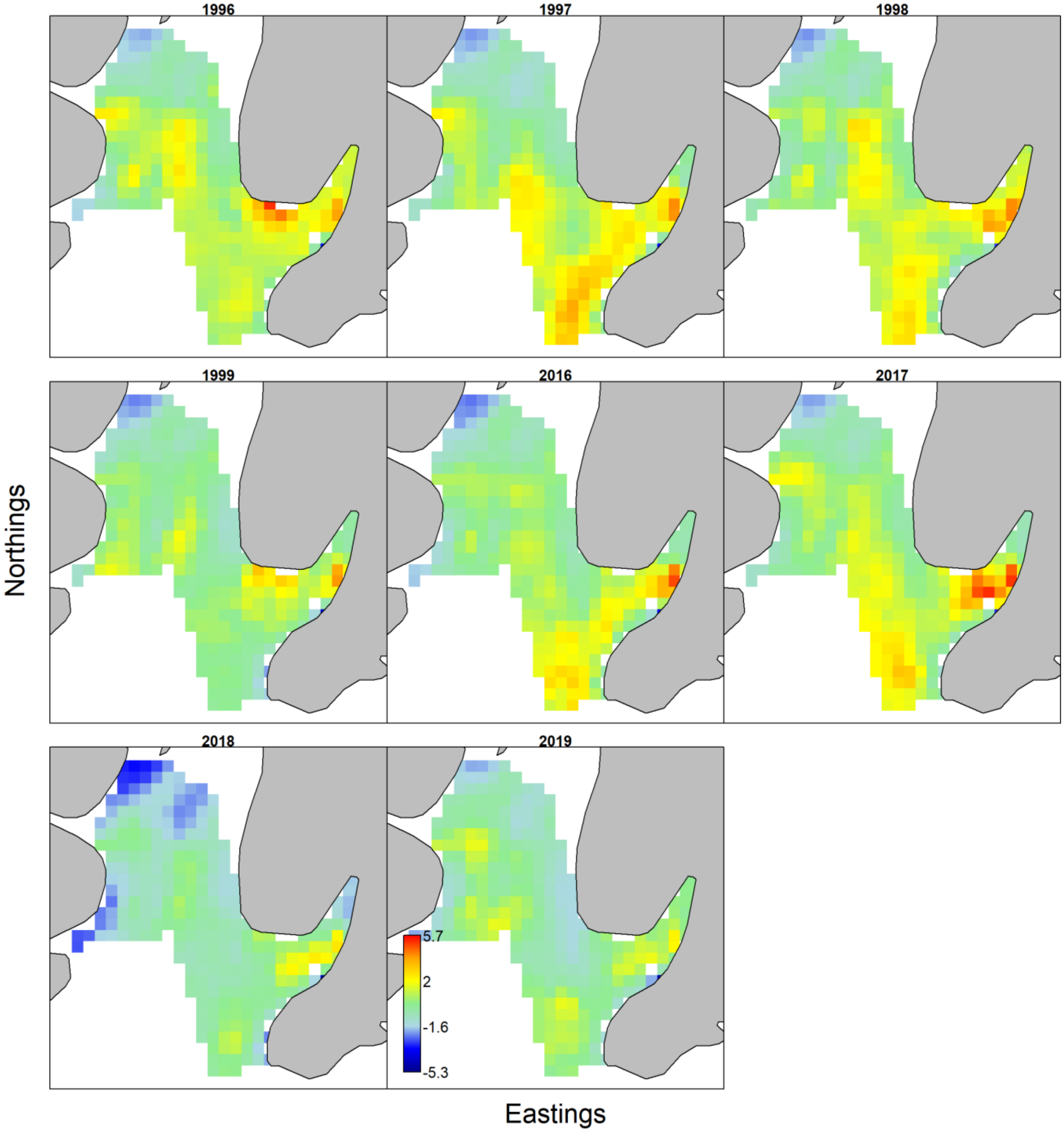

Figure 10. Predicted annual densities- Common Murre
Common Murre log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

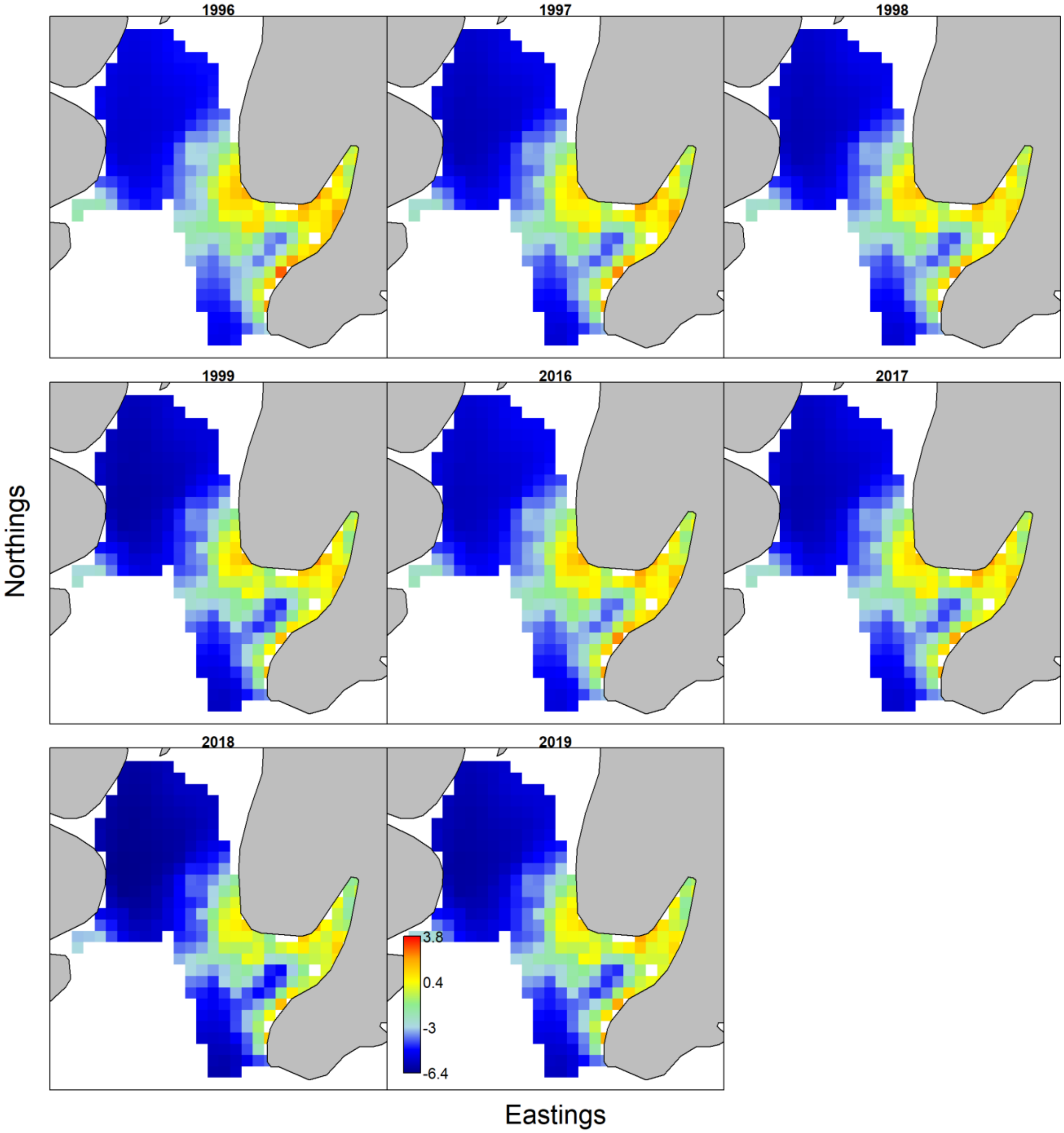

Figure 11. Predicted annual densities- Pigeon Guillemot
Pigeon Guillemot log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

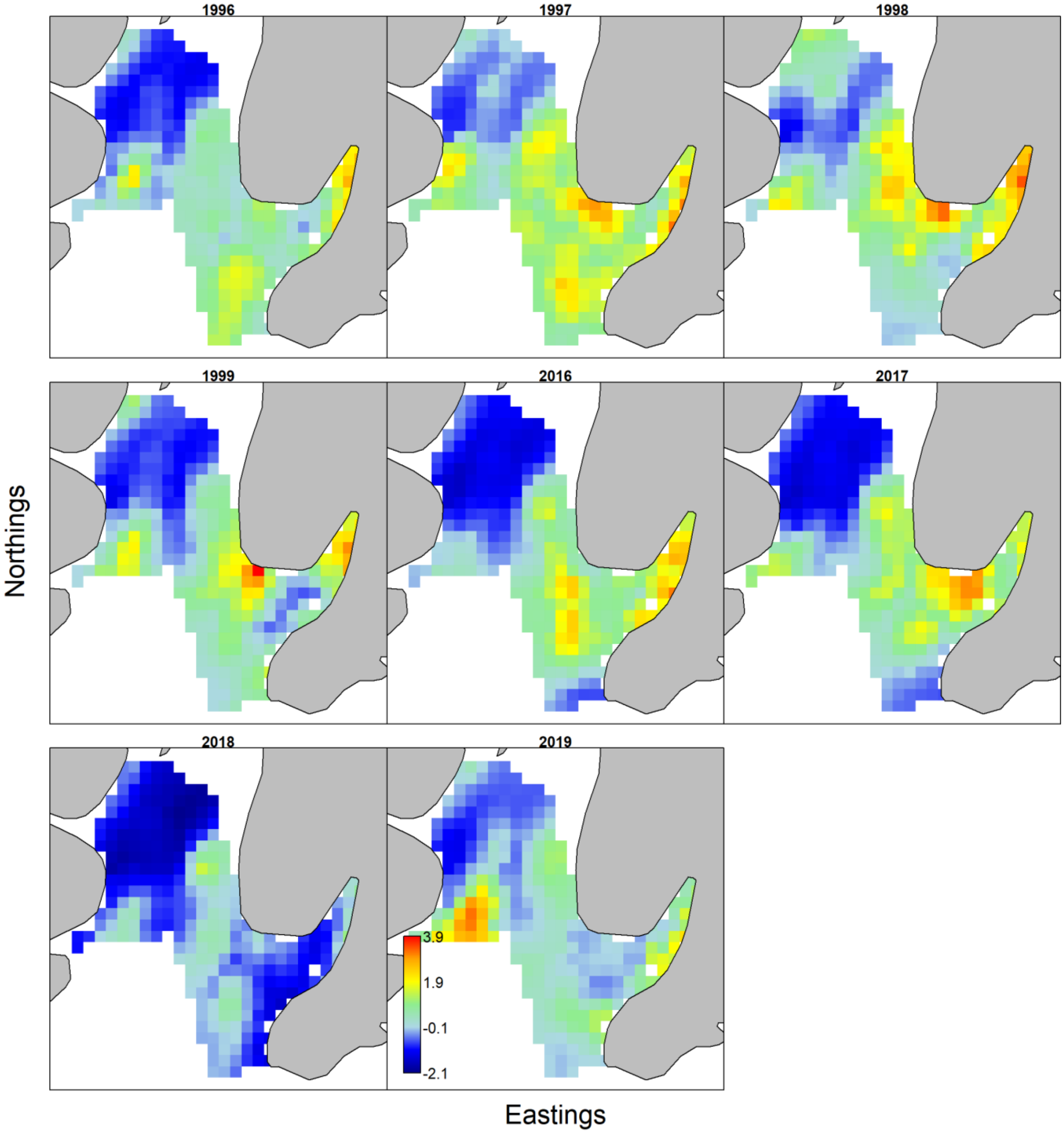

Figure 12. Predicted annual densities- Marbled Murrelet

Marbled Murrelet log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

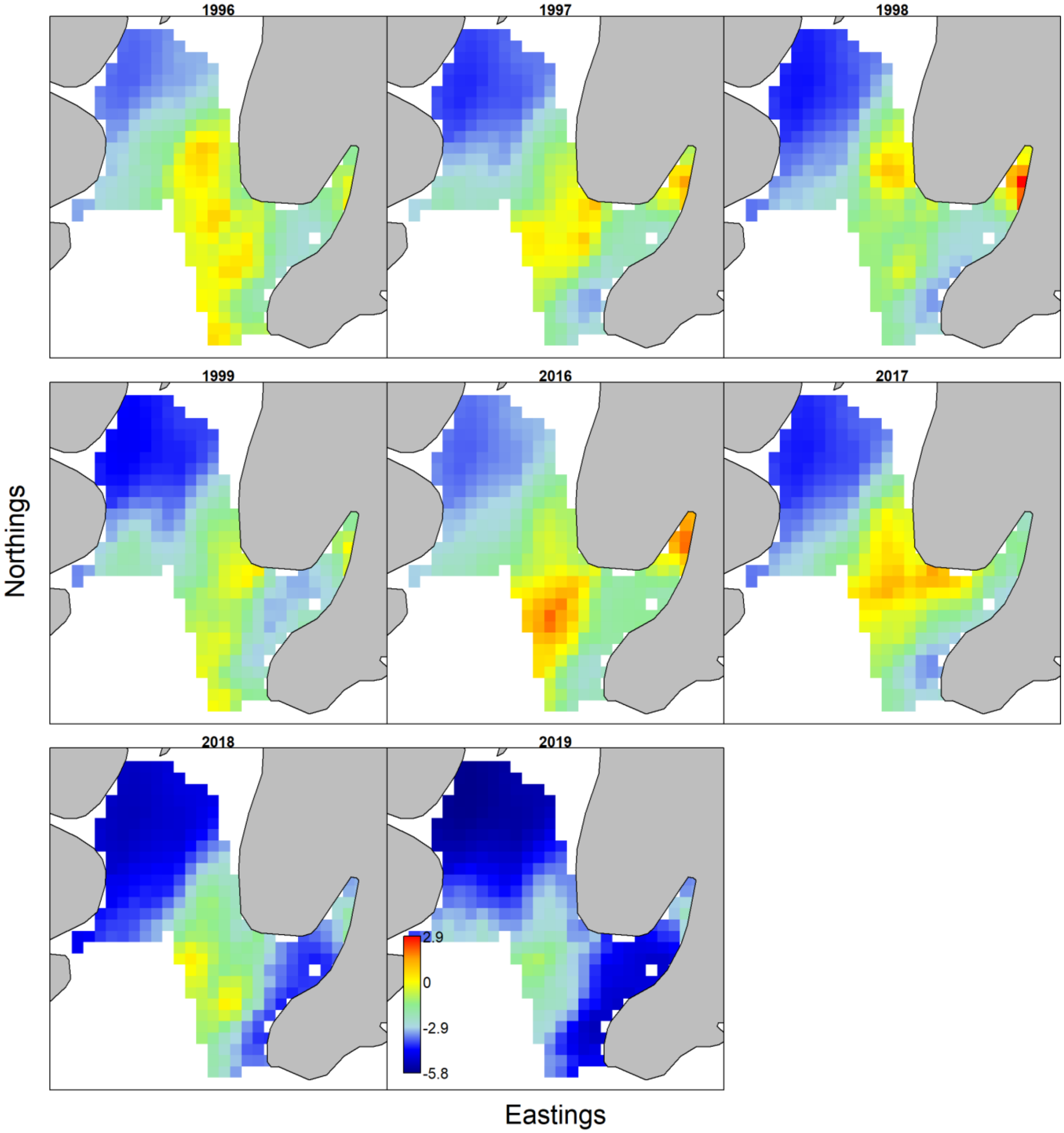

Figure 13. Predicted annual densities- Kittlitz's Murrelet
Kittlitz's Murrelet log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

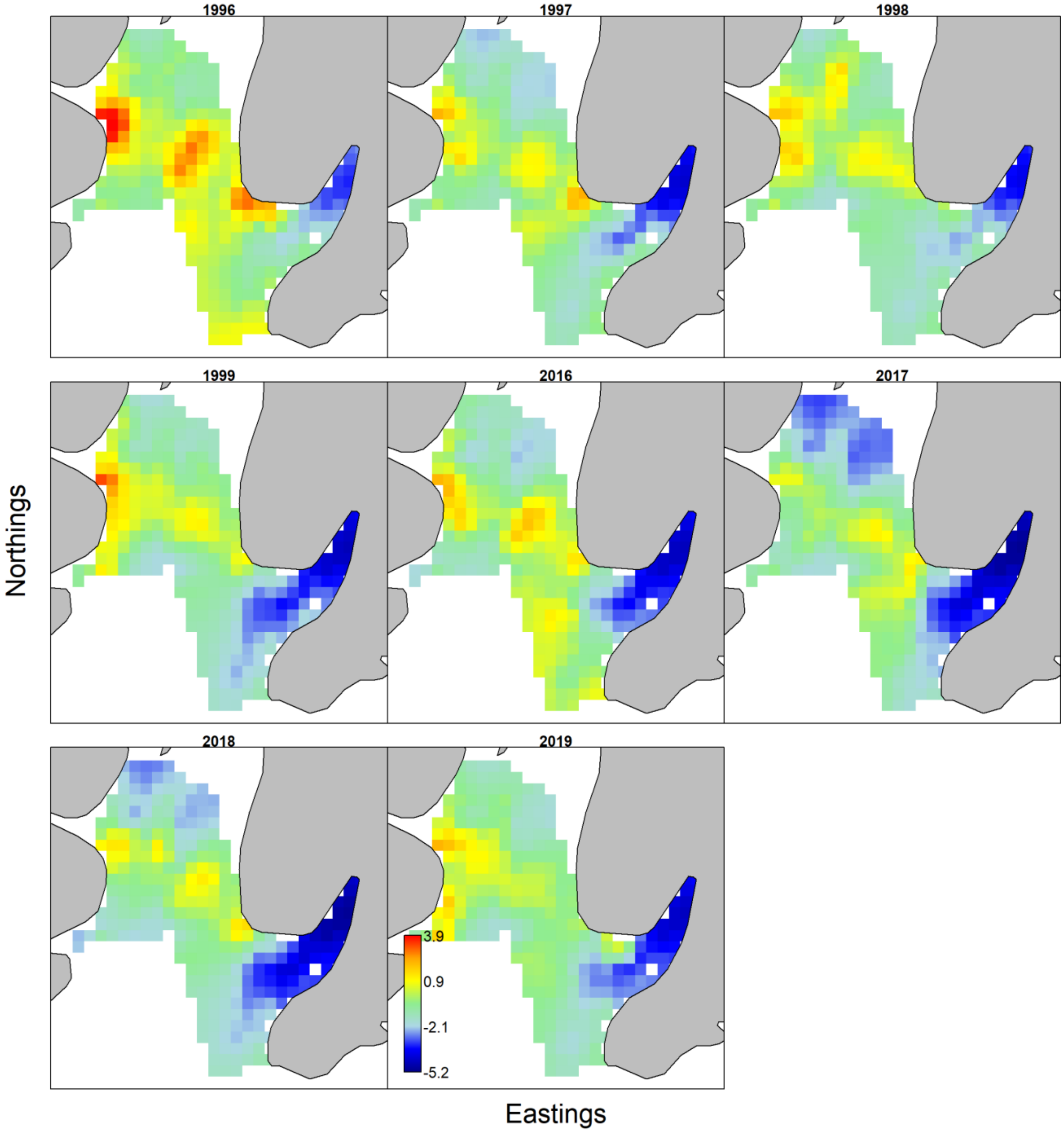

Figure 14. Predicted annual densities- Horned Puffin
Horned Puffin log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

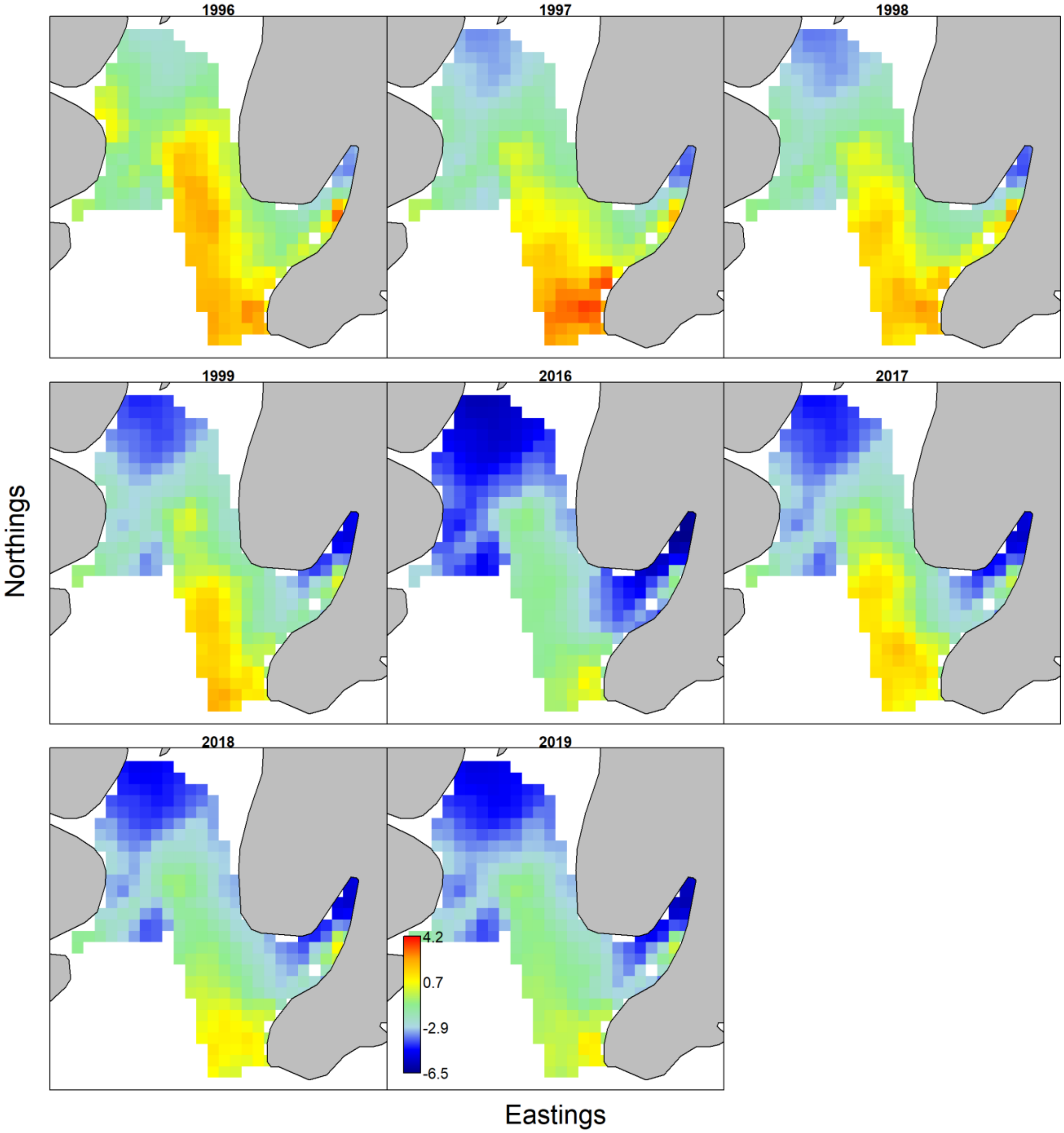

Figure 15. Predicted annual densities-Tufted Puffin
Tufted Puffin log-transformed predicted densities by year on surveys in lower Cook Inlet, Alaska.

Indices of abundance derived from VAST modeled density grids reveal moderately high interannual variability in seabird population estimates within lower Cook Inlet during each of the 4-year sampling periods in the 1990s (CVs 26-66%; mean=41%, excluding migratory shearwaters) and the 2010s (CVs 18-92%; mean=51%) (Table 3, Figure 16). Reflecting their high mobility among rich foraging grounds during their migration to Alaska in summer (their winter), shearwaters exhibited the highest annual variability (CV 148%) in the 2010s, largely owing to a huge influx into Cook Inlet during 2017 that increased their abundance by more than an order of magnitude above normal. While annual estimates varied among resident breeding species as well, it appears that in both the 1990s and the 2010s, the abundance of 9 out of 10 species declined from early to late years of each 4-year study period. In the 2010s, this included significant (p<0.05) or marginally significant (p<0.10) intra-period (average of first 2 years versus last 2 years) declines for kittiwakes (-61%, p=0.0091), murres (-76%, p=0.0048), Pigeon Guillemots (-38%, p=0.047), *Brachyramphus* murrelets (-47%, p=0.074) and Kittlitz's Murrelets (-85%, p=0.039). In the 1990s, only Tufted Puffins declined significantly (-55%, p=0.025). In the 1990s, the average change for declining species was -36% (n=9, range -23% to -56%); in the 2010s it was -54% (n=9, range -14% to -90%). Assuming the odds are equal (50/50) that populations would either increase or decrease among these sampling periods, a Signs Test suggests that a simultaneous decline in 9 out of 10 species between the first 2 and last 2 years was improbable (p=0.0098) in either the 1990s or the 2010s. This perhaps suggests changing environmental conditions affected all seabird populations during both sampling periods in the 1990s and 2010s. The effect was especially notable in 2018, when abundance of most species dropped to unprecedented low levels, and numbers increased only slightly in 2019. Only 2 species showed linear decreases within sample periods: Kittlitz's Murrelet abundance declined linearly (r^2=0.98, p=0.021) from 2016 to 2019, and Pigeon Guillemots declined linearly (r^2=0.91, p=0.048) between 1996 and 1999.

With respect to changes in abundance between past (1996-1999) and recent (2016-2019) surveys, only shearwater numbers increased between these sampling periods (driven by the 2017 influx), while all other taxa counts declined by varying amounts. Most changes were statistically insignificant, owing in part to small sample sizes (n=4 years in each period) and moderate interannual variability. Two taxa exhibited significant differences in average abundance between the 1990s and 2010s, i.e., Tufted Puffin (-81%, *T*-test, p=0.029) and Marbled Murrelet (-35%, p=0.041). Common Murres (-22%) and Black-legged Kittiwakes (-10%) exhibited smaller changes, which were lesser than, or equal to, changes noted on population plot counts for kittiwakes and murres at colonies (below). Declines of 6-46% were also noted for remaining taxa, which may have biological, if not statistical, significance. Taken on the whole, the simultaneous decline (mean= -30%) in numbers of 9 out of 10 species was improbable (Sign Test, n=10, p=0.0098).

Table 3. Seabird abundance indices

Seabird abundance indices (SE) derived from multivariate VAST spatio-temporal model of at-sea survey data in lower Cook Inlet, Alaska.

Species Group	1996	1997	1998	1999	2016	2017	2018	2019
Shearwaters;	41147	101739	83076	20972	47389	361191	13280	26979
Ardenna spp.	(5947)	(11689)	(9533)	(2600)	(7124)	(39177)	(2720)	(4683)
Black-legged Kittiwake;	37028	18790	22772	10442	28302	29574	8985	13662
Rissa tridactyla	(3761)	(2274)	(1805)	(1200)	(2694)	(2899)	(928)	(1303)
Glaucous-wing Gull;	5938	2626	2389	2101	3075	2369	3033	3680
Larus glaucescens	(798)	(424)	(392)	(299)	(379)	(325)	(415)	(448)
Common Murre;	24423	29957	25701	12577	21854	36492	5892	8184
Uria aalge	(2309)	(2728)	(2039)	(1229)	(2853)	(4431)	(806)	(888)
Pigeon Guillemot;	4982	3603	3352	2724	3861	3213	1871	2506
Cepphus columba	(824)	(566)	(559)	(458)	(567)	(605)	(337)	(415)

All *Brachyramphus* Murrelets; *B*. spp.	21482	35825	26375	17822	19443	21827	6809	14959
	(2172)	(3027)	(2399)	(1462)	(1752)	(2042)	(920)	(1631)
Marbled Murrelet; *B. marmoratus*	11472	20690	20336	13662	13250	13497	4086	11919
	(1258)	(1748)	(1902)	(1211)	(1191)	(1319)	(607)	(1408)
Kittlitz's Murrelet; *B. brevirostris*	2361	1775	2107	1007	3654	2239	687	223
	(459)	(378)	(426)	(232)	(784)	(459)	(252)	(100)
Horned Puffin; *Fratercula corniculata*	13677	4310	4605	4883	5361	2610	2816	4071
	(1909)	(635)	(687)	(765)	(675)	(389)	(510)	(574)
Tufted Puffin; *Fratercula cirrhata*	13897	15820	8291	5010	792	4119	2058	1303
	(1788)	(2009)	(954)	(691)	(187)	(633)	(481)	(302)

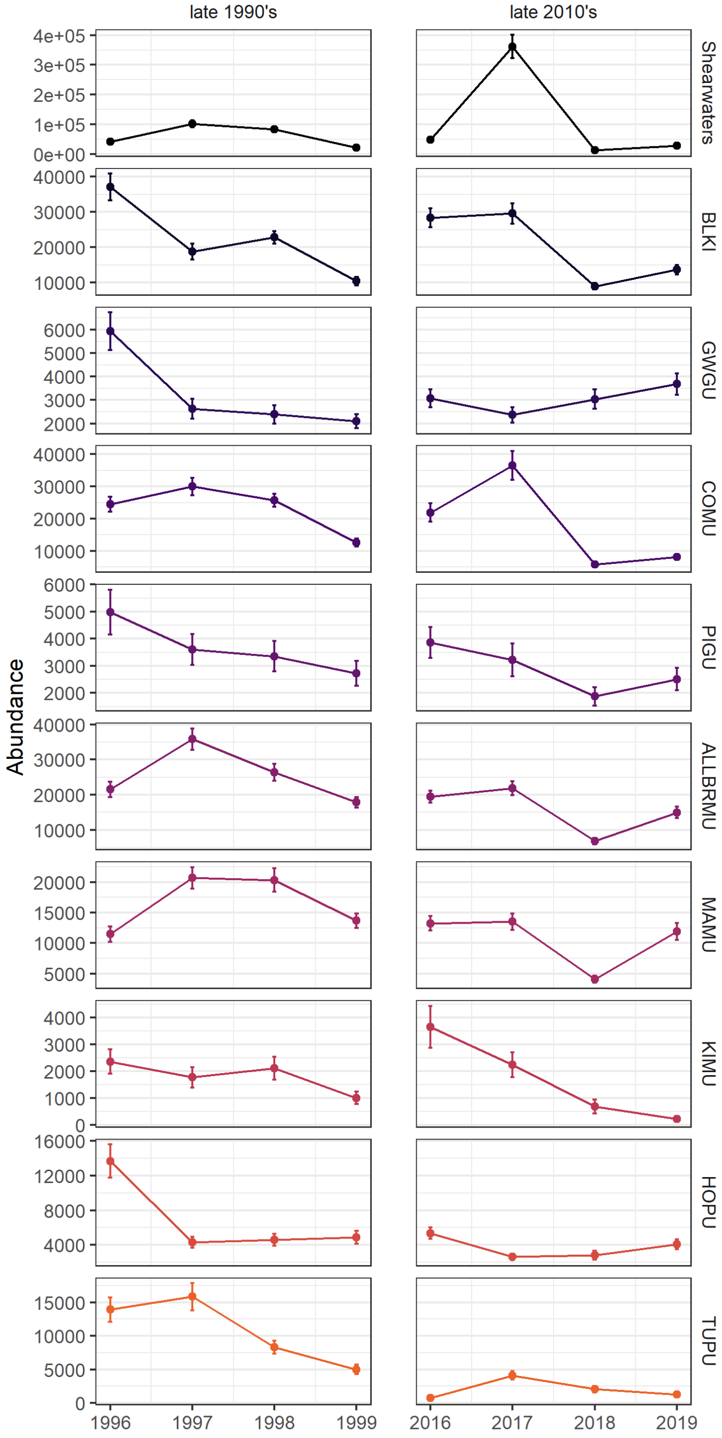

Figure 16. Interannual variability in seabird abundance
Interannual abundance (±SE) indices for Shearwaters, Black-legged Kittiwakes (BLKI), Glaucous-wing Gulls (GWGU), Common Murre (COMU), Pigeon Guillemot (PIGU), *Brachyramphus* Murrelets (ALLBRMU), Marbled Murrelets (MAMU), Kittlitz's Murrelets (KIMU), Horned Puffin (HOPU), and Tufted Puffin (TUPU) on surveys in lower Cook Inlet, Alaska.

5.2 Seabird Colony Monitoring

5.2.1 Population

Whole colony census (WCC) counts for Black-legged Kittiwake populations at Chisik were lower in recent (2016-2019) than past (1996-1999) surveys, but WCC counts at Gull Island were relatively stable over this time period. There were 73% fewer kittiwakes at Chisik Island on recent WCC counts than in the past (Table 4; Figure 17), but because there was only one census conducted in the past (1995), we could not test the difference between years statistically (Figure 17). Furthermore, because the past census was conducted only in the first year (1995) of the study, it doesn't account for a decline of kittiwakes that might have occurred during 1996-1999 (perhaps as much as ~30% noted on population plot counts; below). WCC counts for kittiwakes at Gull Island were 8% lower in recent versus past surveys, but this difference was not significant (Figure 16; F=0.30, *p*=0.614). The power for detecting statistically significant change on WCC counts is low because typically these counts were conducted only once in each year. They were established more for monitoring possible growth and contraction of colonies rather than trend (Piatt 2002).

WCC counts of Common Murre populations declined at both colonies between past and recent censuses. WCC counts for murres were 72% lower (20-125 CI) in recent versus past surveys on Chisik Island (Figure 16; F=14.62, *p*=0.019) and 46% lower (6-86 CI) in recent versus past surveys on Gull Island (Figure 16; F=8.02, *p*=0.030). Confidence intervals were wide because there were substantial fluctuations in murre attendance at both islands following the marine heatwave, and as noted above, sample sizes were small for whole colony censuses.

Table 4. Seabird population and productivity indices

Population and productivity indices by survey type, colony, species and year for Common Murres (COMU) and Black-legged Kittiwakes (BLKI) in lower Cook Inlet during 1995-1999 and 2016-2019. Mean (SD) values were calculated for each time series (1995-1999; 2016-2019). Productivity indices were measured as chicks fledged/nest for BLKI and chicks fledged/eggs laid for COMU (see Methods). Asterisk * indicates counts corrected since previous reports (see Methods).

		Census		Population Plots		Productivity	
Year	Species	Chisik	Gull	Chisik	Gull	Chisik	Gull
1995	COMU	2,246	8,553	64*	384	-	0.61
1996	COMU	-	-	153	340	0.74	0.64
1997	COMU	3,500	6,068	139*	344	0.67	0.53
1998	COMU	-	10,400	69	334	0.18	0.65
1999	COMU	-	10,725	189	407	0.63	0.28
1995-1999	COMU	2,873 (627)	8,937 (1852)	127 (57)	359 (43)	0.56 (0.25)	0.54 (0.15)
2016	COMU	80	7,636	0	297*	0.00	0.00
2017	COMU	1,285	4,658*	20*	366*	0.00	0.00
2018	COMU	971	3,147	89*	217*	0.00	0.00
2019	COMU	854	3,771	76	242	0.00	0.26
2016-2019	COMU	798 (443)	4,803 (1722)	37 (43)	281 (135)	0.00 (0.00)	0.07 (0.11)

1995	BLKI	16,504	8,166	857*	1,341*	-	0.40
1996	BLKI	-	-	890	1,109*	0.05	0.56
1997	BLKI	-	-	591*	1,196	0.01	0.46
1998	BLKI	-	-	584	1,203	0.00	0.28
1999	BLKI	-	5,809	688	1,094	0.09	0.59
1995-1999	BLKI	16,504 (-)	6,988 (1179)	725 (237)	1,197 (122)	0.04 (0.04)	0.46 (0.11)
2016	BLKI	1	5,141	42*	927*	0.00	0.01
2017	BLKI	4,707	6,369	81*	957	0.00	0.61
2018	BLKI	2,552	7,479	27	790*	0.00	0.00
2019	BLKI	5,931	6,719	74	867	0.02	0.67
2016-2019	BLKI	4,397 (1397)	6,427 (844)	58 (35)	884 (151)	0.01 (0.01)	0.32 (0.32)

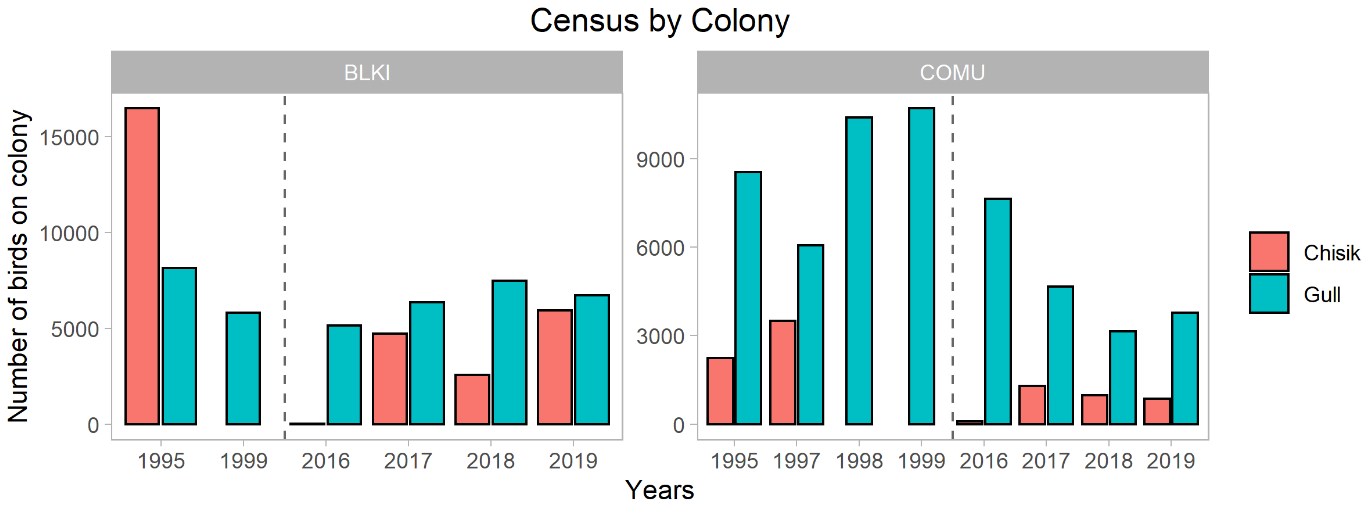

Figure 17. Annual census by colony
Full island census counts for Black-legged Kittiwakes (BLKI) and Common Murre (COMU) on Chisik (red) and Gull (blue) Islands from 1995-1999 and 2016-2019.

Population indices based on population plot counts (PPCs) were significantly lower for kittiwakes (F=80.83, $p<0.001$) in recent years than they were in the past (Table 4; Figure 18). Kittiwake PPCs were 92% lower (69-115 CI) at Chisik (F=69.25, $p<0.001$) and 26% lower (19-33 CI) at Gull (F=61.62, $p<0.001$) in recent surveys compared to the past. Similarly, PPCs of murres at were 71% (27-115 CI) lower at Chisik (F=11.09, $p=0.002$), and 22% lower (7-37 CI) on Gull (F=8.34, $p=0.006$) in recent years than they were in past surveys (Table 4; Figure 18).

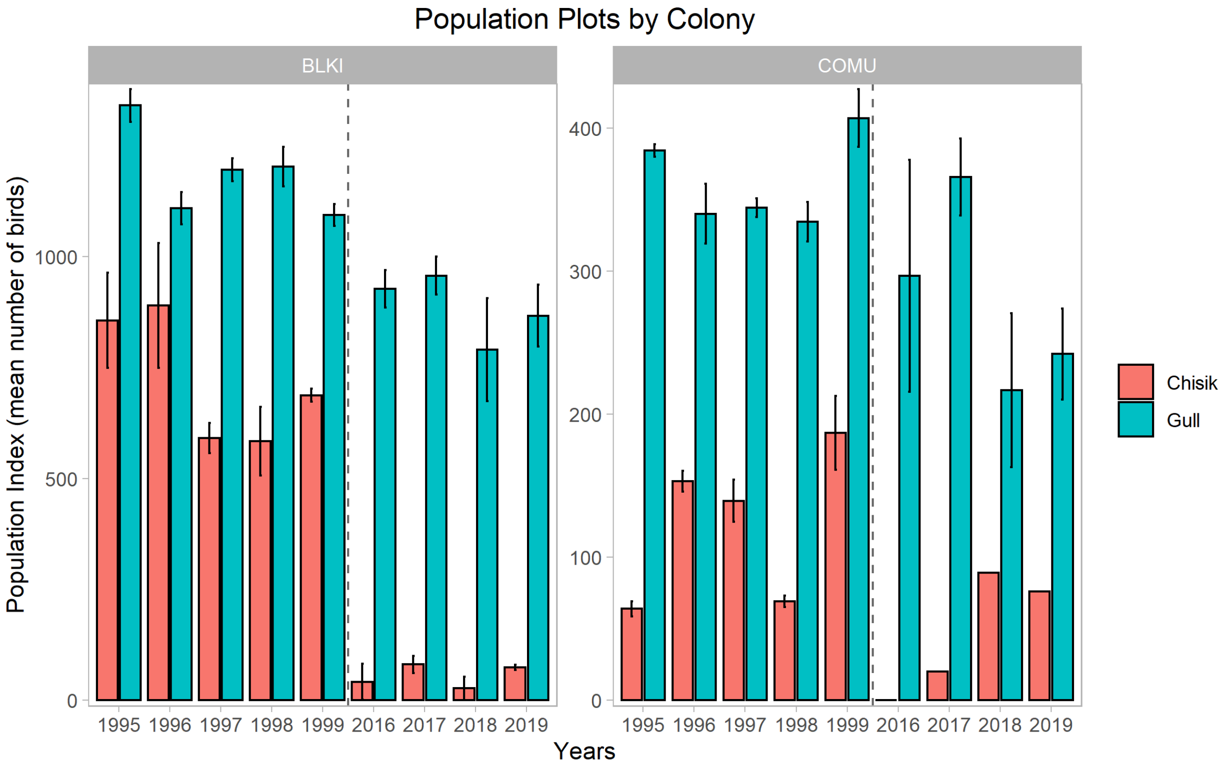

Figure 18. Population plots by colony
Average population plot counts for Black-legged Kittiwakes (BLKI) and Common Murres (COMU) on Chisik (red) and Gull (blue) islands from 1995-1999 and 2016-2019. Error bars indicate standard error from the mean. Years without error bars only had one count.

5.2.2 Productivity and Predation

5.2.2.1 Productivity

Common Murres failed to produce any chicks on study plots at both Gull and Chisik islands during the first 3 years (2016-2018) of recent study (Table 4; Figure 19 and 20). During 2019, murres again failed to produce chicks on study plots at Chisik Island but managed to produce 0.26 chicks fledged per egg (CFE) at Gull Island. This was a marked improvement in breeding success, but still only half the average breeding success (0.54 CFE) observed in past study (Table 4). Overall productivity of murres was 88% lower (46-131 CI) at Gull (F=24.34, *p*=0.002) and 99% lower (44-155 CI) at Chisik (F=19.08, *p*=0.005) in recent years than in the past. Productivity of murres differed significantly between study periods (i.e., recent versus past years; F=45.57, *p*<0.001) but not between colonies (F=0.10, *p*=0.765; Figure 18).

Black-legged Kittiwakes failed (<0.02 chicks fledged per nest; CFN) at both colonies and in most years, except at Gull Island in 2017 and 2019 (Table 4, Figure 18). Kittiwake productivity was the highest (0.67 CFN) ever observed across all survey years monitored in 2019, and many multiple-chick nests were observed (Table 4; Figures 19 and 20). Kittiwakes had a high level (0.61 CFN) of productivity in 2017 as well. Kittiwake productivity differed significantly between colonies (Welch's ANOVA; F=18.775, *p*=0.002), but did not differ significantly between recent and past surveys at either Gull (Welch's ANOVA; F=0.50, *p*=0.524) or Chisik (Welch's ANOVA; F=2.36, *p*=0.213) islands (Figure 18).

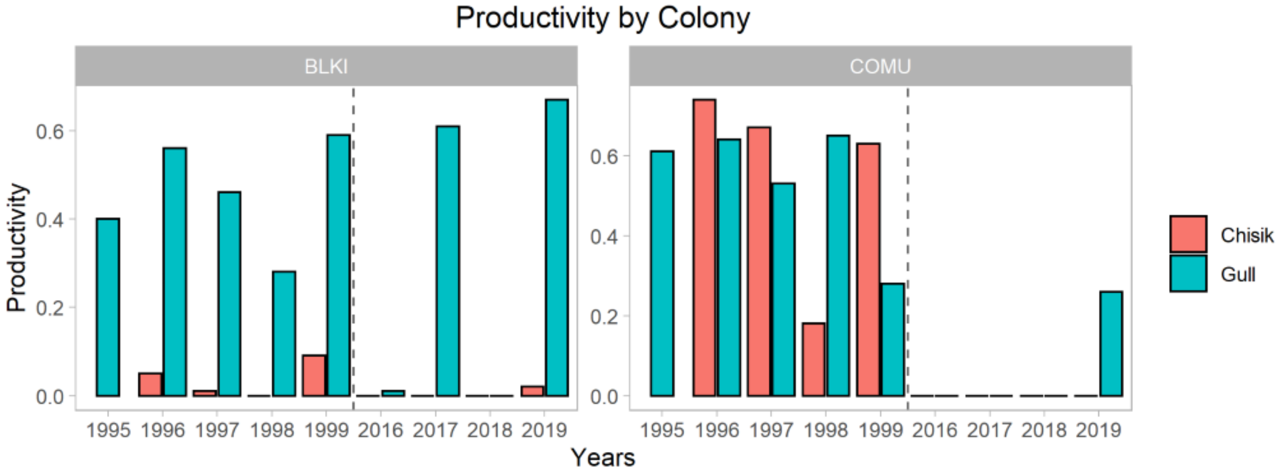

Figure 19. Productivity by colony
Productivity by colony for Black-legged Kittiwakes (BLKI) and Common Murres (COMU) from 1995-2019 at two colonies, Chisik (red) and Gull (blue) Islands.

Figure 20. Black-legged Kittiwake and Common Murre chicks at Gull Island
Two Black-legged Kittiwake chicks (left) and two Common Murre chicks (right) at Gull Island in 2019, the first year that *both* species were successful at producing offspring during the 2016-2019 study. Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

5.2.2.2 Predation

At Gull Island we observed instances of predation on adult and juvenile kittiwakes and murres by Bald Eagles (*Haliaeetus leucocephalus*), Peregrine Falcons (*Falco peregrinus*), and Glaucous-winged Gulls (Figure 21), but the majority of predation was on the eggs of kittiwakes and murres (Figure 22). Kittiwake eggs disappeared from monitored plots on Gull Island in all years (2016-2018), but only in 2018 did video capture images of eggs being eaten by predators (4 of 83 nests). The predators taking kittiwake eggs and captured on camera were primarily Bald Eagles and in one instance a Northwestern Crow (*Corvus caurinus*). We also observed high levels of predation on murre eggs throughout the study period. At Chisik Island, across all years for which we had data (2016-2018), 92% of murre eggs (22 of 24) observed were preyed upon or presumed to be preyed upon by Glaucous-winged Gulls, and 8% of the eggs (2 of 24) disappeared for unknown reasons, although we suspect predation. No chicks were observed to have hatched.

At Gull Island we also observed high levels of murre egg predation by both Glaucous-winged and Herring (*Larus argentatus*) gulls. This predation was often facilitated by a flush of most adults at the colony associated with the presence of a Bald Eagle, or less frequently, a Peregrine Falcon. Across all years (2016-2019) at Gull, 60% of murre eggs were preyed upon or presumed to be preyed upon by gulls, 30% of the eggs disappeared, and 10% of the eggs were observed to have hatched. From 2016-2018, 67% of eggs laid were preyed upon or presumed to be preyed upon and 33% disappeared; no eggs hatched. In 2019, 51% of the eggs were preyed upon or presumed to be preyed upon, 27% disappeared, and 22% hatched.

Figure 21. Bald Eagle and Peregrine Falcon predation on Black-legged Kittiwakes at Gull Island
A Bald Eagle preys upon a freshly hatched Black-legged Kittiwake chick (left) and a Peregrine Falcon preys upon an adult kittiwake (right) at Gull Island in 2018. Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

Figure 22. Glaucous-winged Gulls prey upon Common Murre eggs at Gull Island
Glaucous-winged Gulls capitalize upon a disturbance at the Gull Island colony in 2018 to grab eggs abandoned by breeding Common Murres. One lone incubating Common Murre continues incubation even though the rest of the colony had flushed from nest sites. Credit: U.S. Geological Survey. Public domain.

6 Discussion

A wide variety of fish and wildlife populations in the Gulf of Alaska were negatively impacted by the extreme and persistent marine heatwave of 2014-2016 (Suryan et al. 2021). Warm-water temperature anomalies had a marked effect on pelagic food webs, as evidenced by changes in productivity, plankton community composition and abundance, and declines in abundance of forage fish species and many of their higher predators (Suryan et al. 2021, Arimitsu et al. 2021). Exact mechanisms of change are still under investigation, but a reduction in the growth rates and nutritional quality of forage species has been linked to the high temperature anomalies (Von Biela et al. 2019, Arimitsu et al. 2021), and increased predation by ectothermic predatory fish such as Pacific cod appears to have contributed some top-down reduction in forage fish numbers as well (Barbeaux et al. 2020, Piatt et al. 2020, Arimitsu et al. 2021). Effects on higher predators were likely amplified by the simultaneous and dramatic decline in key forage fish populations, a so-called “portfolio effect” failure which had serious ramifications for highly dependent predators such as Common Murres, Pacific cod, and humpback whales in the Gulf of Alaska (Arimitsu et al. 2021).

These impacts included an unprecedented die-off of an estimated 1 million Common Murres in the Gulf of Alaska in the winter of 2015-2016, and a severe reduction in breeding success of murres at multiple colonies in the Gulf of Alaska and Bering Sea during 2015 and 2016, extending to 2017 as well. In light of these alarming changes in marine food webs and demography of murres, we initiated this study of forage fish and seabirds in lower Cook Inlet in 2016 and continued these studies to 2019. Lower Cook Inlet was selected for study because several important murre colonies are located in lower Cook Inlet, which is oceanographically connected to the Gulf of Alaska, and it was the geographic center of the murre die-off in Alaska. Another important factor was that intensive studies of forage fish adjacent to seabird colonies in lower Cook Inlet were conducted during the 1990s as part of a program to monitor the recovery of seabird populations from the *Exxon Valdez* oil spill of 1989 (Piatt 2002). Therefore, we could examine the forage fish base and seabird populations in Cook Inlet in the aftermath of the heatwave and compare findings to those of the 1990's study in order to better understand the impacts of the heatwave on the marine ecosystem. To our knowledge, there have been no other focused, fine-scale studies on seabirds and forage fish conducted anywhere else in Alaska after the heatwave.

Our study is continuing beyond 2019, but here we have summarized our main findings from our first four years of study. Compared to populations and productivity observed in past years (1996-1999) of study, we detected large reductions in population size and reproductive success of Common Murres and Black-legged Kittiwakes at their colonies in recent years (2016-2019). This was accompanied by high interannual variability in distribution and abundance of seabirds at sea, including significant declines in the abundance of multiple seabird species during the relatively short period of recent study (2016-2019). These changes in bird biology and behavior coincided with observed changes in the abundance, quality, and species composition of forage fish in lower Cook Inlet.

Our recent studies of forage fish did not begin until summer of 2016, and so the mass starvation and mortality of murres that occurred in 2015 and winter of 2015-2016 was in response to conditions for which we have no data. During our study period (summers of 2016-2019), indices of fish biomass were highest in 2016 (relative to 2017-2019) when adult walleye pollock, which are generally unsuitable prey for seabirds, dominated the deeper waters of lower Cook Inlet. At present, we have not yet been able to compare these densities with forage fish densities from the 1990s owing to unresolved issues with the hydroacoustic system used at that time. Still, Piatt et al. (2007) identified key differences between kittiwakes and murres in threshold responses of breeding parameters to forage density. At-sea density was more sensitive to prey density for both murres and kittiwakes, but reproductive parameters (e.g., hatching, fledging, and breeding success) were less sensitive to prey density for murres than kittiwakes. These principles continue to guide our interpretation of results from recent years.

Murres failed to produce any offspring in 2016 and kittiwakes had near total failure, suggesting that the foraging conditions were unsuitable in 2016. Although we observed the highest overall biomass of forage fish in 2016, suitable forage was almost entirely comprised of age-0 classes of sand lance, herring, and walleye pollock, which typically have much lower energy content than older age classes (Van Pelt et al. 1997, von Biela et al. 2019, Arimitsu et al. 2021). Furthermore, these fish would have only recently transformed from their larval state in July, and so the small size of these main forage taxa would have provided low quality prey for seabirds and other predators during their breeding season. By 2017 it appeared that the 2016 cohorts of sand lance and herring were moving through the system, but acoustic surveys reveal that overall abundance declined by about half between 2016 and 2017. Similarly, while the average size and energy content of sand lance increased in 2018 and 2019 (Arimitsu et al. 2021), acoustic biomass bottomed out in 2018 in both shallow and deep strata and recovered slightly in 2019 in the shallow strata only. Thus, it appears that steady improvements in size and quality of forage fish from 2016 to 2019 were counteracted to some degree by changes in prey abundance from 2016 to 2019.

In 2019 we did note some improvements in prey availability. We encountered a few relatively high-density aggregations of pre-spawning capelin mainly outside of Kachemak Bay, off Port Graham, and on the west side of Cook Inlet. We also encountered some larger aggregations of adult sand lance off Anchor Point, and adult herring near Gull Island.

Seabirds are superb marine predators and tend to do a good job of tracking prey aggregations at sea (Piatt 1990). Indeed, 75-85% of the annual variability in murre and kittiwake distribution at sea can be explained by the dispersion of prey schools (Piatt et al. 2007). It was therefore not surprising to see that many of the species we censused at sea in 2016-2019 exhibited fluctuations in abundance (Figure 16) that mirrored the annual trends for acoustic forage fish biomass (Figure 3). Most species occurred in higher abundance during 2016-2017, and declined to a much lower level in 2018, with a moderate up-tick in abundance during 2019. A simple comparison of average abundances in the first two years versus the last two years indicated significant declines in kittiwake, murres, Pigeon Guillemots, *Brachyramphus* murrelets, and Kittlitz's Murrelets. Shearwaters were the only migratory, non-breeding species (Carboneras et al. 2020*a*, *b*) included in the analysis, were most concentrated in outer Kachemak Bay and did not obviously track annual prey abundance. Nor did annual abundances for Glaucous-winged Gulls (opportunistic and inter-tidal forager) or the two puffins, both of which were relatively scarce in the 2010s (few thousands) and declined greatly from numbers observed in the 1990s. Other than a significant decline in Marbled Murrelets, there were no other large declines in any other species between the 1990s and 2010s, suggesting that populations had been fairly stable over three decades of monitoring; at least until 2018 and 2019. The long-term impact, if any, of those recent declines remains to be seen in future surveys.

At colonies, breeding populations of murres and kittiwakes at both Gull and Chisik islands declined precipitously between the late-1990s and the 2010s. Declines were most notable at Chisik Island, where counts for both murres and kittiwakes declined by more than 70% in both census counts and population plots. However, it should be noted that for kittiwakes at Chisik, populations were already declining at rate of 4.3% per annum because adult mortality was not being balanced by chick production (usually <0.03 CFN) or recruitment (Piatt 2004). If that trend had continued through to 2016, then the observed "heatwave effect" on the whole island counts would be closer to 40% than 70%. At Gull Island, kittiwake populations were 26% and 8% lower in recent years than in the past based on population plots and whole colony censuses, respectively. Population plots, with their replicated counts throughout the period of mid incubation to the start of fledging, are a more sensitive metric for detecting population change, especially if there has not been an expansion or contraction of nesting sites on the colony. Most of the population plots on Chisik that had historically been active were no longer in use during this study, indicating a contraction of their range, whereas on Gull kittiwakes have continued to nest on all available cliffside habitat. Murre populations at Gull Island were 46% and 22% lower in census and population plots, respectively. For comparison, the numbers of murres attending colonies in the Bering Sea and Gulf of Alaska were on average 80% and 50% lower, respectively, in the three years following the 2015-2016 murre die-off than in the preceding three years (Piatt et al. 2020). So, it appears that the changes in murre populations that we observed were in the same order of magnitude as those observed at other colonies in the Gulf of Alaska. It is still unclear whether these declines were due to reduced attendance from deferred breeding and/or declines in colony populations due to reduced food availability (Piatt et al. 2020). The continuing failure of colony counts to return to “normal” as food supplies and breeding success recover suggests that the declines were due to adult mortality.

We recorded nearly complete reproductive failures of murres at Gull Island from 2016-2018 and at Chisik Island from 2016-2019. Total reproductive failures are rare for murres (Piatt et al. 2020), and the failures we observed stand in stark contrast to normal breeding success recorded at Gull and Chisik islands from 1995-1999, when murres produced an average of 0.54 and 0.56 chicks/pair, respectively (Piatt 2002). Breeding failures at Gull and Chisik in 2016 mirror those observed elsewhere in Alaska. At least one year of complete reproductive failure was observed at 13 Common Murre breeding colonies in the Gulf of Alaska and Bering Sea in association with the North Pacific marine heatwave (2015-2017), and multi-year failures were observed at 8 colonies (Piatt et al. 2020). Breeding failures (including Gull and Chisik) continued at reduced levels into 2018 (Gulf of Alaska - 2/4 sites failed; Bering Sea - 1/5 sites failed) and 2019 (Gulf of Alaska - 1/4 failed, Bering Sea - 2/5 failed; Dragoo et al. 2020). Given the usual scarcity of murre failures, the continued observation of multi-colony failures in 2018 and 2019 point to lingering impacts of the 2014-2016 heatwave on pelagic food webs in the NE Pacific.

Previous studies in this area have shown murres to be resilient breeders, maintaining high levels of productivity across a wide range of prey conditions by adjusting the time that they spend foraging (Zador and Piatt 1999; Piatt et al. 2007). This remains true until prey availability drops below a certain threshold, as murres prioritize their own body condition above breeding success, which requires consuming roughly half of their body mass in prey per day (Burger and Piatt 1990, Piatt et al. 2007). The reproductive failures we observed suggest that the foraging conditions around these two breeding colonies were insufficient to support breeding success in murres from 2016-2018, and were likely marginal around Gull in 2019, when murres fledged chicks at just over half the rate (0.29 chicks/pair) of the historical average (Piatt 2002). Further support for this hypothesis comes from our observations of abnormally skinny murres attending Gull Island, especially in 2018. We frequently observed murres with concave breast profiles and visible keels (Figures 23 and 24). We can find no reports in literature of such abnormal body conditions at colonies of breeding murres, nor from correspondence with experienced seabird biologists. We believe it reflects conditions of extreme prey scarcity.

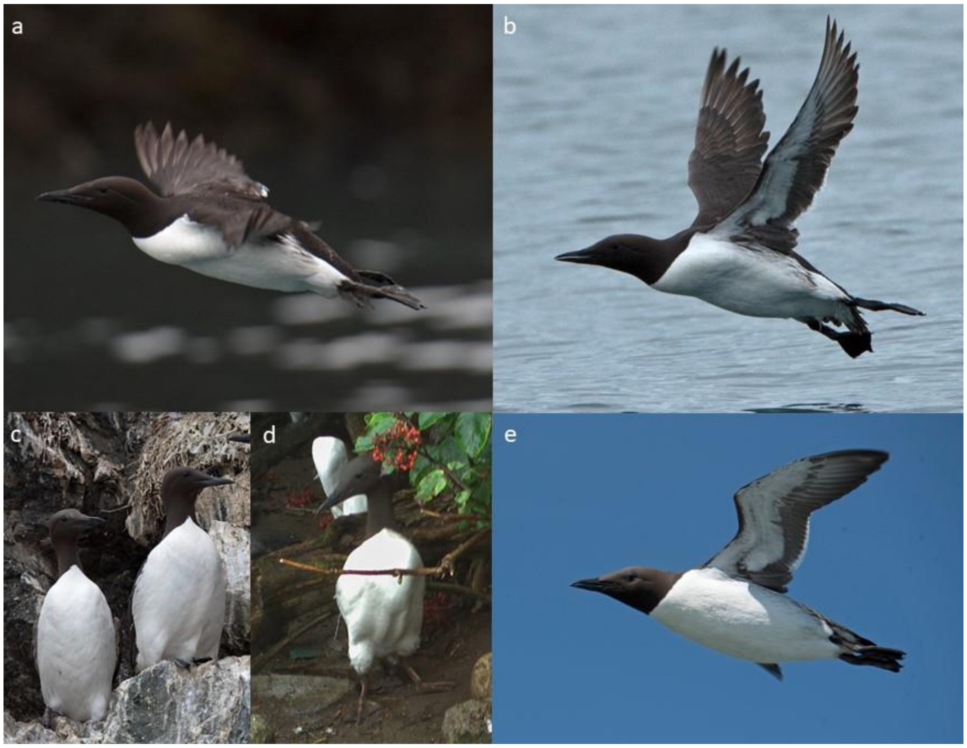

Figure 23. Skinny Common Murres in lower Cook Inlet in 2018
Skinny Common Murres (a, b, c (right), and d) with keel protruding contrasted by normal murres (c (left) and e) in lower Cook Inlet, Alaska. Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

Figure 24. Skinny Common Murres around Gull Island in 2018
Common Murres with visibly protruding keels flush from Gull Island, Kachemak Bay, Alaska. Credit: Mayumi Arimitsu, U.S. Geological Survey. Public domain.

Similarly, kittiwakes had nearly complete reproductive failures at both colonies in 2016 and 2018. Unlike murres, however, kittiwakes had record high productivity in 2017 and 2019 at Gull Island, suggesting that kittiwakes have some life history traits that allow them to subsist at lower prey thresholds—not the least of which is a substantially smaller body mass and requirement to gather a fraction of the food needed daily to support murres (about 37% as much food mass; Piatt et al. 2007). Kittiwakes also have substantially lower wing loading, only 21% the load for murres, and this reduces the cost of foraging considerably (Piatt et al. 2007). Furthermore, kittiwakes provision chicks by ingesting multiple prey items during foraging bouts, which are then stored in their crop, and 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). These differences in foraging and chick provisioning favor kittiwakes when prey items are small, such as in 2017 when sand lance were the most abundant in trawl catches of all years (Table 2) but were primarily smaller fish (Figure 5), since they can collect multiple prey items for chicks on one foraging bout, whereas murres would need to make multiple foraging trips in order to adequately provision chicks when prey items are small or of lower quality (Figure 25). Although murres can adjust their provisioning strategies to compensate when prey resources are poor, there is a limit to their ability to compensate after which chicks are provisioned energy at lower rates (Schrimpf et al. 2012).

Figure 25. Foraging Common Murres and Black-legged Kittiwakes at Gull Island in 2019
A Common Murre carries a single Pacific sand lance (left), and Black-legged Kittiwakes forage on multiple Pacific sand lance and capelin (right), Sand lance and capelin were two of the forage fish species most commonly delivered to murre and kittiwake chicks at Gull Island. Large mixed species forage flocks were observed around Gull Island in 2019, the first year both species successfully reproduced following the Pacific marine heatwave. Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

In addition to, or in concert with, apparently insufficient forage fish supplies, predation played a role in the breeding failures we observed. Both direct and facilitated predation of breeding adults, chicks, and (most often) eggs of both kittiwakes and murres was practiced by Bald Eagles, Peregrine Falcons, Glaucous-wing Gulls and Herring Gulls. Flyovers from Bald Eagles and Peregrine Falcons caused large scale disturbances of breeding colonies, which were most extreme at Gull Island in 2018, when eruptions of thousands of kittiwakes and murres from the colony was a common occurrence (Figures 26 and 27). We also recorded the lowest acoustic biomass of fish in both shallow and deep waters around Cook Inlet in 2018, suggesting that low prey availability exacerbated predator disturbances to breeding birds. As noted above, 2018 was the worst year for reproduction, with both kittiwakes and murres experiencing complete reproductive failures at both colonies. Breeding failures of murres due to Bald Eagles are not uncommon at other colonies, and predation can influence the reproductive performance of murres more when environmental conditions are poor (Parrish et al. 2001, Schrimpf et al. 2012, Horton 2014, Suryan et al. 2017). Increased predation pressure could also be partially responsible for species differences in reproductive success, due to differences in nesting habitat. Although predation of adults, chicks, and eggs of both kittiwakes and murres was observed, predation of murre eggs was the most common. Most murres at Gull Island nest on the flat, open tops of the colony, making their eggs more easily accessible than the eggs of kittiwakes nesting on rocky cliffs.

Figure 26. A Bald Eagle disturbs nesting Black-legged Kittiwakes nesting at Gull Island in 2019
Bald Eagles were common predators at Gull Island, Kachemak Bay, Alaska, predating both on eggs and adult birds. Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

Figure 27. Kittiwakes and murres flush from a Bald Eagle at Gull Island in 2019
Bald Eagles caused large scale disturbances at the Gull Island breeding colony, where they were common predators of both eggs and adult and juvenile birds. Credit: Sarah Schoen, U.S. Geological Survey. Public domain.

Biotoxins associated with harmful algal blooms could have been an additional stressor to the breeding seabirds in this study. Saxitoxin, the neurotoxin involved in paralytic shellfish poisoning, was found in tissues of murres that had died in the 2015-2016 mass mortality event as well as in the tissues of live murres and kittiwakes collected near Gull and Chisik in 2016 (Piatt et al. 2020, Van Hemert et al. 2020). Although saxitoxin was not implicated as the likely cause of death in the die-off birds (Van Hemert et al. 2020), it is unknown how sensitive seabirds are to saxitoxin and what concentrations might elicit behavioral changes in birds.

In summary, we found that in the years following the unprecedented North Pacific marine heatwave—which resulted in widespread seabird die-offs and declines in prey abundance and quality— we documented biological and behavioral responses of forage fish communities, seabirds foraging at sea, and breeding populations of kittiwakes and murres at colonies in lower Cook Inlet. At colonies, we observed large declines in kittiwake and murre populations on Chisik Island, and smaller declines in kittiwake and murre populations at Gull Island following the marine heatwave. Energetically poor age-0 fish were the dominant forage in 2016 and 2017, years in which only kittiwakes at Gull Island (in 2017) were able to reproduce successfully. In 2018 we observed the lowest overall prey densities, coinciding with the lowest densities of birds at sea, signs of malnutrition in murres, increased disturbance and predation on nesting birds, and complete breeding failures of kittiwakes and murres at both colonies. Larger more nutritious sand lance and pre-spawning capelin were more available in 2019 than in previous years, and accordingly, 2019 was the first year that both kittiwakes and murres had breeding success at Gull. Together, these findings are suggestive of multiyear trophic instability in lower Cook Inlet following the marine heatwave. There were signs of recovery starting in 2019, although murre productivity was still only half the rate of that in the past. Recovery will likely take many more years, at the very least because zero (murres) to moderate (kittiwake) numbers of chicks were produced for 4 years after the heatwave, and so recruitment will be extremely limited during the period 2020-2024 when those chicks would have been expected to return and replace older (dying) cohorts at the colonies. Continued food deprivation from 2016-2019 may have had many other negative impacts such as: reduced survival of seabirds of all ages, changes in seabird social structure at colonies, and permanent restructuring of competing populations of forage fish predators such as salmon, groundfish, pinnipeds, and whales. Continued monitoring of forage fish and seabirds across Cook Inlet will aid in understanding the ecosystem response and recovery to marine heatwaves into the future.

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