Exxon Valdez Oil Spill
Long-Term Monitoring Program (Gulf Watch Alaska) Final Report

Monitoring Long-term Changes in Forage Fish Distribution,
Abundance and Body Condition in Prince William Sound

Exxon Valdez Oil Spill Trustee Council Project 21120114-C
Final Report

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Study History: This project was funded as part of the Gulf Watch Alaska long-term monitoring program of the *Exxon Valdez* Oil Spill Trustee Council. This work began during the FY12-16 Gulf Watch Alaska funding cycle and is detailed in annual reports for project 12120114-O and the final report 16120114-O. During the FY17-21 Gulf Watch Alaska funding cycle, forage fish sampling included the annual Fall Integrated Predator-Prey Survey in coordination with the humpback whale (21120114-O) and fall-winter marine bird (2120114-E) projects and seabird diet sampling at Middleton Island. In FY19-21 we received additional funding to reinstate aspects of summer sampling components in Prince William Sound, including the aerial survey validation effort with the Herring Research and Monitoring program (21120111). Annual reports for this work include project numbers 17120114-C, 18120114-C, 19120114-C, and 20120114-C. During this funding cycle, data and findings from the Gulf Watch Alaska forage fish project were summarized in peer-reviewed publications and as the collective Gulf Watch Alaska program synthesis effort.

Abstract: Identifying drivers of change in forage fish populations is key to understanding recovery potential for piscivorous species injured by the *Exxon Valdez* oil spill, and ecosystem response to natural and anthropogenic perturbations. Forage fish are small pelagic schooling fish such as Pacific capelin (*Mallotus catervarius*), Pacific sand lance (*Ammodytes personatus*), Pacific herring (*Clupea pallasii*), and juvenile walleye pollock (*Gadus chalcogrammus*) that are prey of many marine predators. Krill (Euphausiidae) are also an important prey taxa sampled in this study. The goals of the Gulf Watch Alaska forage fish monitoring project are to provide information on the population trends of forage species in the Gulf of Alaska and to better understand how underlying predator-prey interactions influence recovering species and the pelagic ecology of Prince William Sound. The main sampling components of the program include acoustic-trawl surveys for forage fish in Prince William Sound during the Fall Integrated Predator-Prey survey (September), and seabird diet sampling at Middleton Island during spring/summer (April – August). We also validate aerial surveys conducted by the Herring Research and Monitoring program (June), and sample summer spawning capelin and sand lance (July) for condition analyses. This work has provided information important to understanding ecosystem response to perturbations in the northern Gulf of Alaska.

Key words: Aerial survey, Pacific capelin (*Mallotus catervarius*), forage fish, acoustic-trawl, krill (Euphausiacea), Pacific herring (*Clupea pallasii*), Pacific sand lance (*Ammodytes*

personatus), Prince William Sound, walleye pollock (*Gadus chalcogrammus*), Middleton Island, Alaska.

Project Data: All datasets are available in comma delimited format with a unique station ID number. The data include:

- Echointegration data from the fall and summer acoustic forage fish surveys. Acoustic data were obtained from calibrated Simrad EK60 (surveys prior to 2020) or Kongsberg EK80 (surveys during 2021 and later) split beam dual frequency echosounders operating at 120 and 38 kHz.

- Fish catch and morphological data from various net sampling methods including midwater trawls, beach seine, cast net, dip net, jig, gill net and purse seine.

- Prince William Sound aerial survey validation data.

- Prince William Sound forage fish size, age, and energy density data.

- Middleton Island black-legged kittiwake and rhinoceros auklet diets 1978 to present.

- At-sea distribution and abundance of marine birds and mammals. Transects were conducted following standard U.S. Fish and Wildlife protocols for strip transect surveys and modified for work in coastal Alaska.

- Zooplankton biomass. Samples were collected with a 150-micron mesh 0.25 m diameter paired ring net on a 50 m vertical haul during daylight hours.

- Conductivity – temperature – depth (CTD) profiles. Oceanographic parameters were measured with a Seabird Electronics SBE19 (2012) and SBE19Plus v2 (after 2012) CTD equipped with external sensors to measure oxygen, pH, fluorescence, turbidity, beam transmission and photosynthetically active irradiance (PAR).

- Inorganic nutrient concentration, including phosphate, nitrate, nitrite and silicic acid.

These data are archived by the Alaska Ocean Observing System's Gulf of Alaska Data Portal on behalf of the *Exxon Valdez* Oil Spill Trustee Council:

- https://gulf-of-alaska.portal.aoos.org/#metadata/3ca497e2-3421-4fa4-a550-f4d397a73c07/project/folder_metadata/1920957

- https://gulf-of-alaska.portal.aoos.org/#metadata/3ca497e2-3421-4fa4-a550-f4d397a73c07/project

and by the U.S. Geological Survey:

- http://dx.doi.org/10.5066/F74J0C9Z

- http://www.doi.org/10.5066/P93I0P67

- https://doi.org/10.5066/P94KVH9X

There are no limitations on the use of the data. However, it is requested that the authors be cited for any subsequent publications that reference these datasets. It is strongly recommended that careful attention be paid to the contents of the metadata file associated with these data to evaluate data set limitations or intended use.

The data custodian is Carol Janzen, Director of Operations and Development, Alaska Ocean Observing System, 1007 W. 3rd Ave. #100, Anchorage, AK 99501, 907-644-6703. janzen@aoos.org.

Data are archived by Axiom Data Science, a Tetra Tech Company, 1016 W. 6th Ave., Anchorage, AK 99501.

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Citation:

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EXECUTIVE SUMMARY

In this report we summarize field efforts as well as datasets produced and made publicly available by the Gulf Watch Alaska (GWA) forage fish project during the FY17-21 funding period. This work spanned the years following the 2014-2016 Pacific marine heatwave, which included a second extreme marine heatwave in 2019, when lingering impacts were still affecting ecosystem function across the northern Gulf of Alaska (GOA).

We collected data on forage fish abundance, distribution and body condition in Prince William Sound (PWS) and the northern GOA, including summer and fall acoustic–trawl surveys in PWS and spring – summer seabird diets at Middleton Island. We also validated early summer aerial surveys conducted by the Herring Research and Monitoring program in PWS, conducted summer acoustic-trawl surveys in PWS, and sampled summer condition and age-structure of forage fish in PWS. In addition, we sampled forage fish habitat, and characterized biotic and abiotic ocean conditions during our surveys. From all these sampling efforts, we documented changes in biomass and depth distribution of forage species, including capelin, herring, sand lance, age-0 pollock, and euphausiids. We also used acoustic data and trawl catches to identify changes in gelatinous zooplankton (i.e., jellyfish, ctenophores, and large predatory medusae) that are potential competitors for forage fish.

As part of the 2020 GWA synthesis work, we documented large changes to the middle trophic level during the 2014-2016 marine heatwave. The availability and quality of at least three key forage species with different life history strategies were reduced simultaneously in the system. Capelin and sand lance occurrence in predator diets declined abruptly and PWS herring spawning biomass declined to historically low levels. Biomass of euphausiids was also reduced, in part due to the loss of a cold-water species including *Thysanoessa raschii*, *T. longipes*, and *T. inermis*. Changes in age structure, growth, and energy content of capelin, sand lance, and herring were also associated with the heatwave, but not all species responded in the same way. For example, spawning capelin matured at a younger age but at a lower average length than they did prior to the heatwave, while sand lance in PWS experienced anomalously low growth rates and lipid storage in 2015-2016.

After several years of diminished availability and quality of forage fish in the northern GOA, we began to see some improvement in the status of capelin and sand lance populations in the region. By 2018, sand lance age, size, and total energy, and increased occurrence in seabird diets indicated improved health of sand lance compared to the heatwave years. In 2019 we observed that capelin had returned to the system for the first time since the heatwave, though the spawning population sampled in Port Etches was still younger and smaller than prior to the heatwave. To the extent that birds foraged over the shelf in spring, age-1 and older herring were the main fish

prey in seabird diets during 2020, but less so in 2021. Acoustic indices of macrozooplankton also indicated more abundant and diverse euphausiid communities were present in PWS during fall 2022.

In summary, forage diversity, abundance, and body condition in PWS and the northern GOA improved between the beginning and end of our 5-year study cycle. Based on changes in Middleton Island seabird diets over time, however, the current forage fish community still differs from a pre-heatwave state. The composition of seabird diets after 2014 has been more variable than it was prior to the heatwave. Sand lance and capelin dominated seabird diets for nearly three decades prior to the heatwave since the heatwave, these species continue to represent lower than average diet proportions. If or when the ecosystem will return to pre-heatwave conditions remains unclear, but continued monitoring to document changes in middle trophic levels will improve our ability to understand the mechanisms underlying the response of predators to natural and anthropogenic perturbations.

INTRODUCTION

Forage species are important to marine ecosystems because they are key prey for higher marine predators such as marine birds, marine mammals, and predatory fish. They funnel energy between lower and upper trophic levels, and they are capable of regulating their predators and their prey under certain ecosystem states. Important forage taxa in Prince William Sound (PWS) and the northern Gulf of Alaska (GOA) include Pacific herring (*Clupea pallasii*), Pacific capelin (*Mallotus catervarius*), Pacific sand lance (*Ammodytes personatus*), juvenile walleye pollock (*Gadus chalcogrammus*), and euphausiids, all included hereafter under the label of "forage fish".

Forage fish tend to be patchy in their distribution, comprised of species with different life histories and habitats, and most have life history traits that predispose populations to large and abrupt fluctuations in abundance. These traits present major challenges for monitoring changes in forage fish populations over time. In the years following the *Exxon Valdez* oil spill (EVOS), to better understand the natural variability in forage abundance above and separate the EVOS impacts on predators and prey in the marine ecosystem, many investigators set out to document forage fish distribution, abundance, and habitat in PWS and Cook Inlet (e.g., Thedinga et al. 2000, Brown 2002, Ainley et al. 2003, Abookire and Piatt 2005, Ostrand et al. 2005, Speckman et al. 2005, Piatt et al. 2007). Survey methods for estimating abundance and distribution of forage fish included hydroacoustic surveys coupled with trawl-sampling (Haldorson et al. 1998, Speckman et al. 2005) and sound-wide aerial surveys for surface-schooling fish (Brown and Moreland 2000).

Building on this work, during the first 5-year (2012-2016) funding period of the *Exxon Valdez* Oil Spill Trustee Council's (EVOSTC) GWA program, we tested a variety of survey methods for monitoring forage fish in the spill-affected region (Arimitsu and Piatt 2014, Arimitsu et al. 2018). We concluded that systematically surveying all of PWS with boats and nets to locate

scattered and relatively small aggregations of target forage species was not only inefficient but would ultimately require a much greater investment of resources than was available. Like Brown and Moreland (2000), we determined that it would require a combination of different methods to detect change in forage species within PWS, including aerial surveys, using whale predators to lead us to forage aggregations, and sampling of seabird diet composition as an index of relative forage fish abundance (Arimitsu et al. 2021a).

For example, forage fish in PWS tend to occur in nearshore coastal areas, often in waters too shallow for vessels to operate trawls and acoustics. However, schools of Pacific herring and Pacific sand lance are readily observed from fixed-wing aircraft, and this method has been employed to quantify forage fish since the late-1990s (Norcross et al. 1999, Arimitsu and Piatt 2014, Arimitsu et al. 2018). Such surveys proved to be useful for understanding prey resource availability for seabirds in PWS (Suryan et al. 2002, 2006, Ainley et al. 2003). While we adopted some of the earlier survey methods, we also added boat-based ground-truthing efforts to validate identification by observers and to provide a means of estimating error of the aerial survey estimates. In FY19 we received additional funding support to conduct summer sampling, including aerial survey validation in conjunction with the Herring Research and Monitoring Program, collections of spawning capelin and Pacific sand lance for condition analyses, and summer acoustic-trawl surveys.

During the second 5-year (2017-2021) funding period of GWA, we coordinated with other Pelagic Component studies and added a predator-based approach that used humpback whales and seabirds to effectively locate and/or sample forage fish. This included the Integrated Predator Prey survey, a coordinated effort by the humpback whale project (principal investigators [PIs] Moran and Straley) and fall-winter marine bird project (PI Bishop), in which persistent whale foraging areas were sampled with acoustics, midwater trawls, gill nets, dip nets, jigs, purse seines, and underwater video during the period of peak humpback whale abundance in the PWS during late-September. We also collaborated with researchers collecting seabird diet samples from April to August at the breeding colony on Middleton Island, Alaska, where rhinoceros auklets (*Cerorhinca monocerata*) and black-legged kittiwakes (*Rissa tridactyla*) forage in both coastal and shelf neritic habitat and deep ocean waters beyond the shelf break.

One of the most significant accomplishments of the GWA Forage Fish Project is that the information we gathered has been key to understanding the ecosystem response to the multiyear Pacific marine heatwave of 2014-2016, which resulted in a portfolio collapse of forage fish in the GOA and caused unprecedented mortality of marine predators due to starvation, breeding failures, and malnutrition (Barbeaux et al. 2017, Savage 2017, Piatt et al. 2020*b*, Arimitsu et al. 2021*a*). Moreover, continued data collection and synthesis efforts by this project and the GWA scientific team have facilitated understanding of the recovery of the system following this major perturbation in the GOA (Suryan et al. 2021, Weitzman et al. 2021, Danielson et al. 2022).

OBJECTIVES

Obtaining a basic understanding of the status and trends of individual biological members within an ecosystem is fundamental to ecosystem monitoring. It is increasingly clear, however, that understanding mechanisms that underly population change requires knowledge of interactions among predators, prey and the influence of changing habitat conditions. Thus, while the overall goal of this work was to detect changes in distribution, abundance, and body condition of forage fish in marine waters affected by EVOS, we also examined predator-prey interactions and environmental conditions at the same time. The specific objectives of the GWA forage fish monitoring project during the 2017-2021 funding cycle were to:

1. Monitor the status and trends of co-occurring pelagic marine ecosystem components during September in areas with known seasonally predictable aggregations of predators and prey. This included efforts to:

   a. Estimate an index of forage fish abundance, species composition, and biomass within persistent predator foraging areas in PWS,

   b. Identify density and depth distribution of forage fish by species,

   c. Estimate an index of krill abundance, species composition, and biomass within persistent predator foraging areas,

   d. Identify krill density and depth distribution,

   e. Relate whale, marine bird and forage fish indices to marine habitat, and

2. Sample seabird diets at Middleton Island to obtain indices of prey species composition, relative abundance, and size.

In addition, some aspects of the FY12-16 project were resumed with approval of additional funding from EVOSTC in FY19. Objectives for this additional work includes:

3. Summer forage fish sampling in PWS, including:

   a. Validate species composition and size of fish in schools observed during Herring Research and Monitoring program's aerial surveys,

   b. Conduct summer acoustic-trawl surveys, and

   c. Sample sand lance and spawning capelin for condition analyses.

METHODS

Forage fish surveys and sample collection efforts were focused in PWS and extended to the offshore region within a 100 km radius of Middleton Island (Fig. 1). Circulation in the coastal

and shelf regions of the study is influenced by the Alaska Coastal Current as well as by wind mixing and freshwater input, which also drives transport from east to west through two ocean entrances in PWS (Niebauer et al. 1994, Stabeno et al. 2016). Dynamic ocean conditions within the region are driven by complex bottom topography on the shelf and in coastal embayments. Strong winter downwelling relaxes seasonally and enriches nutrient supply to the shelf, which promotes spring and fall bloom activity that drives productivity in the region (Childers et al. 2005, Waite and Mueter 2013). Hydrographic studies in PWS identified a general warming trend of about 0.1 to 0.2 °C per decade, although increased glacier meltwater inputs in the northwestern Sound cause localized cooling and freshening trends in some areas (Campbell 2018). Additionally, the depth of the seasonal mixed layer has decreased over time, with potential impacts to ecosystem productivity in the future (Campbell 2018). Similar warming trends were observed on the shelf, with larger positive trends occurring in more recent decades (Danielson et al. 2022).

Objective 1: Fall Integrated Predator Prey Survey
The Integrated Predator Prey (IPP) surveys were conducted in collaboration with the humpback whale (project 21120114-O) and fall/winter marine bird (project 21120114-E) projects each year during the last two weeks of September. Researchers working from the acoustic vessel collected acoustic backscatter, trawl and marine habitat data (forage fish team) and concurrently conducted surveys for marine birds (fall/winter marine bird team) along fixed transect lines within each sub-region (Fig. 1). While the acoustic vessel conducted sampling, a second vessel was used to assess humpback whale abundance and collected samples as necessary (humpback whale team). During the surveys, the three teams coordinated closely and worked together in the same areas, thus allowing sharing of real time information. For the purposes of this report, we focus on specific objectives and findings of the forage fish project.

Hydroacoustic-trawl survey
In FY17-21 we conducted hydroacoustic surveys with a dual frequency, split-beam echosounder (120-38 kHz EK60 or EK80 in 2021, Kongsberg Maritime, Horten, Norway) during daylight hours along transects in three sub-regions: Bainbridge Passage, Montague Strait, and Port Gravina (Fig. 1) to estimate prey species composition, density, and depth distribution. Our approach to quantifying daytime prey aggregations with hydroacoustics concurrent to predator densities is modeled after work on similar species elsewhere (Gende and Sigler 2006, Friedlaender et al. 2009, Hazen et al. 2009, Boswell et al. 2016, Parker-Stetter et al. 2016).
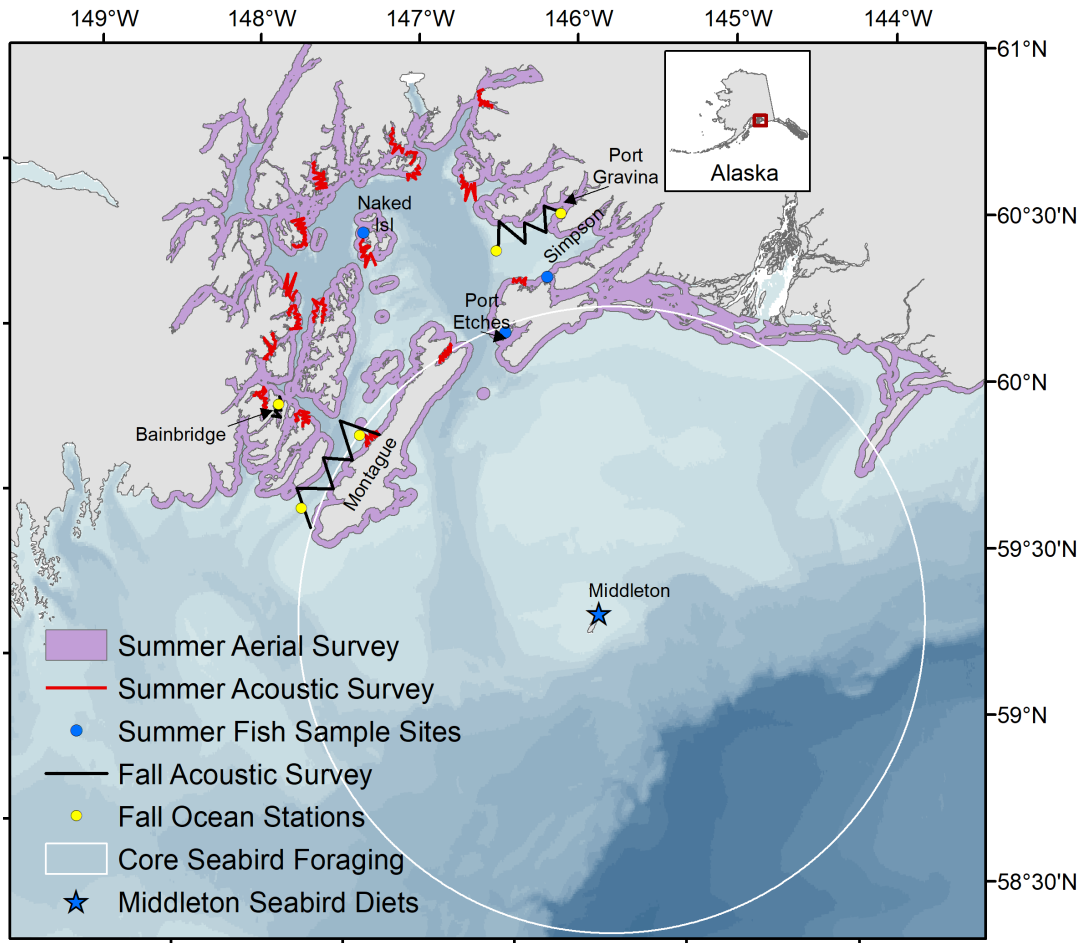
Figure 1. Map of the study area and seasonal Gulf Watch Alaska forage fish sampling effort in Prince William Sound and Middleton Island, Alaska. Bathymetry (Lindquist et al. 2004) is shown in blue with darker shades indicating deeper seafloor depth.

Echosounder calibration was conducted during each survey by suspending a 38.1 mm tungsten carbide sphere of known target strength below each transducer (Foote et al. 1987, Demer et al. 2015). Data were collected using a pulse duration of 0.512 ms at a rate of 1 ping s[-1]. To identify species composition and size of fish and macrozooplankton we conducted fishing with a variety of sampling methods including an Alouette midwater trawl, modified herring midwater trawl, small-meshed gill net, cast net, dip net, and jigs of varying hook sizes. Acoustic data were processed with EchoView (Myriax Pty Ltd, Hobart, Tasmania, Australia).

Passive noise was estimated from data collected in passive mode (i.e., the echosounder system was receiving but not transmitting while the boat was underway) and removed from the raw data for each transducer (Parker-Stetter et al. 2009). We also applied impulse noise (Ryan et al. 2015) and background noise filters (120 kHz only; De Robertis and Higginbottom 2007) to the data using 5x5 smoothing algorithm and signal to noise ratio of 10:1. Sounder detected bottom lines

were offset by 1 m and bottom lines were edited as necessary to remove backscattering signal from the seafloor. Additionally, the surface exclusion zone included the upper 4 m of the water column.

Fish acoustic backscatter was classified to species and size based on catch data and characteristics of backscatter (e.g., school shape and edge characteristics, the presence of shadowing below the first bottom echo). For this analysis we used a minimum threshold of -67 dB to exclude jellyfish, which form weak-scattering bands in the upper water column and overlap in acoustic frequency response with fish at lower thresholds (Parker-Stetter et al. 2013). Regions were drawn around obvious fish aggregations and assigned to species and size categories.

To estimate density and depth characteristics by species, herring (adult and juvenile), walleye pollock (adult and juvenile), capelin, and otherwise unclassified fish regions were exported separately for each 5 m deep by 0.3 km horizontal cell along transects. Sand lance are weak scatterers because they lack a swim bladder, so we used 120 kHz data for this species, but for all other target fish species we used 38 kHz data.

Theoretical target strength (TS) equations were applied for each target species: capelin TS = 20log(L) – 69.3; herring TS = 20log(L) – 2.3log(1+depth/10) – 65.4; walleye pollock = 20log(L) – 67.2; sand lance TS = 20log(L) – 80 (Thomas et al. 2002, Gauthier and Horne 2004, Boswell et al. 2016).

Species-specific fish density (fish m^{-3}) was calculated by scaling the echointegration exports based on average size of fish (cm total length, g weight) caught by region. If size information was unavailable for all species-region-year combinations, we averaged size information across all regions or years, depending on catch data available.

To estimate the species-specific index of fish biomass for each region and year, density (ρ) in each interval was estimated using the standard equations : $\sigma_{bs} = 10^{\frac{TS}{10}}$, where σ_{bs} is the backscattering cross section, and $\rho = \frac{\overline{s_a}}{\sigma_{bs}}$, where $\overline{s_a}$ is the mean of the area backscattering coefficient (ABC, s_a, $m^2\,m^{-2}$) (MacLennan et al. 2002) summed across depths for each interval. Average (SE) density in each region was multiplied by the area of the region and scaled by species and stage-specific weights and to compute biomass indices (mt).

To quantify macrozooplankton abundance and distribution among years, we classified acoustic backscatter in the water column using frequency response methods described for inshore waters (De Robertis and Ormseth 2018). 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 -80 dB. Samples with $\Delta S_{v\,120kHz-38\,kHz}$ values between 8 to 30 dB were classified as macrozooplankton based on

known acoustic scattering characteristics (De Robertis et al. 2010). For each 10 m vertical by 0.3 km horizontal increment along transects in each region and year, we computed the acoustic macrozooplankton index as the mean (SE) area backscattering coefficient (ABC, m^2 m^{-2}) from the 120 kHz acoustic backscattering data (see Arimitsu et al. 2021a for details).

To plot densities by depth, fish density (fish m^{-3}) was calculated as volume backscattering coefficient (s_v, m^{-1}) divided by σ_{bs}. For macrozooplankton, we used volume backscattering coefficient (s_v, m^{-1}) to estimate an index of density by depth layer.

Habitat sampling
At fixed habitat sampling stations (n = 5, one station at Bainbridge and two each in Montague and Gravina sampling areas) we measured oceanographic conditions with a SBE 19 plus v2 conductivity-temperature-depth profiler (CTD) equipped with fluorometer, turbidity sensor, beam-transmissometer, photosynthetically active radiation (PAR) sensor, dissolved oxygen, pH sensor, and water sampler to sample nutrients and chlorophyll *a* at discrete depths (0 m, 10 m, and near bottom). After each CTD cast we collected zooplankton samples with a 50 m vertical haul using a 150 µ-mesh paired ring net equipped with a flowmeter. The CTD and external sensors were calibrated by the manufacturers annually.

Objective 2: Spring-Summer Seabird Diets Middleton Island
EVOSTC support for Middleton Island seabird diet sampling within the GWA program began in FY17-21; however, sampling by the Institute for Seabird Research and Conservation and previously supported by USGS and USFWS began in 1978 (Hatch and Sanger 1992, Hatch 2013). USGS continues to support this effort and has formalized the release of this long-term data stream (Hatch et al. 2023).

Regurgitated food samples are collected annually from adult and/or nestling black-legged kittiwakes at Middleton Island during all months April through August. From an evaluation of alternate methods of analyzing and reporting diet results, the preferred metric for kittiwakes is prey frequency of occurrence.

Bill loads, including whole fish of one or more species at a time, are collected annually during the rhinoceros auklet chick-provisioning period, usually once or twice a week from early July through early or mid-August. Because the adults deliver whole fish to their chicks, these samples are identified to species, and each fish is weighed (to the nearest 0.1 g) and measured (total length to the nearest mm). With individual weights of fish available, the preferred metric for rhinoceros auklets diets is percent biomass.

Objective 3: Summer Forage Fish Surveys in Prince William Sound

Aerial survey validation
Validation efforts to ground-truth school species and fish size and/or age are necessary to estimate error in school identification by aerial observers. From a 16' inflatable skiff we used

jigs of varying hook size, underwater video, cast nets, purse seines, gill nets, and visual identification to identify schools observed by the pilot. Some schools were validated with more than one method (e.g., video and purse seine). Using multiple validation methods was necessary due to the different species and size classes encountered.

Summer acoustic-trawl survey
Summer acoustic-trawl surveys conducted during 2014-2016 were repeated in 2019 to assess interannual variability in forage fish acoustic biomass indices (Fig. 1, Arimitsu et al. 2014). We planned to continue these surveys in 2020 and 2021; however, we were unable to conduct this work during the global COVID-19 pandemic.

Summer survey acoustic data processing methods are detailed in Arimitsu et al. (2018) and differed slightly from those used for fall surveys (as described above) due to different locations, season, and transect layout, and also because we followed the processing methods of summer 2014-2016 surveys to ensure comparability of indices among years. Importantly, the difference in taxa composition across locations, seasons, and years sampled during summers required us to use a lower threshold (i.e., -60 dB) to separate stronger-scattering fish from weaker-scattering gelatinous zooplankton that were widespread in the water column during summer surveys. This relatively strong threshold was necessary to remove the acoustic signal of gelatinous zooplankton aggregations, which regularly occurred in the water column during summer surveys and had similar scattering characteristics on both frequencies (i.e., similar to fish, $\Delta s_{v120-38}$ = -8 to 9.3) but were much weaker scatterers than fish. This threshold also excludes weaker scattering fish, such as larval fish and fish without a swim bladder such as sand lance. However, we didn't encounter sand lance on summer acoustic transects because schools were typically closer to shore in shallower water (i.e., often < 5 m) than our vessel could sample, as confirmed by the aerial survey observations and the lack of sand lance in midwater trawl catches. For the summer gelatinous zooplankton acoustic index we applied an upper and lower threshold of -80 and -60 dB, respectively, which is consistent with what is known about the target strength (Brierley et al. 2004, 2005) of the main species encountered in trawls (see below). Fish and gelatinous zooplankton acoustic indices were integrated from 4 to 125 m (i.e, the maximum depth range of our trawl) (DeRobertis et al. 2010). Echointegration analyses for summer surveys were made at a cell resolution of 5 m depth by 0.1 km horizontal increments. Additionally, we followed the same methods we used for 2014-2016 summer survey analysis for data collected in summer 2019 to ensure indices were comparable among years.

Summer forage fish condition and age structure
To assess forage fish condition and age structure of forage fish in PWS we collected Pacific sand lance and capelin during July to assess energy density and age composition. Pacific sand lance were collected at Naked Island and Middle Ground Shoal, usually with a purse seine (von Biela et al. 2019), and capelin were collected on spawning grounds at Port Etches with dip nets, cast nets, or trawls (Arimitsu et al. 2021a, Fig. 1). Up to 200 fish per species were measured for total length (mm) and weight (g), capelin were identified to sex using external morphology (i.e., males

have a raised lateral line and enlarged anal fin), and all fish were individually labeled and bagged, then frozen at -4°C for later lab analysis.

For both species, age was assigned by counting translucent zones on sagittal otoliths. Otoliths were extracted, dried, and examined under reflected light using a Leica M60® dissection microscope. Under reflected light, translucent zones appear dark and opaque zones appear white. Translucent bands forming on the otolith edge were considered incomplete, assuming a January 1 birth date for sand lance and capelin (Robards et al. 2002, Gjøsæter et al. 2003). Digital images of each otolith were captured using a Leica DFC425 digital camera and translucent zones were counted to determine age.

After otolith removal, a subsample of randomly selected whole fish were freeze dried for a minimum of 48 hours, or until dry weight stabilized. Once dried, fish were weighed (g), homogenized using a coffee grinder and mortar and pestle, and made into pellets. A semimicro Parr 6725 calorimeter was used to measure energy density of the pellets and benzoic acid standards and duplicate tissue samples were used to evaluate precision.

RESULTS

Sampling was accomplished in 2017-2019 as planned. Although the Middleton diet data collection efforts continued during the COVID-19 pandemic, no forage fish sampling occurred aboard the USGS *R/V Alaskan Gyre* during 2020. Additionally, our efforts in 2021 were plagued by logistical complications related to the virus, including logistical constraints on planning and travel, availability of hydraulics specialists for repairing a mechanical problem with our trawl gear during the summer research cruise, supply chain delays on safety equipment that made it impossible to deploy trawl gear for the fall IPP survey, and other significant challenges. Below we summarize findings of the work we were able to conduct as it relates to specific FY17-21 project objectives. All data are publicly available (Arimitsu et al. 2017, Hatch et al. 2023). For timely reporting we include results from 2022 data where available.

Objective 1: Fall Integrated Predator Prey Survey Prince William Sound

Hydroacoustic-trawl surveys
Acoustic fish and macrozooplankton indices reflect interannual variability in abundance by region based on surveys conducted in September of each year during 2017-2019, 2021-2022 (Figs. 2 and 3). Sand lance were encountered infrequently on transects in Montague Strait during 2018 and 2021, and absent other years. Juvenile herring biomass was greatest in Montague Strait during 2018, though they were encountered more commonly in Port Gravina. Juvenile pollock biomass was greatest in Montague during 2017 and in Port Gravina during 2022. Capelin were absent during surveys in most years and regions, however small aggregations were encountered in Port Gravina in 2019 and Montague Strait during 2019 and 2022. Adult herring biomass in Port Gravina and Montague Strait peaked in 2021. Adult walleye pollock biomass was variable

over time but also peaked in Port Gravina and Montague in 2021 (Fig. 2). Macrozooplankton indices were relatively low in years sampled between 2017 and 2021 but increased in all three subregions during 2022 (Fig. 3).

Contours of depth and density indices for macrozooplankton and forage fish aggregations (where present) identify differences in depth distribution among species groups. There were two apparent signals in the macrozooplankton data, including lower density aggregations in shallow (< 50 m) and higher density aggregations at deeper (90 –120 m) water column depths (Fig 4). Juvenile herring occupied shallower depths (0 –50 m) than adult herring (50 –100 m), and a similar segregation of depths was observed for juvenile pollock (25 –100 m) compared to adult pollock (80 – 250 m) (Fig. 4). Capelin aggregations occurred primarily in the upper 100 m of the water column, and there was a relatively wide range of density values concentrated from 35 to 60 m (Fig. 4).
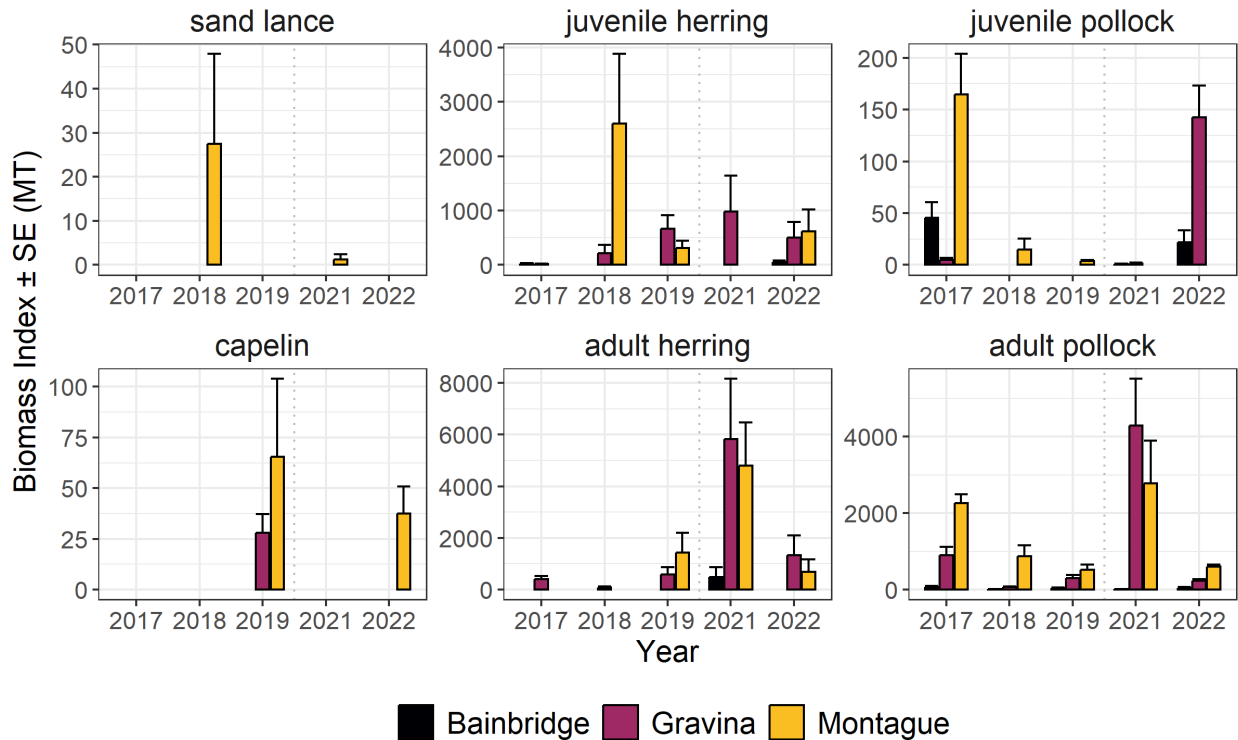
Figure 2. Acoustic indices of forage fish biomass by region and year in Prince William Sound, Alaska during September (±1 SE). No sampling was conducted in 2020 (dashed line).

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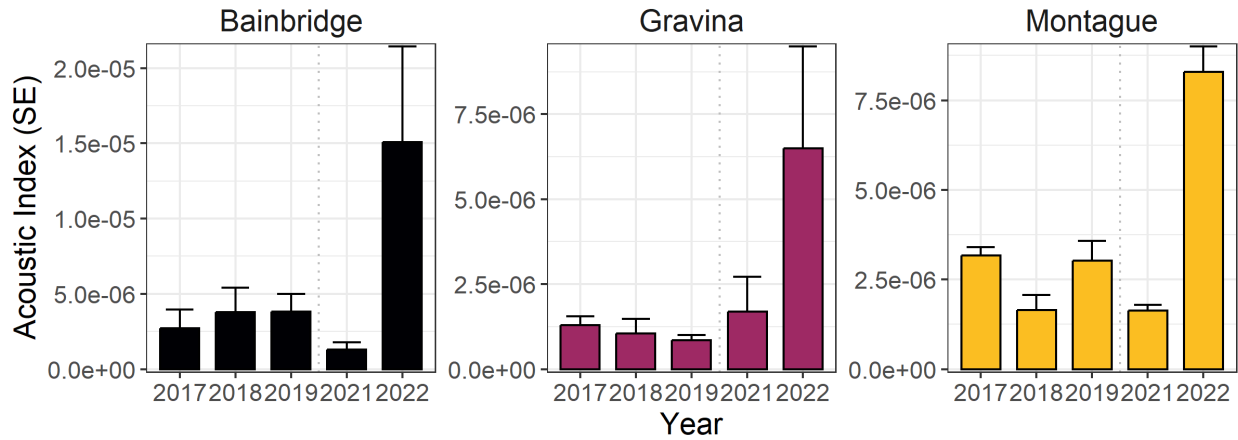
Figure 3. Acoustic indices of macrozooplankton abundance (area backscattering coefficient [ABC] m^2 m^{-2}) by region and year in Prince William Sound during September (±1 SE). No sampling was conducted in 2020 (dashed line).
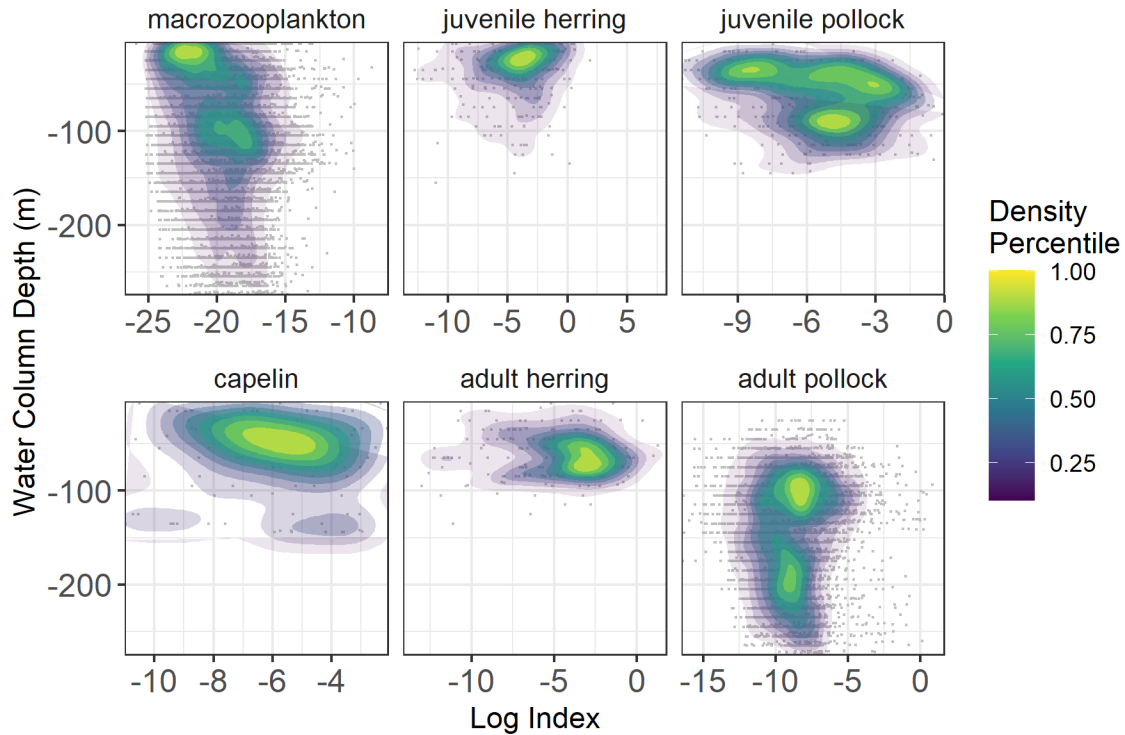
Figure 4. Depth distribution of log-transformed density indices for macrozooplankton (s_v, volume backscattering coefficient, m^{-1}) and forage fish (fish m^{-3}) aggregations in Prince William Sound during September 2017-2019 and 2021-2022. Grey points represent depth and density of aggregations (where present) within each 10 m deep by 300 m long transect interval, and color contours represent a 2D kernel density estimation scaled to a maximum value of 1 for each species and/or life stage.

Macrozooplankton species composition was determined from samples collected in midwater trawls in PWS during summer and fall surveys. Macrozooplankton communities were dominated primarily by two euphausiid species, *Thysanoessa spinifera* and *Euphausia pacifica* starting in 2015 (Fig. 5). *Thysanoessa raschii* and *Thysanoessa inermis* occurred in greater biomass proportions prior to 2015 than in the years following.

Habitat

We sampled water column characteristics with 24 CTD casts during fall surveys in PWS 2017-2022. Surface temperatures were warmest in 2018 and 2019 (Fig. 6). Water column temperatures in 2019 were warmest in Bainbridge Passage, however, in Montague Strait 2019 and 2017 were similar while in Port Gravina 2017 water column temperatures between 25 and 100 m were warmer than 2019. Interannual variability in thermocline depth was most pronounced in Port Gravina, where the thermocline was shallower during 2018 than other years. Surface salinity was consistently lowest at Bainbridge Passage compared to other regions (Fig. 6). Dissolved oxygen concentrations were more variable among regions and years, though lowest values occurred at depth in all regions during 2019 (Fig. 6).
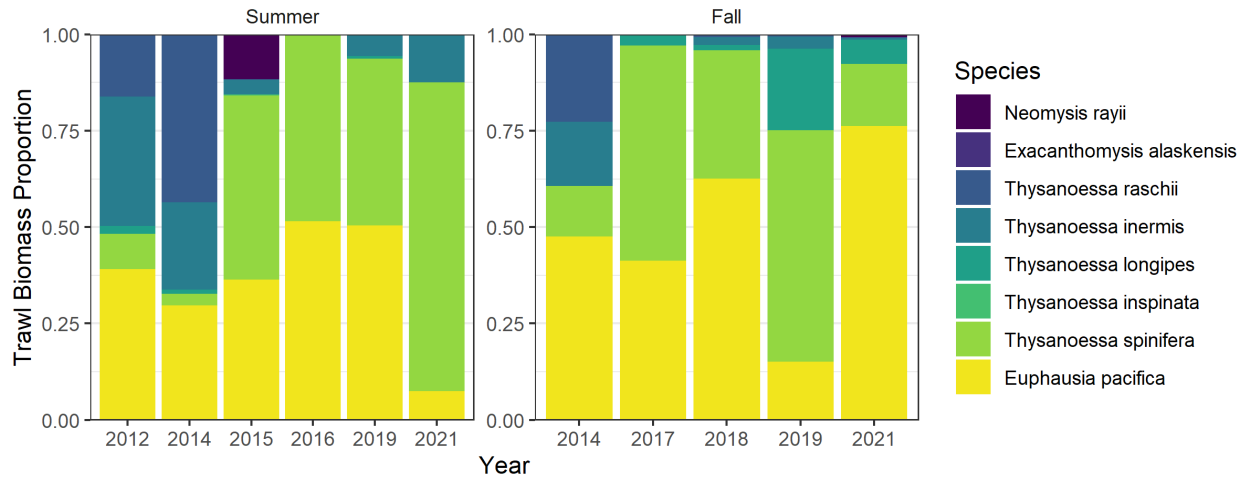
Figure 5. Trawl biomass proportions for macrozooplankton by year and species (color) during summer (June-July) and fall (September) surveys in Prince William Sound.
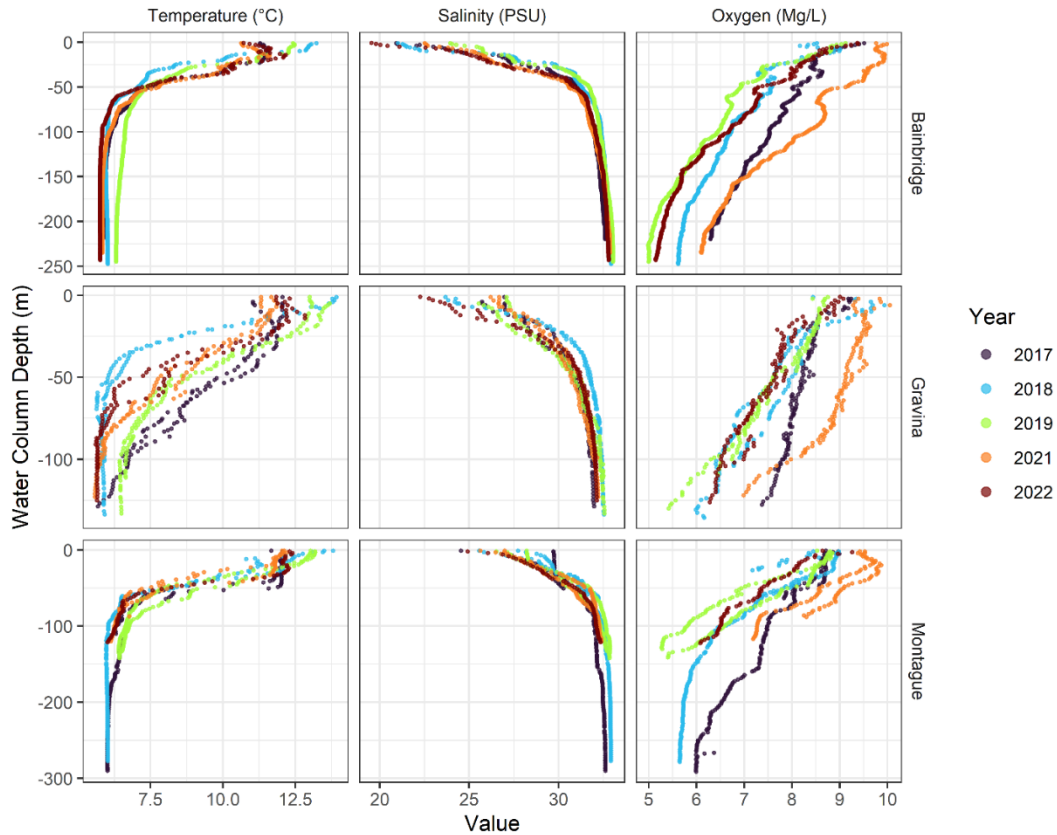
Figure 6. Temperature, salinity, and dissolved oxygen concentration profiles by region during September 2017-2022.Two stations were sampled in Gravina and Montague each year.

In situ fluorescence profiles provide a proxy for relative chlorophyll *a* concentrations (i.e., phytoplankton standing stock) among stations within years (Fig. 7). The outer, more oceanic station on the south end of Montague Strait (Fig. 1) had greater fluorescence values at depth than other stations, especially in 2017 and 2019, but in 2018 it had the lowest peak values of any station at shallower depths (Fig. 7). In general, *in situ* fluorescence profiles suggest high variability in phytoplankton abundance during most years except 2021 when patterns of peak fluorescence depths were more similar among regions.
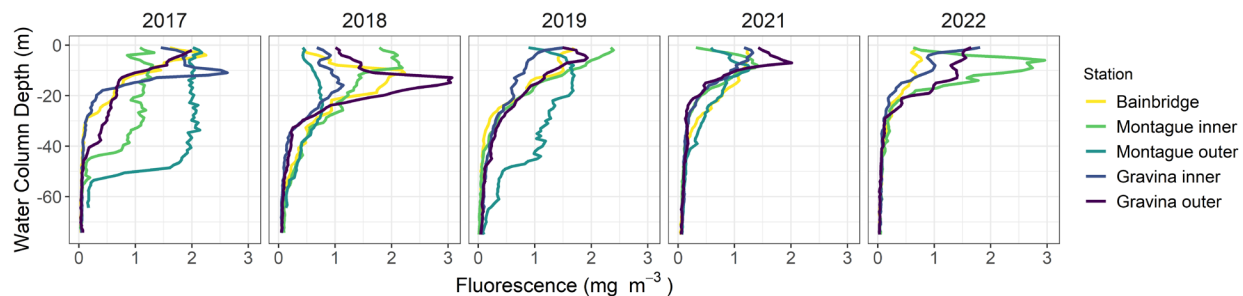
Figure 7. In situ fluorescence depth profiles by year and station (color) during fall surveys in Prince William Sound.

Nutrient samples (nitrate, phosphate, and silica) were also collected at each CTD site (Table 1). These samples were separated into shallow (≤ 10 m) and deeper (> 10 m) habitats to sample above and below the photic zone, respectively. Deep samples were aimed to be collected near bottom depth, however due to an instrument programming error, deep samples in 2018 were collected at 20 m depth and therefore did not exceed the photic zone.

Relationship between whales, birds, and forage fish indices
As part of the 2020 GWA synthesis effort we identified changes in the distribution, abundance, species composition, and condition of forage fish as a driver of shifts in distribution, mortality, malnutrition, and reproductive failures of humpback whales and common murres during or after the marine heatwave (Arimitsu et al. 2020, 2021a). PWS humpback whales encounter rates on fall surveys increased through 2014 and declined by 2017 when surveys were next conducted. The number of calves observed on surveys decreased after 2013, however, even while the abundance of adults in PWS peaked the next year. By fall 2019, humpback whale encounter rates increased slightly but had not returned to pre-heatwave levels. Between fall 2014 and 2017, acoustic macrozooplankton index in humpback foraging habitat declined (Arimitsu et al. 2021a).

Table 1. Mean (±1 SD) nutrient concentrations (µM) by region and depth during September surveys in Prince William Sound. Nutrients were sampled from above ("shallow") and below ("deep") the photic zone at each station, except in 2018.

	2017		2018		2019		2021	
Nitrate	Shallow	Deep	Shallow	Deep	Shallow	Deep	Shallow	Deep
Bainbridge	0.42 (0.44)	21.61 (NA)	0.36 (0.27)	-	2.34 (0.89)	15.26 (NA)	1.48 (0.63)	27.24 (NA)
Gravina	0.33 (0.16)	15.31 (0.65)	0.17 (0.15)	-	0.37 (0.49)	8.70 (0.33)	1.27 (1.15)	21.94 (2.69)
Montague	0.71 (0.35)	11.51 (15.16)	3.16 (2.63)	-	1.35 (0.78)	9.53 (1.97)	1.62 (0.68)	19.91 (1.43)
Phosphate								
Bainbridge	0.15 (0.08)	1.88 (NA)	0.07 (0.03)	-	0.32 (0.08)	1.32 (NA)	0.29 (0.05)	2.13 (NA)
Gravina	0.21 (0.02)	1.535 (0.11)	0.13 (0.06)	-	0.18 (0.06)	0.94 (0.01)	0.36 (0.12)	2.00 (0.36)
Montague	0.36 (0.12)	1.195 (1.10)	0.49 (0.37)	-	0.31 (0.09)	0.95 (0.09)	0.44 (0.08)	1.77 (0.19)
Silica								
Bainbridge	2.90 (1.29)	33.45 (NA)	3.95 (1.93)	-	18.03 (3.29)	58.95 (NA)	7.75 (0.61)	37.75 (NA)
Gravina	3.11 (1.25)	22.07 (1.97)	3.94 (0.85)	-	12.50 (2.42)	42.82 (0.06)	7.73 (1.68)	28.49 (6.46)
Montague	3.86 (0.64)	19.14 (22.79)	7.00 (3.18)	-	17.50 (3.61)	43.71 (3.24)	9.17 (0.54)	26.07 (4.48)

Objective 2: Spring-Summer Seabird Diets Middleton Island

Information from spring-summer seabird diets at Middleton Island provides an index of the availability of forage fish in the northern GOA. Below we summarize main findings on seabird diets from the Middleton Island Field Report in 2021 (see also Appendix A).

Black-legged kittiwake diets

Middleton Island is close to the continental shelf break, and for a few weeks after they arrive in spring kittiwakes typically forage over deep ocean waters at night, taking vertically migrating prey such as lanternfish (myctophids), squids, polychaetes, and crustaceans (Fig. 8). Capelin dominated diets during cool years from 2008 to 2013, but in 2014 the spring diet reverted to a mix of myctophids and invertebrates. For the first and only time observed, kittiwakes continued to rely on oceanic prey throughout the 2014 summer, apparently because prey usually obtained in the neritic (shelf) zone during June-August failed to materialize. In 2015, yet another previously unknown sequence occurred. Neither myctophids nor capelin were available early in the season and large herring supplemented a predominantly invertebrate diet. During later stages of breeding in 2015, large herring and age-0 sablefish comprised the bulk of the diet (Fig. 8). The exceptional warming continued in 2016. The increased use of invertebrates crested that year with a virtual absence of fish in the diet during both April and May (Fig. 8). Typically, the two main contributors to the invertebrate fraction of the diet are squids and polychaetes (the latter being a pelagic species apparently obtained only at night). In 2016, the kittiwake diet in the first week or two after the birds' spring arrival at the colony in late-March consisted almost exclusively of polychaetes. By May, squids were the dominant invertebrates and main prey overall (Appendix A).

In 2017, squids and polychaetes were less prominent in the early-season diet than in several of the immediately preceding, warm-water years. Instead, the dominant fraction of the invertebrate diet that year consisted of crustaceans such as shrimp, amphipods, and copepods (Appendix A). The prevalence of copepods, especially during May, was notable because historically those prey have rarely occurred in the kittiwake diet at Middleton. Copepods arguably are a last resort prey for a bird predator accustomed to having ready access to forage fish like myctophids or herring or energy-rich polychaetes. Also notable in 2017 was the regular occurrence of three-spine sticklebacks during April. Being abundant inhabitants of the intertidal zone and brackish ponds around the island, sticklebacks are an ever-present food source on Middleton, albeit one that is largely ignored by kittiwakes except perhaps when the birds struggle to find much else in the way of oceanic prey. The paucity and generally small mass of regurgitated food samples found on Middleton Island was further evidence of poor foraging conditions in spring 2017.
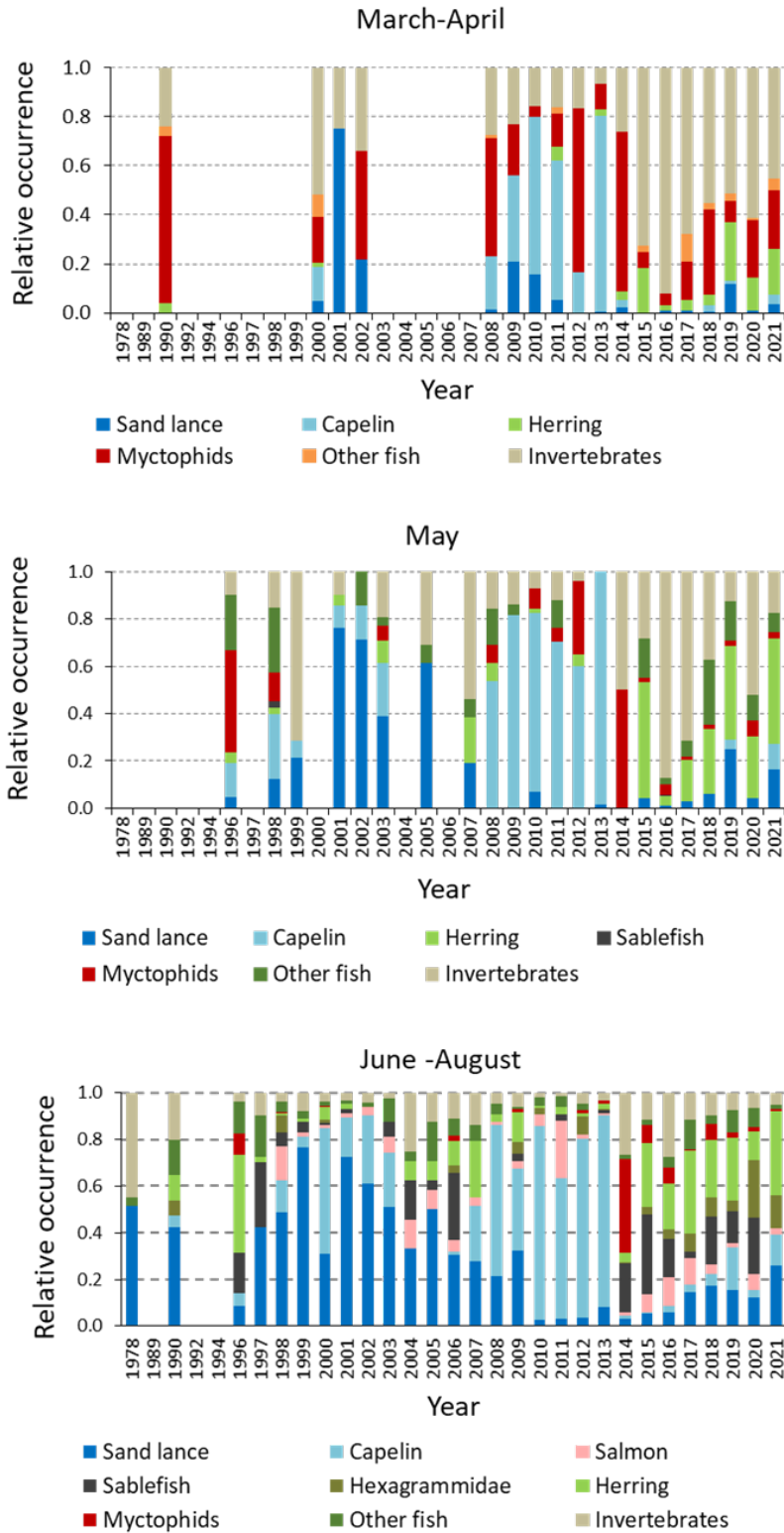
Figure 8. Interannual variation in kittiwake diet composition on Middleton Island, 1978-2021.

The spring diet of kittiwakes in 2018 showed a continuing rebound of myctophids (Fig. 8), perhaps reflecting those species' resumption of near-surface migration at night and not necessarily increased abundance. Such behavior would have been encouraged that year by cool-water conditions, at least in comparison to extreme years of the heatwave, spanning 2014 through 2016. The invertebrate fraction of the diet consisted mainly of squids and amphipods during April, but switched substantially to polychaetes, krill and copepods by May 2018. Temporally, pre-breeding kittiwake seem to forage opportunistically on whatever invertebrate prey happen to be swarming abundantly at the surface over periods of a few nights or up to a week or two. In May 2018, kittiwakes began taking substantial amounts of fish (herring, eulachon, sand lance, and lingcod), implying prey were more abundant compared with several preceding years. During incubation and chick-rearing in 2018, the kittiwake diet favored herring, sablefish, and sand lance (Fig. 8). Consistent with results since 2014, a notable scarcity of capelin continued that year, and juvenile pink and chum salmon had a poor showing in the chick diet (July and August).

Invertebrates comprised a more typical fraction of the kittiwake diet in spring 2019, declining somewhat between April and May as the fish component increased (Appendix A). However, myctophids seemed to be largely unavailable during that time, when the main constituents of the fish diet were herring and sand lance. In fact, kittiwakes made little effort to forage in the pelagic zone during the pre-laying period in 2019 (Appendix A). Herring continued to be important fish prey throughout the summer (Fig. 8). Capelin and sand lance were about equally prevalent in the summer diet, with 18% and 15% relative occurrence, respectively. As such, capelin made a stronger showing in 2019 than in any year since the onset of the heatwave in 2014.

In 2020, invertebrates (especially squids) and myctophids were important in the kittiwake diet during the pre-laying period (Apr-May), indicating that extensive foraging off the continental shelf occurred at that time (Appendix A). To the extent the birds foraged over the shelf in spring, age-1 and older herring were also an important fish prey in 2020. In 2020, capelin were scarce throughout the season—absent in spring and present only in trace amounts from egg-laying through chick-rearing (Fig. 3).

A species new to the list of seabird prey at Middleton Island, chub mackerel (*Scomber japonicus*), was first encountered in 2019 (4 occurrences) and increased to 15 occurrences in 2020. To date the species appears only in late-season samples obtained from black-legged kittiwakes (earliest occurrences 6 August 2019 and 6 August 2020). Co-occurrence in samples with myctophids, squid, and pelagic crustaceans suggests chub mackerel are coming from the pelagic zone south of Middleton Island, where only kittiwakes are known to forage with some regularity.

In 2021, large herring (mean total length 153 mm, range 119-180 mm) continued to be an important component of the pre-breeding diet, and capelin occurred in about 11% of samples. Herring and capelin both persisted as significant components of the diet throughout the summer

(June - August), whereas sand lance increased and greenling declined slightly compared to 2020 (Fig. 8).

Rhinoceros auklet diets

Auklet data plotted separately by prey type highlight large changes in availability of capelin and sand lance starting in 2014 (Fig. 9). Pearson's correlations between time series of surface-feeding kittiwake and diving auklet diets in summer were relatively high for capelin (r = 0.81), sand lance (r = 0.85), and greenling (r = 0.90), indicating these indices are robust indicators of availability in the region, and not just a reflection of preferred prey selection by a predator. Following a period of reduced availability in the mid-1990s, sand lance made a strong comeback by the end of that decade, but steadily declined in importance after 2000 and contributed little to seabird diets from 2009 to 2015 (Fig 9). Capelin replaced sand lance in diets from 2008 to 2013. In 2018 sand lance constituted about 50% of the auklet diet by weight but remained below the long-term average for several years following that.
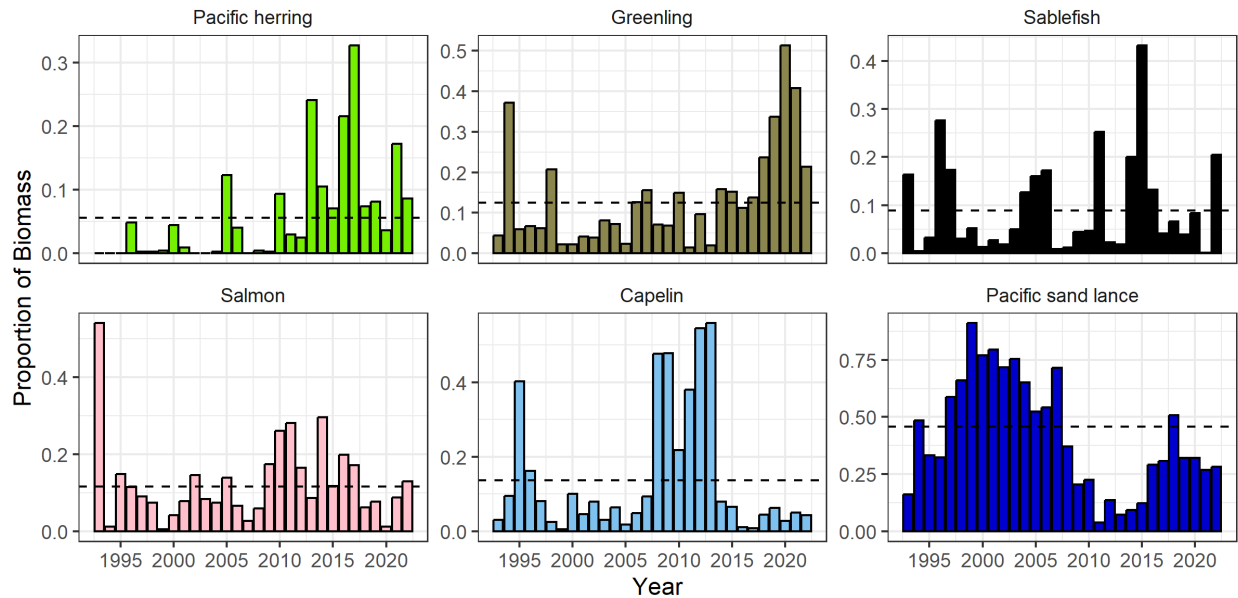
Figure 9. Interannual variation in rhinoceros auklet chick diets on Middleton Island 1993-2022. Mean proportions over time are drawn as dashed lines for each species.

Similar to kittiwake diets, prior to the Pacific marine heatwave either capelin or sand lance made up the majority of rhinoceros auklet diets, but since 2014 indices of both species have been generally below average (Fig. 9). Herring became more common in diets after 2013, and greenlings were prominent in the auklet diets during 2018-2021, to a consistently high degree not seen since sampling began (Fig. 9). Age-0 sablefish were less abundant and much smaller than average during summer 2021, which were likely drivers of their low diet index value in that year (Arimitsu and Hatch 2023).

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Objective 3: Summer Forage Fish Surveys Prince William Sound

Summer acoustic-trawl survey

We conducted summer PWS acoustic-trawl surveys aboard the USGS *R/V Alaskan Gyre* during summers (late-June to July) 2014-2016 and 2019 (Fig. 1). Midwater trawls were conducted to ground truth acoustic signals (Fig. 10) and catch data provided information on forage species composition and size (Fig. 11).
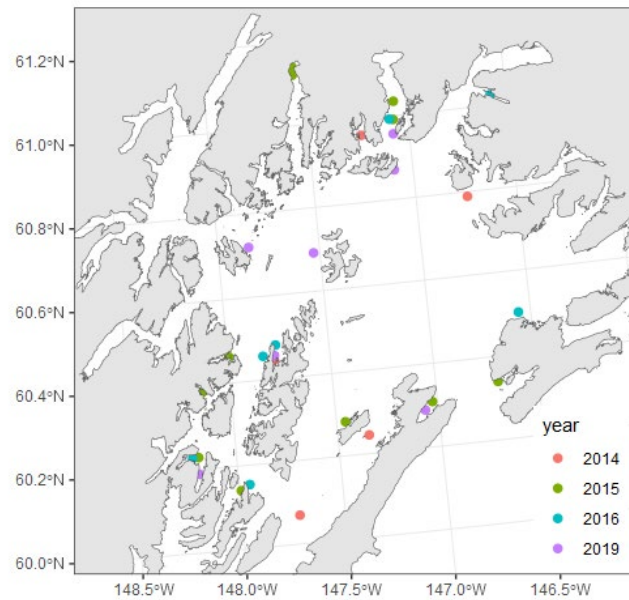
Figure 10. Location of midwater trawl effort (circles) by year (color) during summer surveys in Prince William Sound.
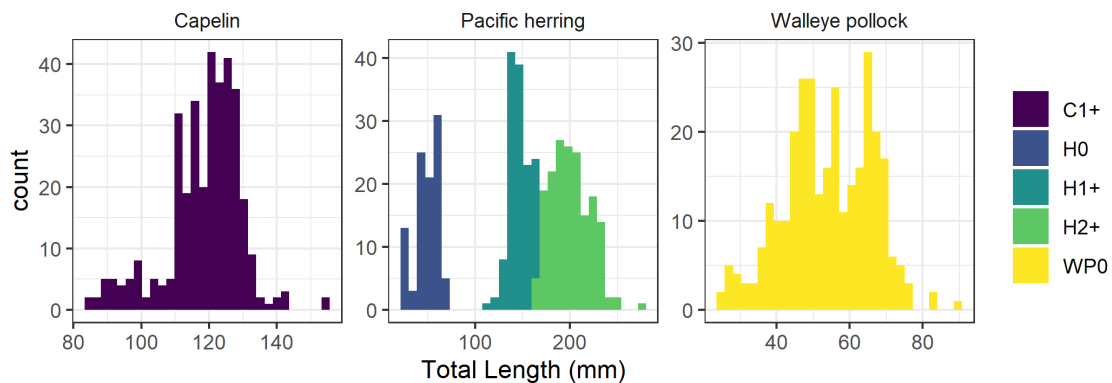
Figure 11. Length frequencies of focal fish species used to estimate target strength for summer acoustic biomass indices. Colors indicate groups by species C = capelin, H = herring, WP = walleye pollock; and size 0 = age-0, 1+ = age-1 or older, 2+ = age-2 or older).

The 120 kHz acoustic fish index, which summarizes average (+1 SE) fish backscatter (including backscatter due to non-target species), was greatest in 2014, lowest in 2015, and of moderate

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values in 2016 and 2019 (Fig. 12). When backscatter was apportioned to species and size based on trawl catch data, 2019 average densities of age-0 herring, capelin, and age-0 walleye pollock increased and age-1+ herring decreased compared to previous years (Fig. 12). Sand lance were not observed on summer acoustic transects or collected in midwater trawls during summer surveys.
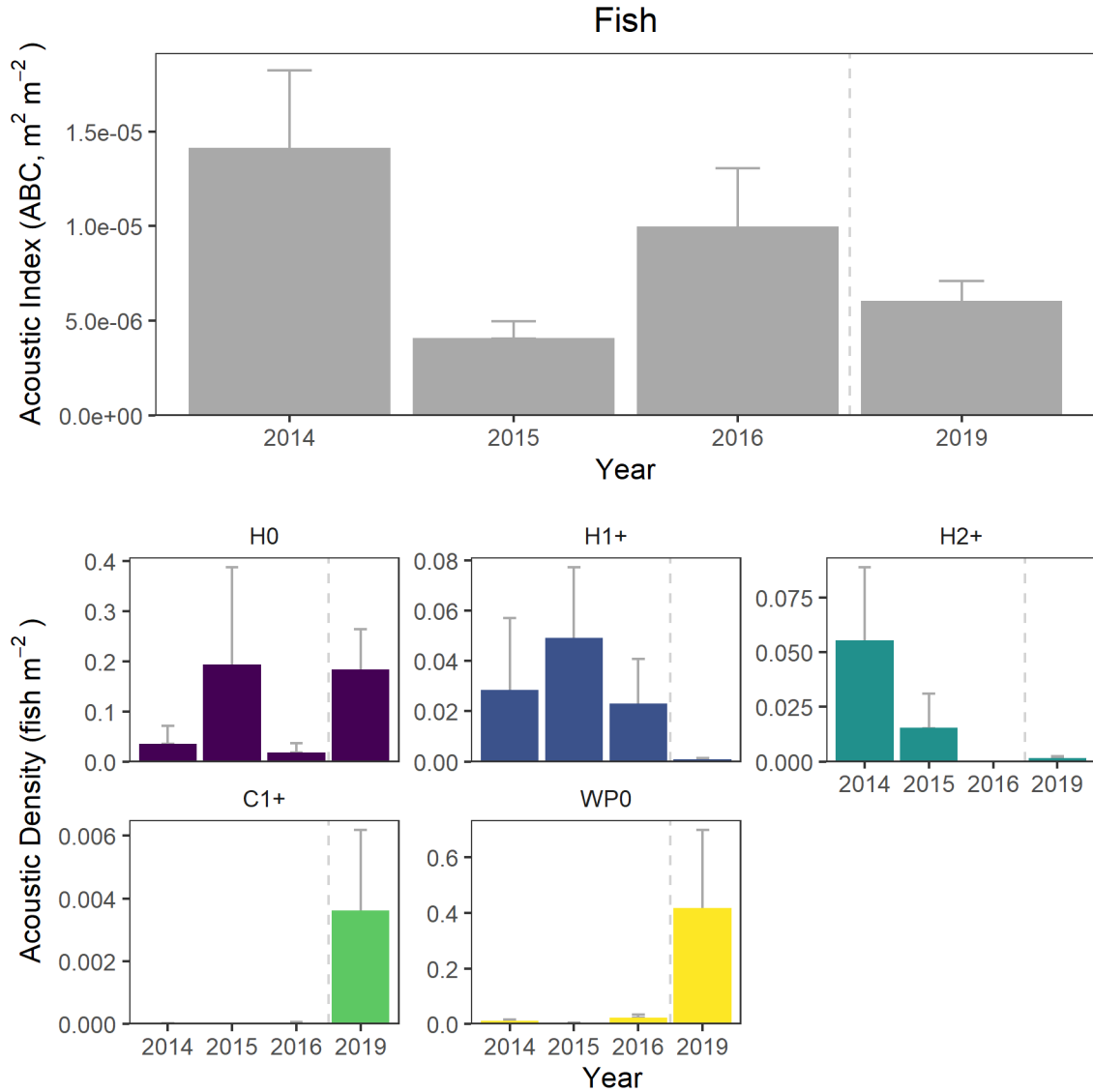
Figure 12. Average (+1 SE) summer acoustic indices for Prince William Sound. (Top) Fish acoustic index (Area Backscatter Coefficient, ABC). (Bottom) Average (+1 SE) fish density by species (H = herring, C = capelin, WP = walleye pollock) and size (0 = age-0, 1+ = age-1 or older, 2+ = age-2 or older).

The gelatinous zooplankton acoustic biomass index was greatest in 2015 compared to other years (Fig. 13). When scaled to catch biomass proportions, large medusae species including *Aurelia* sp., *Chrysoara melanastor*, *Cyanea capillata,* and *Phacellorphora camtschatica* were dominant species comprising jellyfish communities in 2015. *Aequroea* sp. comprised more than 50% of gelatinous zooplankton biomass during 2016 and 2019.
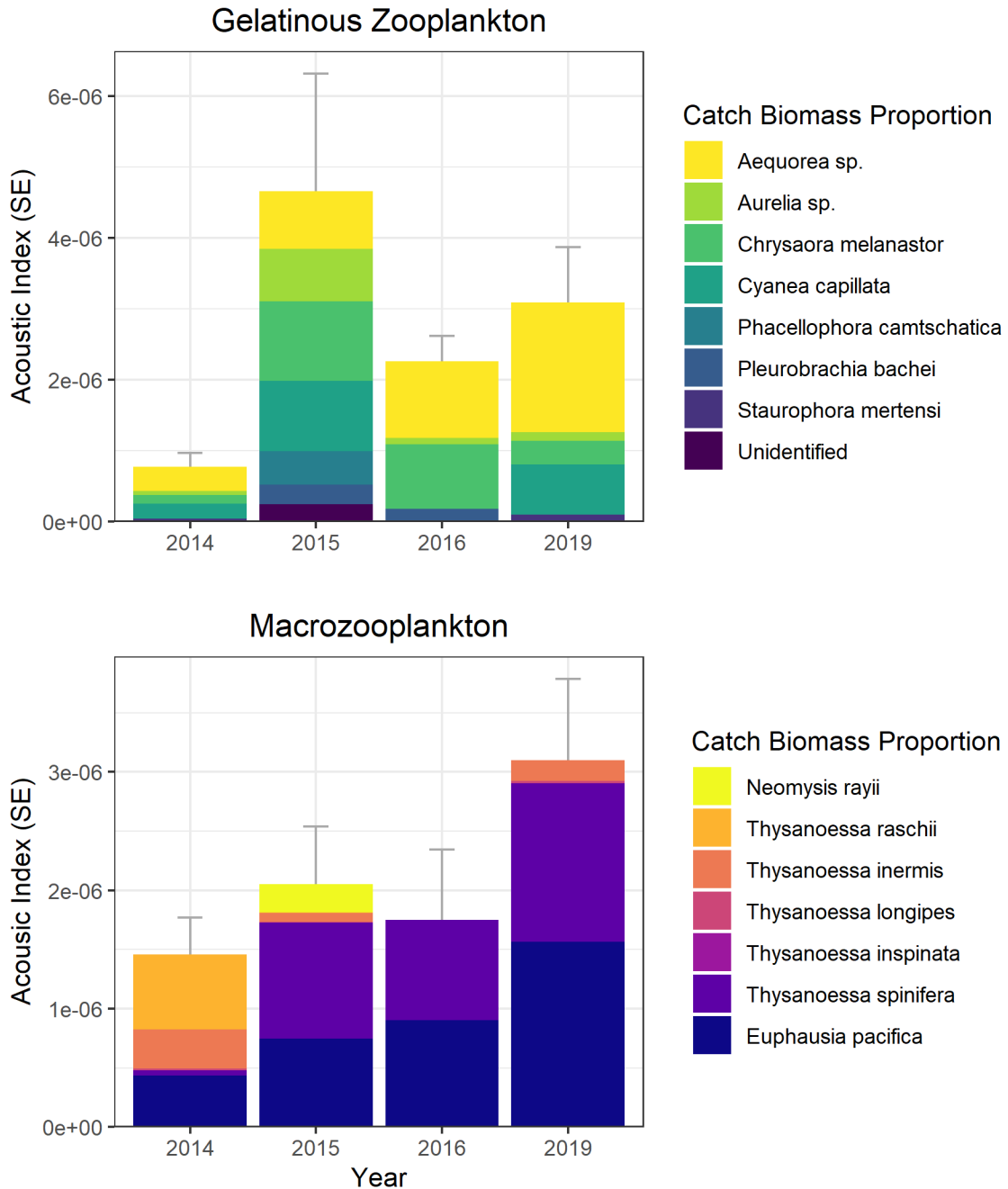
Figure 13. Interannual variability in gelatinous zooplankton (top) and macrozooplankton (bottom) acoustic indices (mean Area Backscattering Coefficient, m^2 m^{-2}) and proportion of trawl catch biomass by species (color) during summer surveys in Prince William Sound.

Acoustic indices of macrozooplankton increased in 2019 compared to 2014-2016 (Fig. 13). Biomass indices of *Thysanoessa raschii* and *T. inermis* decreased after 2014, when the community was dominated by *Euphausia pacifica* and *T. spinifera* in 2015, 2016, and 2019.

Aerial survey validation
We validated 88 schools during aerial surveys conducted in 2014-2016 and 2019-2022, of which 86% were correctly identified to species, 10 11% of schools were misidentified, and one school was found to be mixed species of age-0 herring and sand lance (1%). In one instance (1%) a patch of shallow rocks was misidentified as a school.

Of 56 herring schools correctly identified to species and in which age class could be determined by the ground crew (either by inferring age from length of fish or by age determined from scales), 82% were correctly identified to age, 9% were found to be a different age than called by aerial observers, and 9% schools contained multiple age-classes. Specifically, of five herring schools that were identified by aerial observers as age-1 herring, two were found to be age-0 herring, and three were found to be age-2+ herring. Of five schools found to be mixed-age herring schools, four were identified by aerial observers as age-1 herring but contained age-1 and age-2+ fish, and one was identified by aerial observers as age-0 herring but contained age-0 herring and age-0 sand lance.

Notably, during validation efforts in June 2021 we sampled spawning adult herring schools in Simpson Bay. Most spawning occurs in PWS during spring, so this represented an unusually late spawning event.

Summer forage fish condition and age structure
During summer 2019, we collected Pacific sand lance samples in PWS to continue the energy time series for age-1 fish. We did not sample sand lance in 2017, however, by July 2018 the age-1 sand lance whole fish energy had returned to pre-heatwave levels and remained so in 2019 and 2021 (Fig. 14).
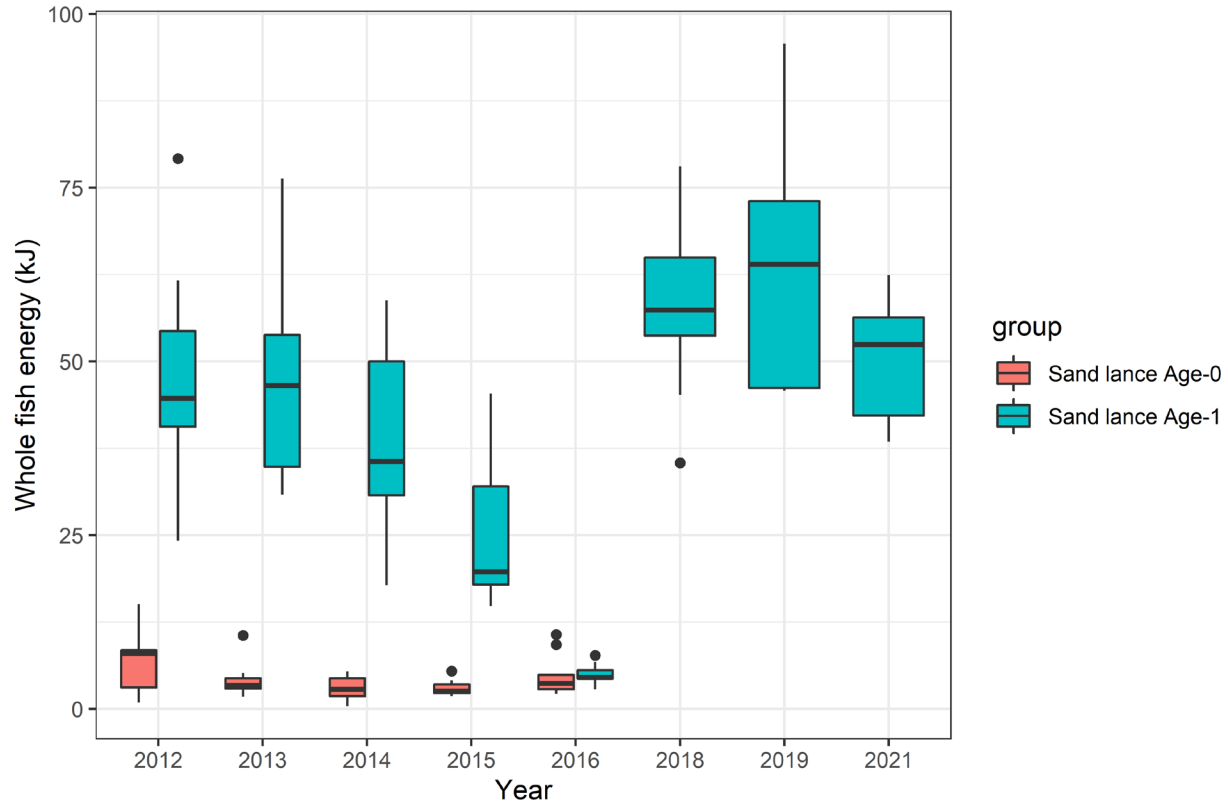
Figure 14. Pacific sand lance whole fish energy (kJ) by age (color) in Prince William Sound from 2012-2021.

Despite a return of marine heatwave conditions during our 2019 summer survey, we encountered adult capelin in trawls for the first time in several years, and larval capelin were first observed during the fall cruise in 2018. Spawning capelin were collected at Port Etches and Zaikof Bay in 2019. Although surface water temperatures were unusually high, below 10 m depth our CTD measurements indicated that water temperatures were within the range considered suitable for capelin spawning (8-10 ºC). We encountered spawning capelin in Port Etches (PWS) in July 2020. Through an outreach effort to get more information on spawning capelin in Alaska (Appendix B), we also obtained samples from beach spawning events in Kachemak Bay (Cook Inlet) and Kodiak in May of that year. In all three locations the spawning capelin were primarily age-1 individuals, a contrast to primarily age-2 individuals observed in PWS in 2013 (Fig. 15).
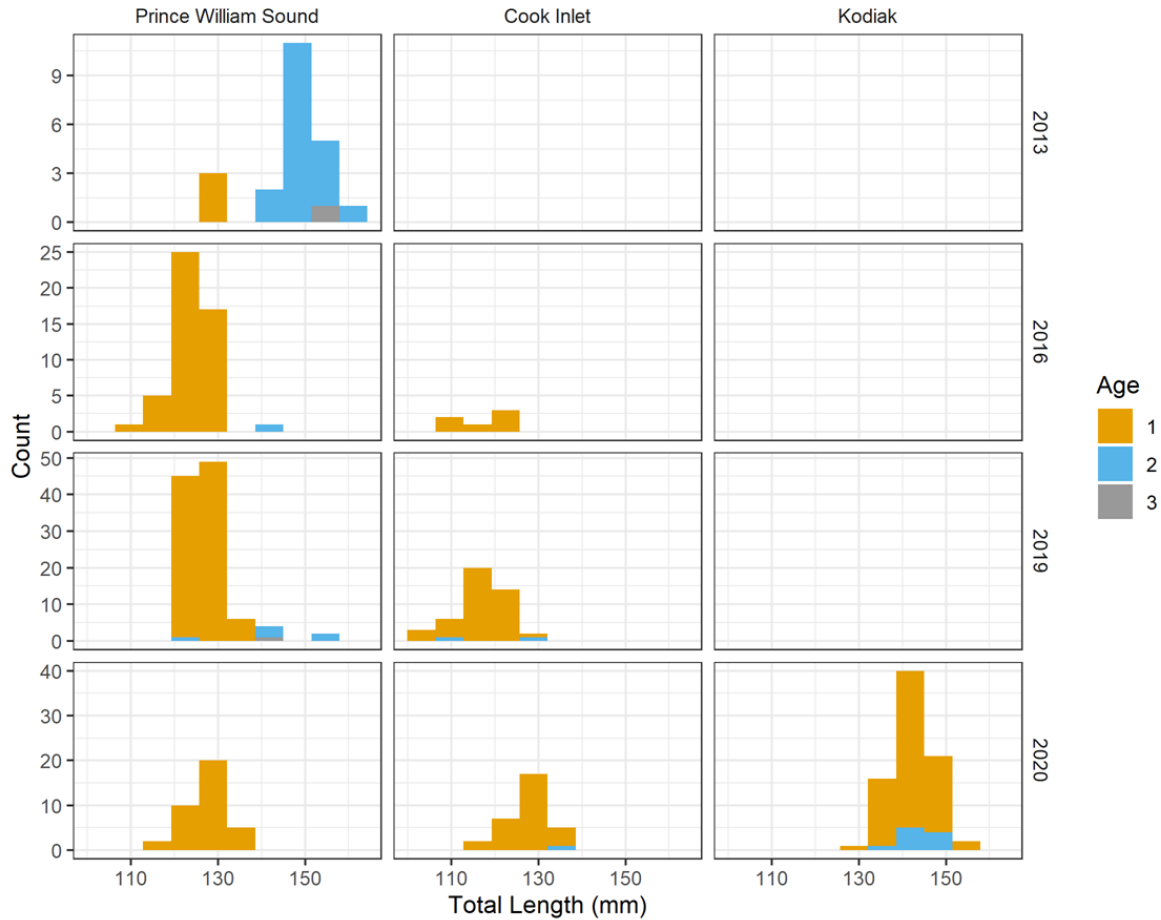
Figure 15. Capelin length histograms by age (color), region (columns), and year (rows). Spawning capelin were younger and smaller during (2016) and after (2019, 2020) the Pacific marine heatwave than they were before (2013).

DISCUSSION

A synthesis of datasets on middle trophic level forage taxa from PWS and the northern GOA demonstrated the unique ability of the GWA forage fish monitoring effort to provide a basis for understanding large-scale changes in higher-level predators in response to the 2014-2016 Pacific marine heatwave (Arimitsu et al. 2021a). This effort further highlighted GWA time series on forage fish abundance and quality in the region most affected by the heatwave, and when integrated with information from other agencies, provided a mechanistic understanding of the role that forage fish played in a large-scale disruption in the pelagic food web (Arimitsu et al. 2021a, Suryan et al. 2021). We found a primary mechanism of trophic disruption by the multi-year marine heatwave. The marine heatwave reduced the abundance of several key forage fishes along with some cold-water-associated euphausiids (e.g., *T. raschii*, *T. inermis*, and *T. longipes*), while it simultaneously lowered nutritional quality of key forage species. For example, in 2016 we identified an 89% reduction in age-1 Pacific sand lance whole body energy compared to

2012-2014. This change in nutritional value was attributed to poor growth during the marine heatwave, especially in 2016 when age-1 fish were indistinguishable in size from age-0 fish (von Biela et al. 2019).

Not surprisingly, the decrease in humpback whale encounter rates coincided with reduced macrozooplankton biomass and historically low herring indices in PWS. We also documented unusually high densities (> 2SD) of common murres in PWS during fall 2014 and late-fall 2015, within nearshore areas of Katmai during summer 2015, and on the GOA inner shelf during spring and fall 2015 (Arimitsu et al. 2021a). These high densities suggest inshore movement of murres preceded the unprecedented mass mortality of the species during winter 2015-2016 (Piatt et al. 2020).

Much of the information summarized in this GWA final report for work in 2017-2021 was used for the synthesis described above, including data from 3 years (2017-2019) of the project. Since then, we have continued our annual monitoring necessary for documenting the long-term impact of the Pacific marine heatwave. Continued monitoring is essential to understanding mechanisms for the recovery of the pelagic ecosystem and resumption of healthy predator-prey relationships. For example, by 2018, sand lance age, size, total energy and an increase in consumption by seabirds indicated improved health of sand lance compared to the heatwave years. In 2019, another extreme marine heatwave year, we saw spawning capelin returning to the system for the first time since the population collapsed abruptly at the onset of the 2014-2016 heatwave (Arimitsu et al. 2021a), though the spawning population sampled in Port Etches was still younger and smaller than we sampled prior to the heatwave. During ongoing and complementary work on seabirds and forage fish in lower Cook Inlet, we also found significant improvement to prey quality and quantity, and significant aggregations of pre-spawning capelin and sand lance in 2019 led to improved breeding success of common murres that year (Arimitsu et al. 2021*b*, Schoen et al. 2022).

Since 2019, however, the recovery of the middle trophic level has not been sustained. Though spawning reports are rare in any year, in 2020 and 2022 (samples obtained from Kodiak, lower Cook Inlet, and Sitka were being processed at the time of this report) capelin spawned in several locations around the northern GOA but none were reported in 2021. Capelin are known to undergo 2-year cycles off the coast of Russia, with stock biomass fluctuations differing on an even-odd year pattern for decades at a time (Naumenko 2002). Whether a life history trait causes 2-year cycles in capelin populations in the GOA remains to be seen, but from our collective work on capelin in the region, we have documented large changes in size, growth, and age at maturity since the late-1970's (Pahlke 1985, Brown 2002, Arimitsu et al. 2008, McGowan et al. 2020, Arimitsu et al. 2021*a*).

Moreover, the composition of seabird diets after 2014 has been more variable than it was prior to the heatwave. Sand lance and capelin dominated seabird diets for nearly three decades prior to the 2014-2016 marine heatwave, yet in nearly every year since then, these species continue to

represent lower than average diet proportions. The seabirds switched to mainly herring and greenling in recent years. It's not yet clear if or when the ecosystem will return to pre-heatwave conditions but continued monitoring to document changes in middle trophic levels will improve our ability to understand the mechanisms underlying the response of predators to natural and anthropogenic perturbations.

Monitoring forage species in this region requires a multi-pronged approach including acoustic-trawl surveys to identify interannual variability of prey resources within predator hotspots, legacy time series data from seabird diets at Middleton Island, aerial surveys to monitor nearshore and shallow forage schools inaccessible to larger vessels, summer acoustic-trawl surveys, and forage fish sampling to monitor condition over time. Future work will involve more detailed analyses and modeling efforts to document changes in forage fish in the region. This work has demonstrated success through multiple publications and productive collaborations that have brought a more comprehensive understanding of forage fish abundance, distribution, and condition in PWS and the northern GOA.

CONCLUSIONS

When tens of thousands of common murres washed ashore during the Pacific marine heatwave (Piatt et al. 2020), monitoring by the extended GWA team provided timely data to conclude that widespread malnutrition, reproductive failures, and mortality of predators was due to lower availability and lower quality of prey resources in the GOA (Arimitsu et al. 2021a). A forage fish portfolio collapse underlay the murre die off during the heatwave, based on long-term data on seabird diets from Middleton Island (Arimitsu et al. 2021a). Since then, lingering impacts of the marine heatwave have impacted marine food webs in the northern GOA (Suryan et al. 2021, Schoen et al. 2022). More recently, monitoring indicates a slow recovery of the pelagic marine food web, yet the middle trophic system remains distinctly different from the community composition before the 2014-2016 marine heatwave.

Data collected on forage fish, in addition to coordinated efforts of GWA scientific and program management teams and other collaborators, will provide timely information and important context for understanding the response of marine ecosystems to current and future perturbations. Continued monitoring of forage fish as part of the GWA program is essential for understanding trends in both prey and predators and mechanisms by which the marine ecosystem responds to climate change.

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Robinson, C. L. K., D. F. Bertram, H. Shannon, V.R. von Biela, and M. **Arimitsu**. 2021. Haro Strait habitat as a refuge from ocean warming for Pacific sand lance and its importance to seabirds. World Seabird Conference, October.

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Sydeman, W., S.A. Thompson, S. Zador, K. Shotwell, M. **Arimitsu**, H. Renner, J. **Piatt**, S. Hatch, and Y. Watanuki. 2019. Oral Presentation. Potential application of seabird data on groundfish stock assessments. PICES annual meeting. Victoria, British Columbia, Canada, October.

Thompson, S. A., M. García-Reyes, W. J. Sydeman, M. L. **Arimitsu**, S. A. Hatch, and J. F. **Piatt**. 2019. Effects of ocean climate on the length and condition of forage fish in the Gulf of Alaska. Poster Presentation. PICES annual meeting. Victoria, British Columbia, Canada, October.

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Outreach

Arimitsu, M. L. 2019. Forage fish in changing seas. Guest lecture at the Sitka Whalefest, a Community Science Symposium. Sitka, AK. November.

Arimitsu, M. 2019. Hands-on presentation about pelagic marine organisms in Prince William Sound to pre-school through high school students at Chenega School, September.

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Arimitsu, M., and S. Schoen mentored ANCEP student Tatiana Kortuas during field work in Prince William Sound in June-July 2019. Tatiana gained valuable experience while helping with marine ecosystem field research including at-sea marine bird surveys, acoustic-trawl surveys for forage fish, zooplankton and oceanography sampling.

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Institute for Seabird Research and Conservation

Middleton Island Seabird Research and Monitoring

2021 Field Report
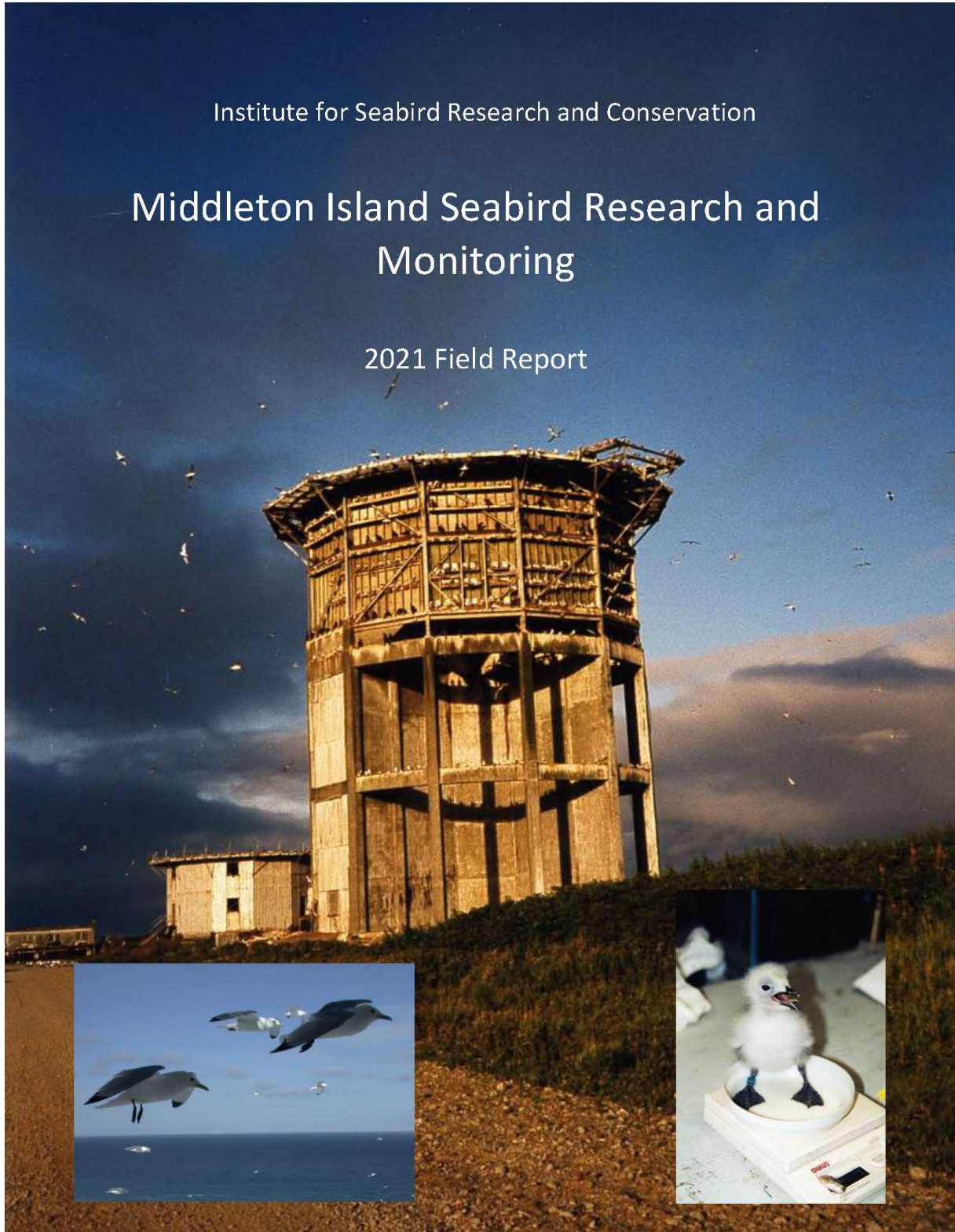
INTRODUCTION

The Middleton Island Marine Biological Station is a facility owned and managed by the Institute for Seabird Research and Conservation (ISRC) in support of long-term seabird research and monitoring in the Gulf of Alaska. The 2021 season marked the fifth year the project has contributed to Gulf Watch Alaska, a 20-year effort (2012-2031) funded by the Exxon-Valdez Oil Spill Trustee Council. The program is intended to uncover and monitor natural and anthropogenic factors affecting ecosystem function in the Gulf of Alaska and Prince William Sound. The specific contribution of the Middleton project includes quantifying dietary shifts in predator species, especially black-legged kittiwakes and rhinoceros auklets, as indicators of forage fish dynamics in the region.

Following best practices for Covid-19 safety, the project was able to avoid any significant disruption of the field effort caused by the ongoing pandemic in 2021. Of greater significance this year was the occurrence of an unusual die-off of adult and nestling seabirds (mostly kittiwakes and gulls) that began in mid-July and continued for nearly two weeks. This event necessitated a special effort to collect dead birds and environmental samples and send them off-island for diagnostic purposes. While awaiting the results of those analyses, much of the normal work routine in the tower and elsewhere on the island was suspended in the interest of worker safety. Nonetheless, the overall effort was successful in maintaining the continuity of long-term data sets— sampling effort for kittiwake and rhinoceros auklet diets, in particular, was comparable to recent years.

Special lines of research in 2021 included tagging black-legged kittiwakes with GPS trackers to identify the principal foraging areas used during pre-laying, incubation, and chick-rearing, and treatments designed to detect and quantify carryover (cross-seasonal) effects on kittiwakes of supplemental feeding. Participants in the latter effort (remotely and on-site) included researchers from McGill University (Montreal), University of Milan (Italy), University of Tsukuba (Japan), and University of Aberdeen (UK). Some geolocator (GLS) devices previously deployed on tufted puffins were recovered for Prince William Sound Science Center (PWSSC) investigators to assist in wrapping up their project to identify the wintering areas of puffins. With the partial exception of GPS tracking results for kittiwakes, the outcomes of those special investigations are not included in this report.

In 2021, the Middleton research station was occupied by members of the field crew from 8 April through 15 August.

always, the project benefitted from favors coming from many quarters and we are especially grateful to our friends and island neighbors with the Federal Aviation Administration.

RESULTS AND DISCUSSION

PRODUCTIVITY

Rhinoceros Auklet—In general, rhinoceros auklets have consistently high breeding success on Middleton (Coefficient of variation, CV = 10.0) (Fig. 1), and their population is increasing (currently ~20,000 individuals). At 0.77 chicks/egg laid (Table 1), production in 2021 was a little higher than the long-term average of 0.67 (n = 24 years, 1997-2021).

In 2017, we began a project to provide artificial breeding sites (wooden nest boxes, Middleton Report Appendix Fig. 1) for rhinoceros auklets on ISRC property. As of 2021, 121 nest boxes have been installed. Box occupancy (percentage of boxes with an egg laid) and fledging success (percentage of eggs that successfully hatch and fledge) has steadily increased in the nest-box population. For example, in 2021, 68% of the "old" boxes (installed before spring 2021) and 49% of the "new" boxes (installed in spring 2021) were occupied (egg laid); 79% of the "old" boxes and 81% of the "new" boxes in which eggs were laid produced fledged chicks.

Tufted Puffin—For 5 years prior to 2015, the virtual absence of fish-carrying adults seen around the island was a clear indication of scant chick production by tufted puffins on Middleton. During seven seasons subsequent to that period, puffins have achieved at least a partial return to normal production—between 0.17 and 0.43 late-stage chicks produced per egg-laying pair—despite ocean conditions in some years unfavorable to surface-feeders such as black-legged kittiwakes (see below). Production of 0.31 chicks per egg in 2021 continued that trend (Table 1), and despite their comparatively poor breeding performance (vis-à-vis rhinoceros auklets), puffin numbers have increased substantially on Middleton—i.e., roughly 20,000 individuals today versus 5,000 in the 1970s.

Pelagic Cormorant—Since 2002, pelagic cormorants have been monitored in the tower colony. Numbers (31-145 nest-building pairs) have varied greatly (less so in recent years), whereas breeding success (from ~0.45 to 2.0 fledglings per nest built) is relatively constant (Fig. 1, CV = 91.5; Table 2). Production in 2021 (2.3 fledglings/nest) was the highest observed since 2002, and more than double the long-term average of 1.05 fledglings/nest. On average, about 90 nests are constructed annually by cormorants on the tower, versus 59 nests in 2021. Thorough banding of adults and chicks done annually on the tower will support a future analysis and report of cormorant survivorship spanning the years since 2002.

Black-legged Kittiwake—Among fed pairs on the tower (n = 72 excluding fed pairs specially added for experimental purposes in 2021), production was 1.00 fledglings/nest, whereas 217 unfed pairs produced 0.43 chicks/nest (Table 3). The sizeable difference between food-treatment and control groups in 2021 indicated only fair foraging conditions for surface-feeding kittiwakes, as compared to the excellent performance of diving auklets and cormorants. The 2020 and 2021 seasons seemed decisively to end a period of poor breeding performance of kittiwakes that began with the emergence in 2014 of an unusual warm-water event in the northeast Pacific. Interannual variation in kittiwake production (naturally foraging pairs) is high on Middleton (CV = 113.8), especially in comparison to rhinoceros auklets (Fig. 1).

PHENOLOGY

Breeding phenology of pelagic cormorants varies by at least 3 weeks on Middleton, with the mean date of clutch initiation ranging from 18 May to 10 June in yearly samples averaging ~80 pairs on the tower (Fig. 2, upper panel). For reasons unclear in their particulars—but pertaining presumably to food supply—cormorant breeding was progressively delayed in the decade from 2002 through 2011. The reverse occurred more recently, with the timing of breeding having advanced steadily, or nearly so, after 2011.

The grand average of clutch initiation dates (mean of annual means) among naturally foraging kittiwakes on Middleton is 5 June. Thus, timing in 2020 (3 June) was about average, and that was true for both food-supplemented pairs and controls (Fig. 2, lower panel). As a rule, clutch initiation occurs about 4 days earlier in fed pairs (range 0-9 days) as compared with unfed pairs, and the treatment effect on laying date covaries ($r = 0.56$) with the treatment effect on chick production (i.e., fed pairs lay earlier and, in most years, fledge more chicks). Not surprisingly, because both parameters reflect foraging conditions in spring, the covariation of food-treatment effect on laying dates and clutch sizes (not shown) is stronger ($r = 0.72$). Supplemental feeding usually commences about 4-6 weeks after kittiwakes recolonize the island (which occurs in late March or early April), and a month or so prior to the mean date of clutch initiation.

DIETS

Black-legged Kittiwake—In most years since 1996, regurgitated food samples have been collected from adult and/or nestling kittiwakes on the tower from April or May through August (Table 4). From an evaluation of alternate methods of analyzing and reporting diet results (Hatch 2013, Middleton Report Appendix 2), the preferred metric for kittiwakes is prey relative occurrence, for which the relevant sample units are numbers of identified prey types in a given collection of samples (Table 5).

On average, Middleton kittiwakes take about equal amounts of Pacific sand lance, capelin, and invertebrates, and lesser amounts of herring, sablefish, salmon, and myctophids, depending on stage of the season (Fig. 3). A salient finding during the previously mentioned warm-water event was the virtual disappearance of capelin from the kittiwake diet on Middleton, following 6 prior years when capelin were abundant (Fig. 4).

Middleton Island is close to the continental shelf break, and for a few weeks after they arrive in spring kittiwakes typically forage over deep ocean waters at night, taking vertically migrating prey such as lanternfish (myctophids), squids, polychaetes, and crustaceans (Fig. 3). This was clearly the case in 2012, a year in which kittiwakes switched to capelin as the primary prey during incubation and chick-rearing (Fig. 4). Notably, because it had never been seen previously, capelin dominated throughout the following year, including even the spring arrival stage (a sizable sample having been obtained in late March 2013). In 2014, the spring diet reverted to a mix of myctophids and invertebrates, and for the first and only time observed, kittiwakes continued to rely on pelagic prey throughout the summer, apparently because prey usually obtained in the neritic (shelf) zone during June-August failed to materialize. In 2015, yet another previously unknown sequence occurred, as neither myctophids nor capelin were available early in the season, and large herring supplemented a predominantly invertebrate diet. During later stages of breeding in 2015, large herring and first-year sablefish comprised the bulk of the diet (Fig. 4).

The 2016 season was another extreme year within an ongoing, exceptional warming event. Increased use of invertebrates seen over the course of the heatwave crested that year with a virtual absence of fish in the diet during both April (Fig. 5) and May (Fig. 6). Typically, the two main contributors to the invertebrate fraction of the diet are squids and polychaetes (the latter being a pelagic species apparently obtained only at night). In 2016, it seemed the kittiwake diet in the first week or two after the birds' spring arrival at the colony (which normally occurs in late March) consisted almost exclusively of polychaetes. By May, squids were the dominant invertebrates and main prey overall (Figs. 5 & 6). As in other years, small numbers of the amphipod *Paracallisoma alberti* appeared regularly in the spring diet. The first occurrence of the hydrozoan *Velella velella* in 2016 was unexpected because the species is normally associated with warmer water than what usually occurs in the northern Gulf of Alaska.

In 2017, squids and polychaetes were less prominent in the early-season diet than in several of the immediately preceding, warm-water years. Instead, the dominant fraction of the invertebrate diet that year consisted of crustaceans such as shrimp, amphipods, and copepods (Figs. 5 & 6). The prevalence of copepods, especially during May, was notable because historically those prey have occurred but rarely in the kittiwake diet at Middleton. Copepods arguably would be a food source of last resort for a bird predator accustomed to having ready access to forage fish like myctophids or herring or energy-rich polychaetes. Also notable in 2017 was the regular occurrence of threespine sticklebacks during April (Fig. 5). Being abundant inhabitants of the intertidal zone and brackish ponds around the island, sticklebacks are an ever-present food source on Middleton, albeit one that is largely ignored by kittiwakes except perhaps when the birds struggle to find much else in the way of oceanic prey. The paucity and generally small mass of regurgitated food samples found around the grounds of the research station was further evidence of poor foraging conditions in spring 2017.

The spring diet of kittiwakes in 2018 showed a continuing rebound of myctophids (Fig. 5), perhaps reflecting those species' resumption of near-surface migration at night. Such behavior would have been encouraged that year by cool-water conditions, at least in comparison to extreme years of the heatwave, spanning 2014 through 2016. The invertebrate fraction of the diet consisted mainly of squid and amphipods during April, but switched substantially to polychaetes, krill and copepods by May 2018. Temporally, an even finer-grained depiction of kittiwake prey during pre-breeding would portray the fact that kittiwakes seem to forage opportunistically on whatever invertebrate prey happen to be swarming abundantly at the surface over periods of a few nights or up to a week or two. In May 2018, kittiwakes began taking substantial amounts of fish (herring, eulachon, sand lance, and lingcod), and the number and size of samples obtained from the grounds around the Middleton station indicated a relative abundance of food as compared with several preceding years.

During incubation and chick-rearing in 2018, the kittiwake diet favored herring, sablefish, and sand lance (Fig. 4). Consistent with results since 2014, a notable scarcity of capelin continued that year, and juvenile pink and chum salmon had a poor showing in the chick diet (July and August).

Invertebrates comprised a more typical fraction of the kittiwake diet in spring 2019, declining somewhat between April and May as the fish component increased in the samples (Figs. 5 & 6). However, myctophids seemed to be largely unavailable during that time, when the main constituents of the fish diet were herring and sand lance. In fact, kittiwakes made little effort to forage in the pelagic zone during the

pre-laying period in 2019 (see below). Herring continued to be important fish prey throughout the summer (Fig. 4). Capelin and sand lance were about equally prevalent in the summer diet, with 18% and 15% relative occurrence, respectively. As such, capelin made a stronger showing in 2019 than in any year since the onset of the heatwave in 2014.

In 2020, invertebrates (especially squids) and myctophids were important in the kittiwake diet during the pre-laying period (Apr-May), indicating that extensive foraging off the continental shelf occurred at that time (Fig. 7). To the extent the birds foraged over the shelf in spring, age-1 and older herring were the main fish prey in 2020, as was true also the previous year. Despite an amelioration of warm conditions at the ocean surface in 2020 (see below), capelin were scarce throughout the season—absent in spring and present only in trace amounts from egg-laying through chick-rearing (Fig. 4). Rather, cooling conditions were associated with the emergence of hexagrammid species, especially age-0 greenlings, as an important part of the kittiwake diet at Middleton (Fig. 7).

A species new to the list of seabird prey at Middleton—chub mackerel (*Scomber japonicus*)—was first encountered in 2019 (4 occurrences), increasing to 15 occurrences in 2020. To date the species appears only in late-season samples obtained from black-legged kittiwakes (earliest occurrences 6 August 2019 and 6 August 2020). Co-occurrence in samples with myctophids, squid, and pelagic crustaceans suggests chub mackerel are coming from the pelagic zone south of Middleton, where only kittiwakes are known to forage with some regularity.

In 2021, kittiwake prey during the pre-breeding period (Apr-May) was similar to 2020, except that polychaetes largely replaced squid in the invertebrate fraction of the diet (Fig. 7). Large herring (mean total length 153 mm, range 119-180 mm) continued to be an important component of the pre-breeding diet, and capelin occurred in about 11% of samples, possibly an incipient response to cooling ocean conditions. Herring and capelin both persisted as significant components of the diet throughout the summer (Jun-Aug), whereas sand lance increased and greenling declined a little compared with their respective showings in 2020 (Fig. 4).

Rhinoceros Auklets—Auklet diets are monitored by collecting bill-loads from chick-provisioning adults, usually once or twice a week from early July through early or mid-August. Sampling in 2021 yielded 306 bill loads and ground samples, comprising nearly 10 kg of auklet prey in total (Table 6). Overall, the auklet diet at Middleton is composed largely of a few species of forage fish, especially Pacific sand lance, capelin, salmon (including both pink and chum), and sablefish, in that order of importance (Fig. 8). The years 2014 through 2017 saw significant breaks from the past, with historically dominant species—sand lance and capelin—being largely supplanted by sablefish, salmon, and herring (Fig. 9).

Since 1978, about 154 kg of auklet prey samples have been collected on Middleton (Table 6), and auklet diet monitoring provides our single best indicator of forage fish dynamics in the region. By all appearances, sand lance were the overwhelmingly dominant forage species in the late 1970s through the early 1980s. Following a period of reduced availability in the mid 1990s, sand lance made a strong comeback by the end of that decade. Sand lance steadily declined in importance after 2000, however, and contributed little to seabird diets during a cold-water phase that materialized in 2008 (Fig. 9). The appearance of about 30% sand lance in the auklet diet in 2016-2017, and more than 50% by weight in 2018 was consistent with a known association of sand lance with warm-water conditions (Hatch 2013). While herring appeared superficially to have benefitted during a period of warming of surface waters

(Fig. 10), the absence of such a signal in herring data generally (PWSSC 2018) suggests that shifts in foraging locations have occurred that may account for the increased capture of herring by auklets and kittiwakes from Middleton (see below). Noteworthy in 2019 was an unusual spike in the occurrence of juvenile gadids—as yet unidentified to species, but definitely not walleye pollock—in the diet of rhinoceros auklets (Fig. 10).

As in three prior years (2018-2020), but to a slightly smaller degree in 2021, greenlings were a substantial part of the diet in both kittiwakes (above) and rhinoceros auklets (Figs. 9 & 10). While this analysis focuses on hexagrammid species (greenlings, lingcod, and Atka mackerel) as a group, it is noteworthy that in addition to kelp and rock greenlings (similar fish not identified to species in the field or lab), Atka mackerel (large-bodied relative to other hexagrammids collected) showed a marked increase, in 2019-2020, but receded in 2021 (only 1 occurrence in 306 auklet samples). Collectively, hexagrammids in 2021 (mostly kelp and rock greenlings) constituted about 40% of the auklet diet (biomass) and 14% of kittiwake prey (relative occurrence, Jun-Aug) (Figs. 9 & 10).

The juxtaposition of time series for kittiwakes and rhinoceros auklets since 1978 (Fig. 9) shows general agreement vis-à-vis the decline of sand lance and, after 2008, the emergence of capelin as a dominant forage species. However, in several recent years, when neither sand lance nor capelin were prevalent, the diets of surface-feeding kittiwakes and diving auklets diverged substantially (Fig. 9). In 2019, the trade-off appeared to occur primarily between herring (more prevalent in kittiwake diet) and juvenile greenlings (taken mainly by auklets). Both predators took substantial quantities of herring and greenlings in 2020 and 2021.

FORAGING AMBITS OF KITTIWAKES AND AUKLETS

From an initial application of GPS tracking devices in 2008 we learned—or rather, confirmed an inference from prior diet analyses—that Middleton kittiwakes shift their foraging strategies between different stages of breeding on Middleton Island (Fig. 11). The 2008 study was conducted during a time of food abundance at the outset of what proved to be a 6-year span of capelin dominance of the kittiwake diet—during incubation and chick-rearing at first, then throughout the breeding season from arrival through departure (Fig. 4). That initial study serves as a baseline for comparison with more recent telemetry that reveals the great extent to which kittiwakes vary their foraging behavior both within and between years.

For instance, whereas kittiwakes in 2008 (June - August) foraged mostly within a radius of about 50 km from the colony, during 2019 (post cold, capelin-dominated conditions that ended in 2014) the birds typically flew 100 km or more each way on a foraging trip, vastly enlarging the ocean area they exploited in summer (Fig. 12). We found a continuing pattern of long-distance foraging in 2020 and 2021, with nearshore waters along the outer coasts of Montague, Hinchinbrook, and Kayak islands being the prime foraging habitats of Middleton kittiwakes during incubation and chick-rearing (Fig. 13).

The pre-laying period following spring arrival at the colony (which occurs in late-March or early April) is of particular interest as Middleton kittiwakes reveal their choice whether to forage pelagically, over deep ocean habitat south of the island, or to forage over neritic waters of the continental shelf. In 2008, their clear preference—presumably driven by prey abundance—was to forage mainly at night for lanternfishes (Myctophidae) and other mesopelagic prey seaward of the continental slope (Fig. 11). The same behavior

has prevailed in some years subsequently, but in other cases we find the birds exploiting mainly shelf habitat, presumably because myctophids, which are energy-rich prey available only when and if they migrate diurnally to within a meter or so of the ocean surface, were unavailable (Fig. 14). Spring foraging by kittiwakes in 2019 (Fig. 14, upper panel) was more widespread than previously recorded or anticipated, with some individuals traveling far to the east and west of Middleton or visiting interior waters of Prince William Sound. Foraging tracks gave the impression of birds sampling intermittently the pelagic zone off the continental shelf, but not staying or foraging extensively, as though food-searching there was generally unproductive.

By correlating regurgitated prey samples with the preceding movements of tracked individuals, we aim eventually to identify the particular areas used by foraging seabirds to obtain specific prey. For example, large specimens of Pacific herring have in recent years been an important constituent of the kittiwake diet at Middleton, including samples obtained in the pre-laying period. In 2021, the foraging tracks of 5 birds that regurgitated herring upon returning to the tower indicated the fish were probably captured in an area extending some 50-80 km east and west of Middleton along the outer shelf (Fig. 15). Herring are thought to be restricted to continental shelf habitats (Mecklenburg et al. 2002), and visits by kittiwakes to barrier islands and beaches at the Copper River mouth (e.g., Figs. 11, 15) seem to occur most years during a narrow period in spring when pre-spawning eulachon aggregate at that location (Willson et al. 2006).

No tracking of rhinoceros auklets was undertaken in 2020. In 2019, however, the foraging area of chick-rearing rhinoceros auklets overlapped that of kittiwakes and was concentrated in nearshore waters of southeast Montague Island from Patton Bay to Cape Cleare (Fig. 16). That would seem to be the location where age-0 greenlings and gadids were unusually abundant in 2019. Chick-rearing auklets displayed a similar foraging ambit in 2021, although some individuals apparently located prey more to the northeast and further offshore from Montague this year (Fig. 16).

It is noteworthy that auklets deliver fish from as far away as 100 km from their nest sites on Middleton. Additional telemetry may find considerable flexibility in that regard, but the early lesson is that rhinoceros auklets, consistent with their reliable success at breeding, are well adapted for coping whenever local food shortages occur. Similar to kittiwakes, the information they furnish as prey samplers is relevant to a sizable portion of the northern Gulf of Alaska.

SPECIAL PROJECTS

Rhinoceros Auklet Population— Rhinoceros auklets burrow in several locations along the eroding cliffs around Middleton Island, usually under cover of salmonberry bushes and/or elderberry trees. The most recent census took place in 2008-2009, when approximately 11,450 rhinoceros auklet burrows were counted island-wide (comprising an estimated 15,000-20,000 adults; Hatch 2011). Continued growth of the colonies has made traditional burrow-counting methods impractical. During spring 2021, station personnel conducted an exhaustive search for currently occupied auklet habitat. This survey identified eight distinct sub-colonies, which were mapped by walking the perimeter of each sub-colony using a handheld GPS unit (Middleton Report Appendix Fig. 2). The total nesting habitat in use comprised 8.7 acres. The field crews observed prospecting activity (i.e., shallow burrows and evidence of recent digging) along the periphery of colonies where salmonberries extended beyond the current

colony limit, suggesting a trend of gradual colony expansion. Periodic mapping and measurement of rhinoceros auklet nesting habitat will be the preferred method of documenting future changes in this species' breeding population on Middleton.

Seabird Mortality Event, July 2021—As mentioned, a conspicuous die-off of black-legged kittiwakes in July 2021 caught the attention, and then dominated for several weeks the activities of, the Middleton field crew. The following account of the event is taken largely verbatim from a write-up prepared by S. Schoen (USGS), F. Tremblay (ISRC), and others (Ferriss and Zador 2021).

In mid-July 2021, a large number of sick and dying seabirds were observed. During a 10-day period, 250 kittiwakes, 70 glaucous-winged gulls, and 2 herring gulls were found dead, and 220 kittiwakes and 19 glaucous-winged gulls were observed sick. Affected birds exhibited neurological signs and abnormal behavior. At first, sick birds lost their ability to fly, then gradually lost their ability to move, and all died within ∼5 days of the first signs of sickness. Large numbers of carcasses, blood, feces, and food samples were collected from all seabird species monitored on the island. A coordinated response to determine the cause of this die-off was launched by ISRC personnel in coordination with scientists at the University of Alaska Fairbanks, the University of Alaska Anchorage, McGill University (Quebec, Canada), Frostburg State University, the U.S. Fish and Wildlife Service, and the U.S. Geological Survey (Alaska Science Center and National Wildlife Health Center, Madison, WI). The University of Alaska INBRE program provided funding for the collection, shipment, and initial molecular analyses of various samples and carcasses. The National Oceanographic and Atmospheric Administration (NOAA) Alaska Sea Grant provided additional funding to assist with transportation of personnel to participate in training and sample processing.

The cause of death was not immediately clear. Many sick and deceased birds were emaciated or in poor condition, but tested negative for highly pathogenic avian influenza, and the biotoxins saxitoxin (STX) and domoic acid. Blue mussels, plankton, and forage fish samples from recent kittiwake foraging locations near the outer islands of Prince William Sound (PWS) also tested negative for STX, as did blue mussels and feces from both outwardly healthy and sick kittiwakes collected at Middleton during the die-off. However, next generation sequencing (metagenomics) of RNA samples collected from sick and dead kittiwakes indicated the presence of Clostridia *spp.* in all birds, and significant reads in cloacal swabs classifiable as *C. botulinum* (n=2/12 birds, 17% prevalence). Clostridia are a group of bacterial species that produce botulinum neurotoxins, which can cause botulism. Further analysis of blood from two deceased kittiwakes revealed a positive bioassay test for (avian) botulinum toxin type C in one bird and a suspected positive result for the other; both birds tested negative for botulinum toxin type E, the botulinum toxin type that has been found to cause botulism in humans in the Arctic. Researchers plan to conduct additional tests to establish conclusively whether botulinum toxin type C was the culprit of the die-off and to investigate sources of this neurotoxin. This appears to be the first verified case of botulinum toxin type C in Alaska. Botulism can cause large die-offs of waterbirds, but botulinum toxin type C has not been associated with disease in humans.

The ecological implications of this mortality event are still being explored. Seabird die-offs in Alaska have increased in magnitude, duration, and frequency since 2015. Whereas most seabird die-offs have been attributed to starvation from a presumed lack of available food, this die-off appears likely to have been caused by disease. The origin of the botulinum toxin remains unknown, but fresh or brackish

water pools in which kittiwakes rest and bathe on Middleton contain dipteran populations, which are viewed as potential vectors. Diet and reproductive data for kittiwakes collected during the die-off show no indication of poor foraging conditions that might have contributed to changes in behavior (i.e., feeding in the brackish pools of Middleton Island). The diet composition and GPS tracking data indicate the kittiwakes were feeding distantly, closer to PWS than to Middleton, continuing a trend observed since the 2014–2016 marine heatwave. While extended foraging trips, and reduced capelin in kittiwake diets may contribute to a level of foraging stress, as shown in supplemental feeding experiments, other 2021 indicators, such as reproductive success and timing were close to 40-year averages. If the cause of this event is confirmed to be botulism, the 2021 die-off could be a harbinger of more such events as the distribution of naturally occurring toxins expands northward in concert with a warming ocean and changing weather patterns.

OCEAN REGIME INDICATORS

Using data from seabird monitoring on Middleton Island through 2011, Hatch (2013) described an apparent regime shift in the Gulf of Alaska ecosystem that occurred around 2008. This transition entailed: (1) a switch from mostly positive PDO indices (since 1977) to negative values after 2008, (2) the emergence of capelin as a dominant prey species at Middleton, and (3) markedly improved breeding performance by black-legged kittiwakes. These patterns persisted for at least 6 years (i.e., through 2013) and, all else being equal, would be expected to continue (with occasional interludes of opposing conditions) for another 2 decades or longer (Hatch 2013). One such interlude is now evident for the period 2014-2017, a widespread anomaly nicknamed "The Blob." Examples of dramatic species range shifts associated with that warm-water event are listed in Bond et al. (2015), to which we added the first-ever appearance of male California sea lions (*Zalophus californianus*) among ~100 Steller sea lions hauling out on Middleton in April, May and June of 2016. A similar complement of California sea lions was observed among the males hauling out on Middleton in April 2017.

Anomalous conditions are also reflected in monthly PDO indices and in seabird indicators from Middleton Island—namely, dietary capelin and kittiwake productivity—both of which dropped precipitously beginning in 2014 (Table 7, Fig. 17). The prevalence of invertebrates (mainly polychaetes and squids, but also including copepods and the normally warm-water hydrozoan *Velella velella*) in the spring diet during 2016-2017 is especially noteworthy. As nocturnal vertical migrants from mesopelagic depths, myctophids are available to foraging kittiwakes only at night, and then only if the fish rise to within a meter or so of the ocean surface. Evidently, anomalous surface conditions in 2015 and 2016 prevented myctophids from doing so in April, and mesopelagic fish remained a relatively minor component of the spring diet through 2019, April 2018 being a partial exception. While seabirds and forage fish gave early signs of returning to normal in 2018, a constellation of physical conditions in fall 2019 prompted references in the popular media to "Son of Blob" (e.g., Yulsman 2019). That event did not materialize, however, as cool conditions returned in early 2020, and Middleton seabirds had an exceptionally good year. If the incipient change to cool conditions seen in 2020 and 2021persists and strengthens, we predict a re-emergence of capelin as a dominant part of the food base in the Gulf of Alaska and correspondingly high breeding performance in seabirds.

The comparison of breeding performance in fed and unfed kittiwake pairs on Middleton furnishes a powerful indicator of ocean conditions, for the simple reason that kittiwakes prefer to feed themselves. In

poor years, characterized by positive PDO, low capelin availability, and poor kittiwake breeding performance, the difference between fed and unfed treatment groups is accentuated, and vice versa (Table 8, Fig. 18). The events of 2014-2021 have only increased the strength and predictive power of relations among the PDO, prey dynamics, and kittiwake breeding performance (Table 9). As of winter 2021/22, the PDO showed signs of a possible return to ocean conditions expected if a predominantly negative phase of the PDO would prevail in spite of temporary disruptions such as the warm-water anomaly so notorious of late. Thus, we look forward to the next iteration, if it comes, of this natural experiment, when a return to cold water conditions, capelin, and high kittiwake performance would more or less clinch these simple, yet portentous, relationships. As noted, a predominantly cold phase of the PDO is expected to last through the 2030s, all else being equal. Global warming and climate change could have countervailing effects, however, with far-reaching consequences for seabirds, marine mammals, and fisheries. It remains to be seen whether the recent and exceptional warm-water event in the Gulf of Alaska, was really an "anomaly" or, rather, a window on the future.

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Table 1. Productivity of rhinoceros auklets and tufted puffins breeding on Middleton Island in 2015-2021.

Parameter	2015	2016	2017	2018	2019	2020	2021	$\bar{x} \pm \text{se}$
				Rhinoceros auklet				
Burrows with eggs	60	61	62	61	72	62	100	
Eggs hatched	42	38	40	35	51	54	79	
Late-stage chicks	38	33	32	33	44	47	77	
Chicks/egg laid	0.63	0.54	0.52	0.54	0.61	0.76	0.77	0.62 ± 0.039
				Tufted puffin				
Burrows with eggs	52	82	71	71	60	32	78	
Eggs hatched	21	27	17	17	19	16	27	
Late-stage chicks	18	20	12	12	19	12	24	
Chicks/egg laid	0.35	0.24	0.17	0.43	0.32	0.38	0.31	0.31 ± 0.033

Table 2. Breeding performance of pelagic cormorants on the Middleton tower, 2002-2021.[a]

	A-egg date (Julian day)				Clutch size				Chicks fledged/nest built			
Year	n	Mean	SE	SD	n	Mean	SE	SD	n	Mean	SE	SD
2002	77	139.7	0.95	8.325	86	3.7	0.18	1.707	86	1.6	0.15	1.371
2003	78	138.2	0.97	8.540	80	4.0	0.16	1.441	80	1.9	0.16	1.400
2004	62	144.0	0.88	6.941	76	2.8	0.18	1.607	76	0.4	0.07	0.650
2005	31	142.5	1.32	7.352	31	3.5	0.18	1.028	31	1.2	0.23	1.283
2006	92	148.3	0.90	8.635	101	3.0	0.12	1.228	101	1.1	0.12	1.156
2007	142	147.8	0.93	11.130	144	3.8	0.11	1.275	144	1.6	0.12	1.425
2008	145	146.4	0.94	11.370	145	3.8	0.10	1.165	145	1.6	0.11	1.319
2009	113	155.0	0.68	7.223	128	2.9	0.11	1.232	128	1.4	0.10	1.175
2010	71	154.7	0.72	6.037	71	2.6	0.10	0.851	71	0.1	0.05	0.445
2011	95	161.3	0.96	9.314	109	2.5	0.12	1.281	109	0.5	0.07	0.741
2012	85	159.4	0.86	7.884	85	3.0	0.12	1.107	85	0.5	0.08	0.765
2013	89	150.3	0.73	6.842	90	3.4	0.09	0.880	90	1.9	0.12	1.167
2014	--	--	--	--	--	--	--	--	~87	~1.2	0.13	1.170
2015	58	155.0	0.91	6.910	85	2.1	0.16	1.470	85	0.6	0.09	0.823
2016	53	152.8	1.62	11.78	53	2.9	0.17	1.210	53	0.9	0.14	1.050
2017	69	150.9	1.08	8.951	69	3.3	0.10	0.845	69	1.6	0.16	1.306
2018	84	150.8	1.14	10.492	84	3.4	0.10	0.898	84	0.8	0.09	0.784
2019	75	149.3	1.03	8.918	75	3.6	0.10	0.841	75	0.4	0.10	0.838
2020	64	145.6	0.81	6.478	76	3.4	0.11	0.938	76	2.0	0.15	1.322
2021	59	146.5	0.77	5.946	59	3.6	0.11	0.828	59	2.3	0.17	1.308
Totals	1,542	149.4	0.96	8.37	1,588	3.2	0.13	1.149	1,647	1.175	0.12	1.075

[a] Productivity data for 2014 based on final count of chicks in tower nests on 14 July. This is at least 3 weeks before final checks in other years, and thus the count of chicks does not include additional mortality that would have occurred before fledging. On the other hand, 10 nests were still being incubated on 14 July. Those nests assumed to produce zero fledged chicks, offsetting perhaps the premature count of late-stage chicks. Thus, the estimate of fledglings in 2014 is 102 chicks from 87 nests built, a relatively crude value that should not be taken as strictly comparable to other years.

Table 3. Breeding performance of supplementally fed and unfed pairs of black-legged kittiwakes on the Middleton tower, 1996-2021.[a]

| | Unfed pairs | | | | | | | | | | | | Fed pairs | | | | | | | | | | | |
| | Julian lay date | | | | Clutch size[a] | | | | Chicks fledged | | | | Julian lay date | | | | Clutch size[a] | | | | Chicks fledged | | | |
Year	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.	n	Mean	s.e.	s.d.
1996	59	159	0.75	5.728	63	1.73	0.07	0.574	63	0.60	0.08	0.636	25	157	1.07	5.342	27	1.74	0.11	0.594	27	1.22	0.15	0.801
1997	59	158	0.44	3.386	65	1.48	0.08	0.664	65	0.32	0.06	0.503	25	155	1.09	5.427	25	1.80	0.08	0.408	25	0.96	0.16	0.790
1998	59	160	0.92	7.032	70	1.29	0.09	0.745	70	0.36	0.06	0.539	27	155	1.12	5.797	29	1.69	0.14	0.761	29	0.62	0.12	0.622
1999	65	169	0.59	4.771	156	0.47	0.05	0.606	156	0.21	0.04	0.468	44	161	1.01	6.684	46	1.61	0.09	0.614	46	0.59	0.11	0.717
2000	135	151	0.63	7.322	152	1.68	0.06	0.706	152	0.99	0.07	0.814	67	149	0.66	5.403	71	1.83	0.07	0.609	71	1.18	0.10	0.833
2001	166	153	0.46	5.942	174	1.78	0.04	0.560	174	1.03	0.06	0.853	67	151	0.41	3.342	71	1.93	0.07	0.569	71	1.28	0.10	0.848
2002	168	149	0.66	8.581	179	1.73	0.04	0.586	179	0.97	0.06	0.796	70	149	0.94	7.825	72	1.83	0.06	0.475	72	0.97	0.09	0.769
2003	95	157	0.47	4.600	102	1.67	0.06	0.603	102	0.50	0.06	0.609	66	152	0.74	6.003	69	1.81	0.07	0.550	69	0.91	0.10	0.836
2004	88	154	0.42	3.949	102	1.58	0.07	0.750	102	0.18	0.04	0.432	68	151	0.70	5.742	69	1.99	0.04	0.364	69	0.97	0.10	0.804
2005	214	157	0.30	4.321	221	1.67	0.04	0.553	221	0.37	0.04	0.553	71	151	0.57	4.775	72	1.86	0.05	0.421	72	1.03	0.08	0.712
2006	216	158	0.38	5.537	233	1.56	0.04	0.627	233	0.47	0.04	0.587	71	151	0.43	3.642	73	1.90	0.05	0.446	73	1.14	0.10	0.822
2007	172	163	0.43	5.606	197	1.34	0.05	0.693	197	0.42	0.04	0.606	63	158	0.74	5.900	73	1.58	0.08	0.725	73	0.77	0.10	0.874
2008	125	153	0.58	6.498	130	1.73	0.05	0.554	130	0.78	0.06	0.707	70	150	0.70	5.887	71	1.92	0.06	0.470	71	0.90	0.10	0.813
2009	90	155	0.57	5.439	98	1.69	0.07	0.649	98	0.20	0.04	0.405	75	150	0.81	7.056	76	1.89	0.04	0.386	76	0.75	0.10	0.656
2010	68	148	0.87	7.160	74	1.81	0.07	0.612	74	0.78	0.09	0.815	58	150	1.07	8.174	61	1.82	0.07	0.563	61	0.89	0.10	0.819
2011	41	158	0.64	4.092	42	1.62	0.08	0.539	42	0.50	0.09	0.552	47	152	1.26	8.624	48	1.83	0.07	0.519	48	0.92	0.11	0.794
2012	72	153	0.78	6.582	78	1.82	0.07	0.619	78	0.87	0.09	0.779	72	152	0.86	7.262	75	1.88	0.06	0.544	75	0.93	0.09	0.811
2013	63	148	1.06	8.413	68	1.84	0.06	0.507	68	1.00	0.10	0.792	67	148	0.97	7.965	70	1.97	0.06	0.538	70	1.04	0.10	0.842
2014	--	--	--	--	--	--	--	--	143	0.45	0.04	0.526	--	--	--	--	--	--	--	--	--	--	--	--
2015	296	153	0.29	4.986	352	1.51	0.04	0.762	352	0.21	0.02	0.422	70	152	0.47	3.895	72	1.90	0.05	0.449	72	0.96	0.09	0.740
2016	79	165	0.73	6.444	155	0.74	0.06	0.806	155	0.08	0.02	0.301	73	156	0.99	8.434	74	1.80	0.05	0.437	74	0.81	0.06	0.541
2017	72	161	0.52	4.407	104	0.95	0.07	0.755	104	0.22	0.04	0.417	72	155	0.58	4.948	74	1.82	0.04	0.371	74	0.76	0.08	0.679
2018	113	155	0.56	5.981	134	1.48	0.06	0.752	134	0.31	0.04	0.492	72	151	0.70	5.958	72	1.97	0.03	0.238	72	0.99	0.08	0.687
2019	326	154	0.30	5.471	368	1.61	0.04	0.691	368	0.50	0.03	0.586	73	150	0.46	3.922	73	1.99	0.04	0.311	73	1.07	0.09	0.770
2020	316	154	0.28	4.919	404	1.69	0.03	0.615	404	0.83	0.04	0.724	20	154	1.61	7.210	24	1.71	0.11	0.550	24	1.04	0.15	0.751
2021	217	155	0.45	6.693	217	1.76	0.03	0.441	217	0.43	0.04	0.532	72	149	0.50	4.275	72	1.97	0.04	0.335	72	1.00	0.09	0.732

[a] Clutch size (and chicks fledged) include zero-egg nests, thus incorporating breeding propensity into clutch size and reflecting (for fledging) the overall productivity of site-holding pairs.

Table 4. Temporal distribution of diet samples from black-legged kittiwakes on Middleton Island, 1978 – 2021.

Year	Adults			June			July			August			Total
	Mar	April	May	Adults	Chicks	Total	Adults	Chicks	Total	Adults	Chicks	Total	Total
1978								38	38		2	2	40
1989		2	2				5		5				9
1990		17	7	18		18	21	9	30				72
1992			1							3		3	4
1994		3											3
1996			19					37	37		17	17	73
1997			4	4	3	7	3	107	110	1	35	36	157
1998			32	11	16	27	13	130	143	7	64	71	273
1999			11	11		11	9	51	60	2	45	47	129
2000		41	7	13	1	14	4	87	91		29	29	182
2001		10	19	7	23	30	10	321	331		31	31	421
2002		26	14	2	22	24	1	193	194		22	22	280
2003		4	22	24	3	27	22	15	37	5	2	7	97
2004		9	8		1	1	11	7	18				36
2005		4	12	3		3	5	10	15	1	2	3	37
2006			6	6	8	14		100	100		19	19	139
2007		1	21	4		4	13	3	16	1	3	4	46
2008		44	10	4	2	6	2	40	42	2	13	15	117
2009		36	21	16	2	18	22	27	49	2	7	9	133
2010		39	51	39	34	73	27	128	155	4	36	40	358
2011		32	14	3		3	9	18	27	8	13	21	97
2012		10	75	5	10	15	60	238	298	11	67	78	476
2013	114	7	64	50	17	67	23	110	133	8	26	34	419
2014		179	6	1	1	2	3	100	103	14	14	28	318
2015		63	63	12	4	16	33	32	65	4	12	16	223
2016		135	129	27	5	32	42	123	165	3	26	29	490
2017		87	67	34	0	34	69	77	146	6	31	37	371
2018		197	40	18	5	23	27	92	119	4	53	57	436
2019		58	45	11	11	22	17	187	204	7	54	61	390
2020		58	34	1	18	19	1	351	352	4	142	146	609
2021		126	62	33	25	58	36	143	179	1	14	15	440
Total	114	1188	866	357	211	568	488	2774	3262	98	779	877	6875

Table 5. Numbers of prey types identified in kittiwake food samples—the basis for computations of

relative occurrence—by month on Middleton Island from 1978 through 2021.

| Year | Prey type identifications | | | | | | |
	March	April	May	June	July	August	Total
1978					56	4	60
1989		4	3		10		17
1990		25	9	34	46		114
1992			1			4	5
1994		7					7
1996			21		38	19	78
1997			4	9	132	47	192
1998			40	34	190	111	375
1999			14	15	75	65	169
2000		64	7	16	108	41	236
2001		12	21	30	409	44	516
2002		41	14	24	222	28	329
2003		6	31	34	47	9	127
2004		11	10	2	22		45
2005		5	13	3	17	4	42
2006			7	17	143	24	191
2007		1	26	4	21	4	56
2008		69	13	6	44	15	147
2009		48	22	23	65	11	169
2010		45	58	78	160	48	389
2011		37	17	3	34	29	120
2012		12	80	20	339	89	540
2013	129	7	64	68	139	44	451
2014		218	6	2	156	39	421
2015		77	71	23	88	20	279
2016		202	158	45	260	46	711
2017		134	74	46	207	48	509
2018		329	51	29	190	70	669
2019		68	48	29	289	83	517
2020		98	46	23	543	200	910
2021		176	74	62	225	20	557
Total	129	1696	1003	679	4275	1166	8948

Table 6. Food samples (bill loads, partial bill loads, and ground samples) obtained annually from rhinoceros auklets on Middleton Island from 1978 through 2021.

Year	No. samples	TotalMass (g)
1978	72	3109.2
1986	4	97.7
1990	17	199.4
1993	70	1407.2
1994	190	3680.1
1995	146	2217.1
1996	78	1488.0
1997	138	1707.6
1998	315	7816.6
1999	100	2688.3
2000	106	2537.8
2001	126	3888.6
2002	95	2706.7
2003	121	3461.6
2004	107	2889.9
2005	95	2749.3
2006	113	4393.8
2007	100	2470.0
2008	130	4514.9
2009	111	3079.4
2010	175	6297.6
2011	115	3430.8
2012	260	7011.6
2013	248	8732.3
2014	180	5920.0
2015	334	9351.0
2016	306	8988.5
2017	328	10,056.8
2018	210	6,989.0
2019	319	10785.9
2020	322	9691.0
2021	306	9606.4
All years	5337	153,964.1

Table 7. Time series of kittiwake productivity, dietary capelin and PDO index during the breeding season on Middleton Island from 1978 through 2021.

Year	Mean PDO index (Jun-Aug)	Productivity	Capelin in diet (Jun-Aug)
1978	-0.55	0.14	0.0000
1979	0.51	--	--
1980	0.17	--	--
1981	0.90	0.47	--
1982	0.06	0.30	--
1983	2.57	0.03	--
1984	-0.01	0.76	--
1985	0.69	0.04	--
1986	0.83	0.05	--
1987	1.86	0.00	--
1988	0.52	0.21	--
1989	0.43	0.00	--
1990	0.27	0.00	0.0500
1991	-0.40	0.22	--
1992	1.53	0.24	--
1993	2.46	0.01	--
1994	-0.09	0.32	--
1995	1.06	0.17	--
1996	0.58	0.60	0.0526
1997	2.63	0.32	0.0000
1998	0.05	0.42	0.1373
1999	-0.97	0.19	0.0452
2000	-0.76	0.99	0.5394
2001	-0.85	1.03	0.1677
2002	-0.02	0.97	0.2956
2003	0.84	0.50	0.2333
2004	0.44	0.20	0.0000
2005	0.69	0.37	0.0000
2006	0.25	0.47	0.0163
2007	0.46	0.42	0.2414
2008	-1.57	0.78	0.6462
2009	-0.25	0.20	0.3535
2010	-0.85	0.78	0.8322
2011	-1.43	0.50	0.6061
2012	-1.44	0.87	0.7634
2013	-1.02	1.00	0.8247
2014	0.73	0.45	0.0152
2015	1.65	0.21	0.0076
2016	1.27	0.08	0.0313
2017	0.33	0.22	0.0332
2018	0.08	0.31	0.0519
2019	0.83	0.50	0.1820
2020	-0.25	0.83	0.0287
2021	-1.39	0.43	0.1336

Table 8. Effects of supplemental feeding on laying dates, clutch sizes and overall productivity of black-legged kittiwakes on the Middleton tower since 1996.

| Year | Treatment effect (Fed - Unfed pairs) | | |
	Julian lay date	Clutch size	Chicks fledged
1996	-2.30	0.01	0.62
1997	-3.23	0.32	0.64
1998	-5.19	0.40	0.26
1999	-8.78	1.14	0.38
2000	-2.03	0.15	0.19
2001	-2.65	0.15	0.25
2002	0.79	0.10	0.00
2003	-4.58	0.14	0.41
2004	-2.87	0.41	0.79
2005	-6.67	0.19	0.66
2006	-7.09	0.34	0.67
2007	-4.90	0.24	0.35
2008	-3.13	0.19	0.12
2009	-4.40	0.20	0.55
2010	2.24	0.01	0.11
2011	-5.55	0.21	0.42
2012	-1.55	0.06	0.06
2013	0.15	0.13	0.04
2014	--	--	--
2015	-1.62	0.39	0.75
2016	-8.52	1.06	0.73
2017	-6.00	0.87	0.54
2018	-4.00	0.49	0.68
2019	-4.70	0.38	0.57
2020	0.10	0.02	0.21
2021	-6.55	0.22	0.57
Mean	-3.72	0.31	0.42

Table 9. Pearson correlations among the Pacific Decadal Oscillation (PDO) index (June to August), relative occurrence of dietary capelin, and kittiwake chick production on Middleton Island over 42 years between 1978 and 2021.

Variable	Statistic	Variable	
		Chick production	Capelin in diet
Capelin in diet			
	Pearson's r	0.637	---
	P (2-tailed)	<0.001	---
	n (years)	28	---
PDO (Jun-Aug)			
	Pearson's r	-0.575	-0.633
	P (2-tailed)	<0.001	<0.001
	n (years)	42	28

Rhinoceros auklet

Pelagic cormorant

Black-legged kittiwake
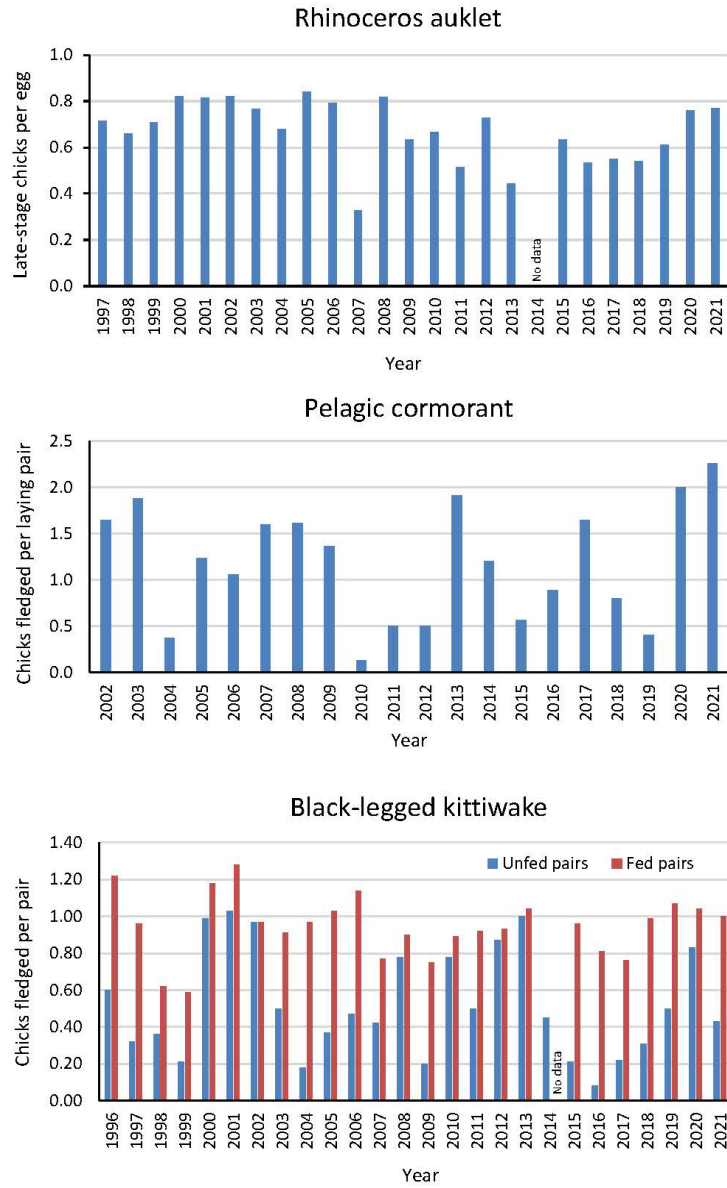
Figure 1. Annual production of offspring in three species of seabirds monitored on Middleton Island in the north-central Gulf of Alaska. Lower panel compares the breeding performance of kittiwakes subjected to supplemental feeding (ad libitum) at the nest site with control samples of naturally foraging pairs.

Pelagic cormorant

Black-legged kittiwake
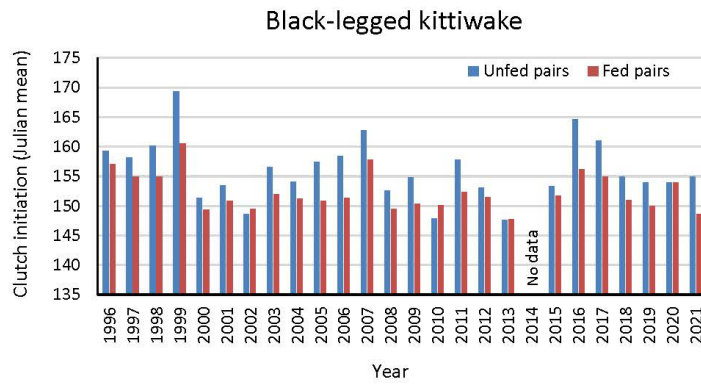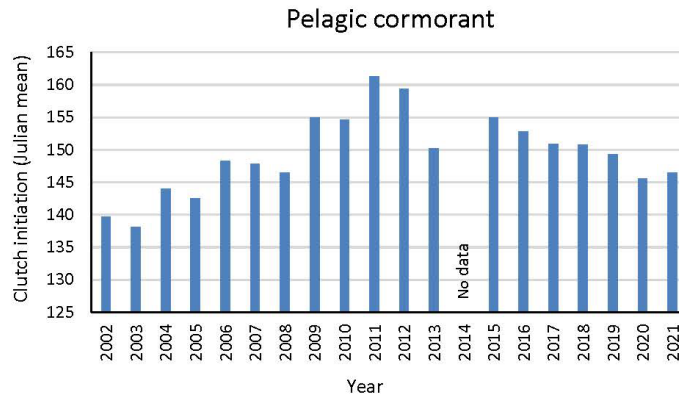
Figure 2. Breeding chronology of pelagic cormorants and black-legged kittiwakes on Middleton Island. On average, food-supplemented kittiwake pairs breed 4 days earlier than controls (lower panel).

1978-2021

All months

April

May

Jun-Aug
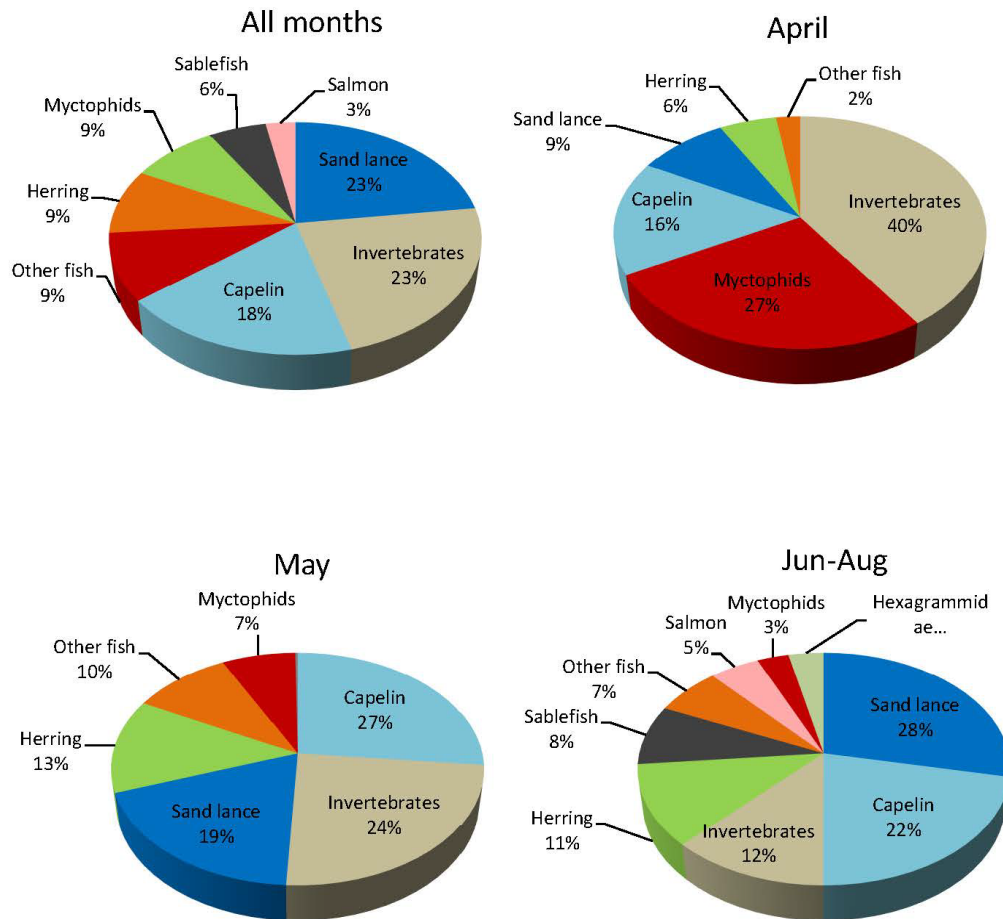
Figure 3. Overall composition of food samples obtained from black-legged kittiwakes (relative occurrence, April – August) on Middleton Island from 1978 to 2021.   .
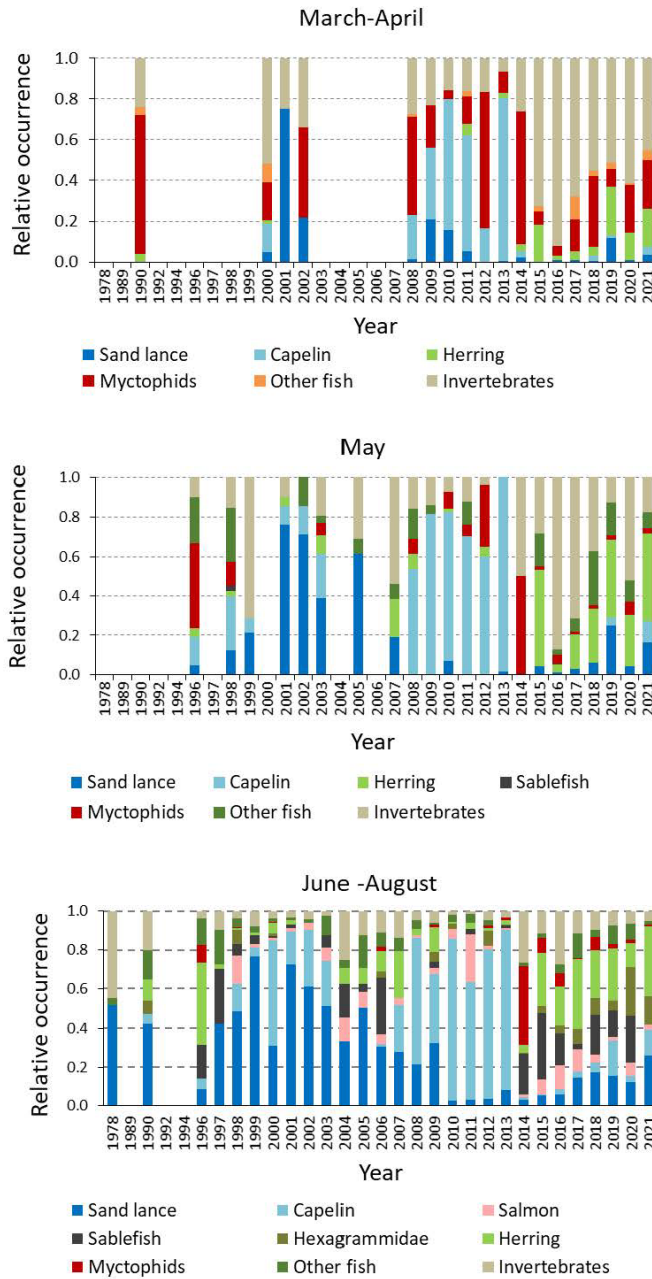
Figure 4. Interannual variation in kittiwake diet composition at three stages of breeding on Middleton Island, 1978 to 2021. Sample sizes as listed in Tables 4 and 5.

March - April

2012 (n = 10)

Myctophids 67%
Capelin 17%
Inverte-brates 16%
Amphipods 8%
Squid 8%

2013 (n = 121)

Myctophids 10%
Herring 3%
Other fish 1%
Capelin 79%
Invertebrates 7%
Amphipods 5%
Krill 1%
Squid 1%

2014 (n = 179)

Herring 3%
Other fish 2%
Inverte-brates 27%
Myctophids 65%
Capelin 3%
Amphipods 10%
Squid 13%
Other invertebrates 4%

2015 (n = 63)

Other fish 3%
Herring 18%
Inverte-brates 75%
Myctophids 7%
Polychaetes 31%
Squid 5%
Amphipods 10%
Krill 12%
Other invertebrates 14%

2016 (n = 135)

Other fish 1%
Herring 2%
Invertebrates 97%
Myctophids 5%
Squid 26%
Other invertebrates 3%
Velella 4%
Amphipods 13%
Polychaetes 46%

2017 (n = 87)

Herring 4%
Other fish 3%
Stickle-back 9%
Inverte-brates 68%
Myctophids 16%
Squid 17%
Amphipods 20%
Shrimp 16%
Isopods 2%
Copepods 2%
Polychaetes 11%

2018 (n = 197)

Capelin 3%
Other fish 3%
Herring 4%
Inverte-brates 55%
Myctophids 35%
Squid 30%
Amphipods 18%
Other invertebrates 1%
Shrimp 6%

2019 (n = 68)

Myctophids 9%
Other fish 4%
Pacific sand lance 12%
Inverte-brates 51%
Pacific herring 24%
Polychaetes 32%
Amphipods 12%
Squid 3%
Other invertebrates 3%
Shrimp 1%

Figure 5. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island from spring arrival through April in 2012-2019.

May
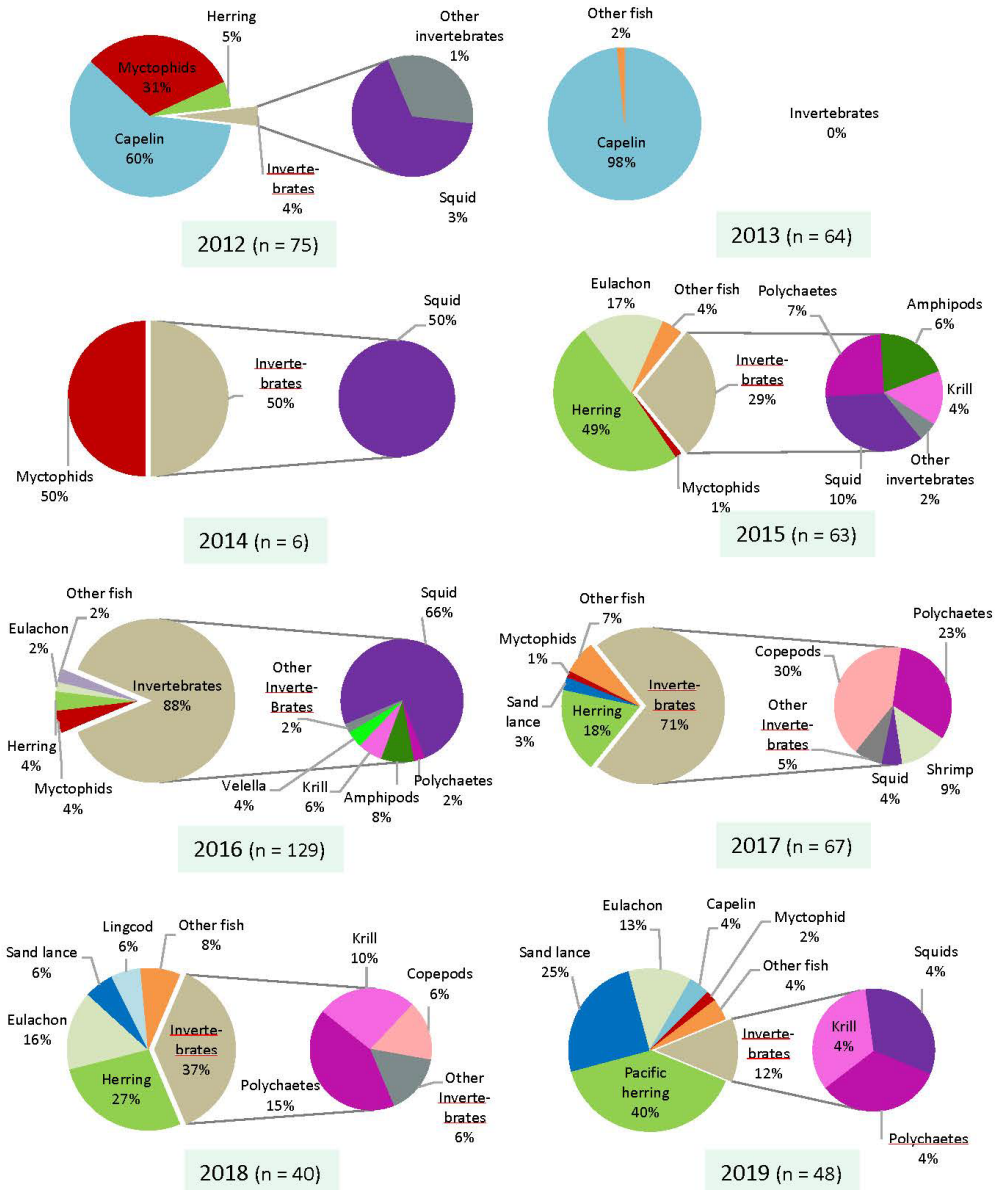
Figure 6. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island during May in 2012-2019.
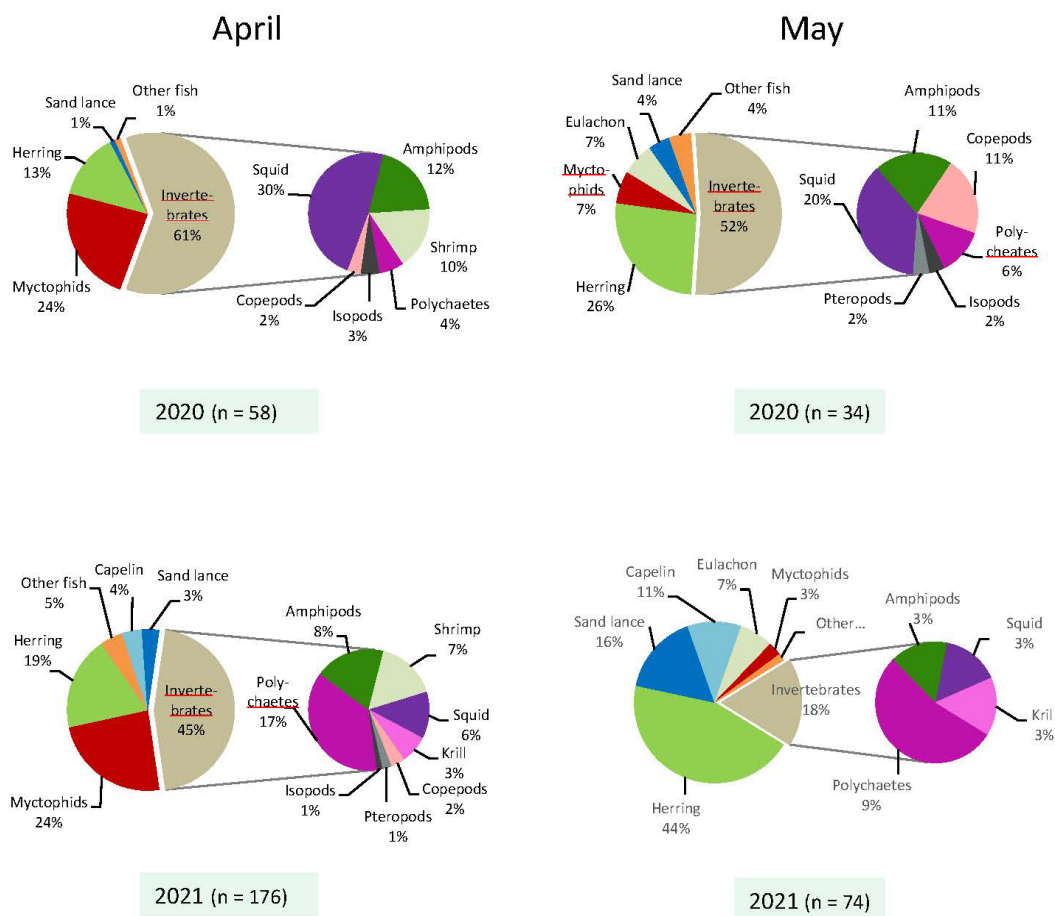
Figure 7. Variation in the relative occurrence and composition of fish and invertebrates in the diet of black-legged kittiwakes on Middleton Island during April and May, 2020-2021.

RHAU overall diet, 1978-2021

Sand lance 46%
Capelin 14%
Salmon 12%
Sablefish 10%
Greenling 9%
Herring 5%
Other 4%

n = 5,337 samples
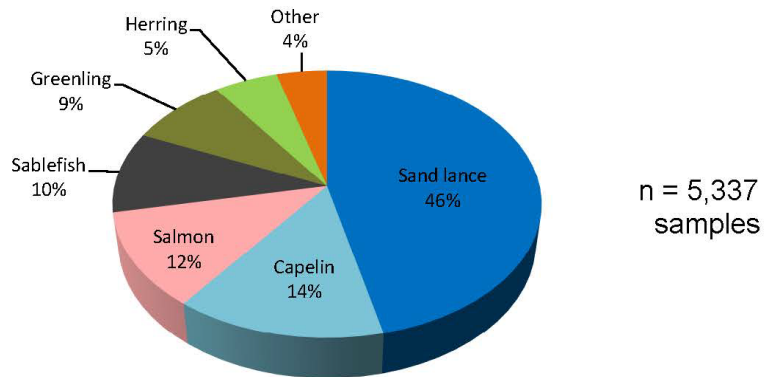
Figure 8. Overall composition of food samples obtained from chick-rearing rhinoceros auklets (% biomass, July-August) on Middleton Island from 1978 through 2021.

RHAU chick diet

Kittiwke diet Jun-Aug
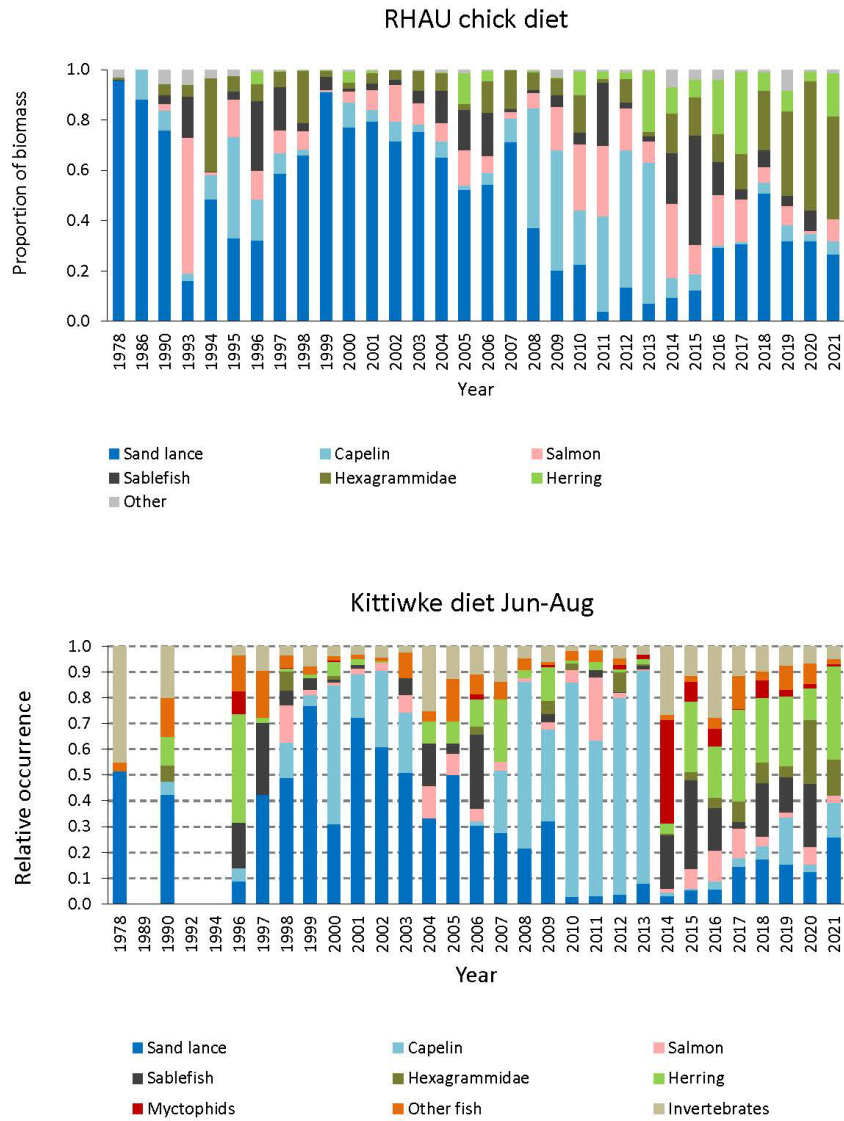
Figure 9. Interannual variation in diet composition of chick-rearing rhinoceros auklets on Middleton Island, 1978 to 2021 (upper panel), with a similar time series for black-legged kittiwakes (lower panel) for comparison. Sample sizes as listed in Tables 4, 5 and 6.
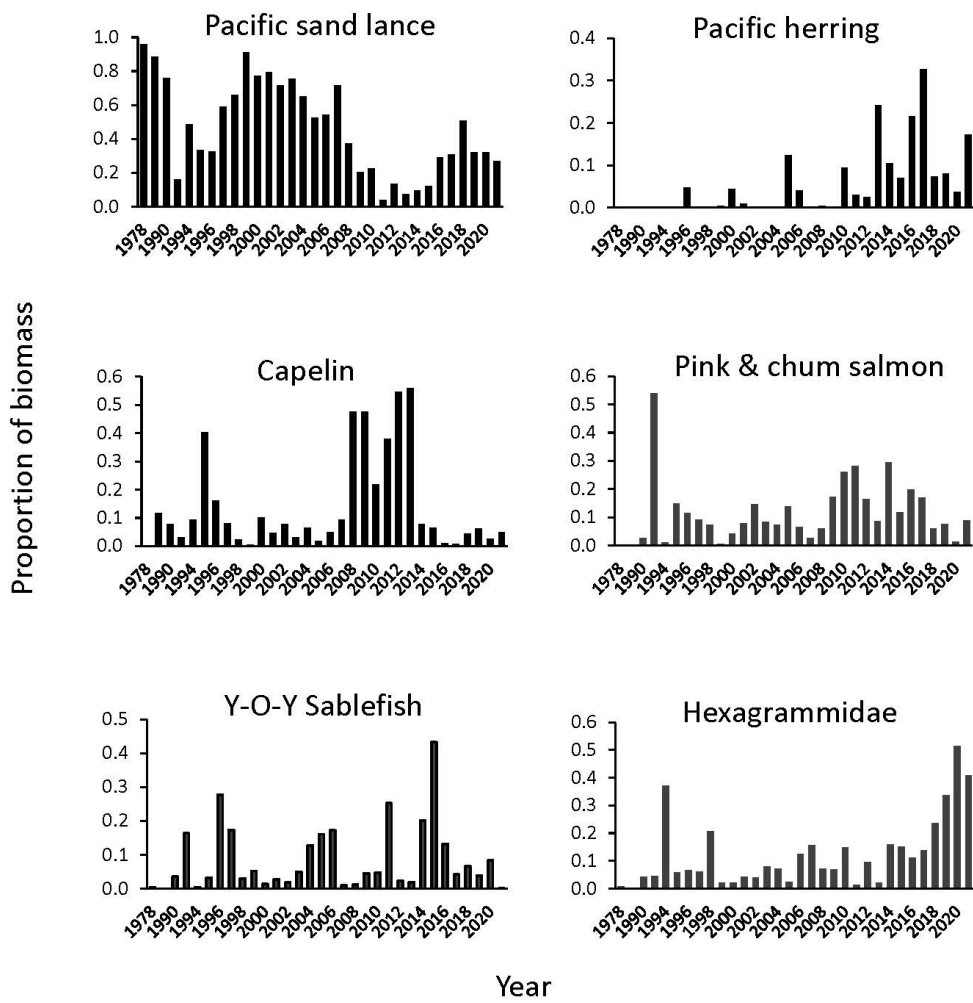
Figure 10. Indices of prey species occurrence in the nestling diet of rhinoceros auklets on Middleton Island from 1978 through 2021.
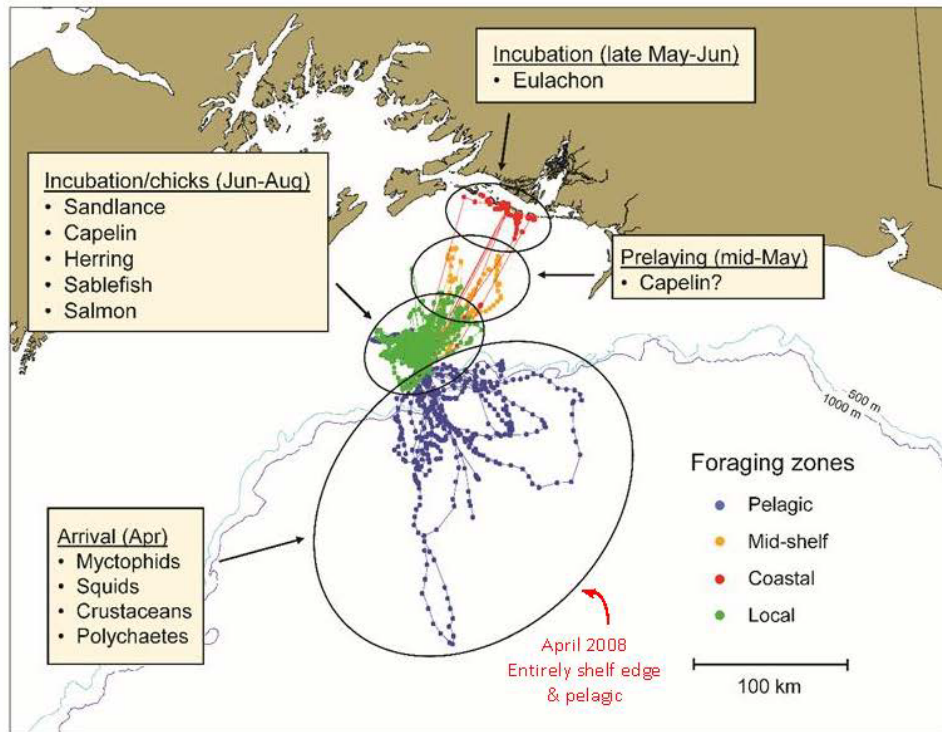
Figure 11. Seasonal shifts in foraging activity of black-legged kittiwakes from Middleton Island as revealed by deployments of GPS tracking devices in 2008.
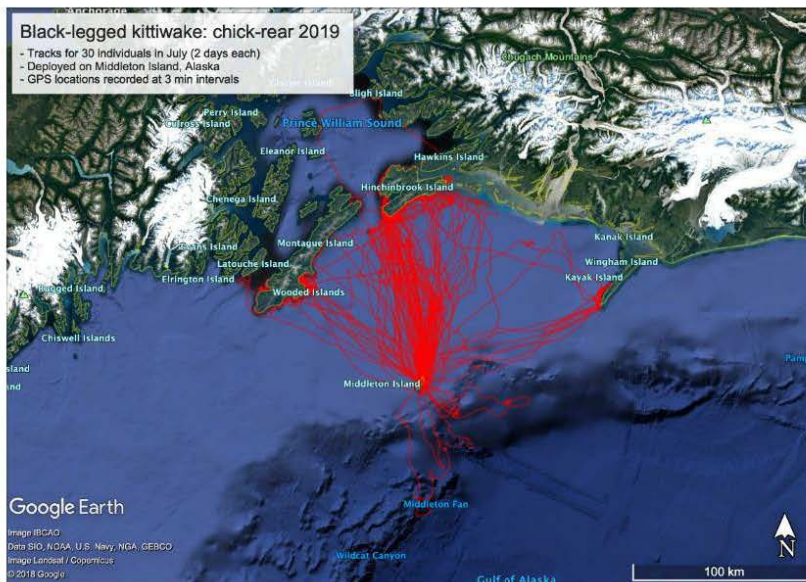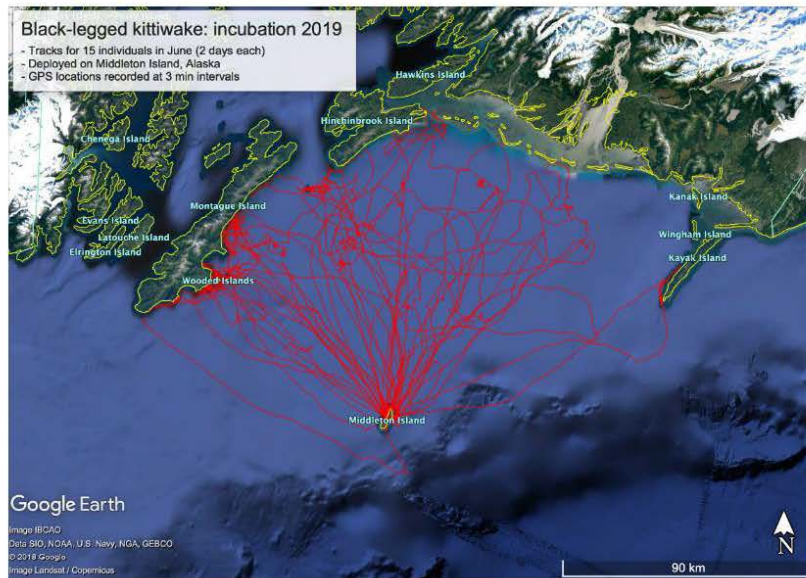
Figure 12. Flight paths of Middleton kittiwakes foraging during incubation (upper panel) and chick-rearing (lower panel) in 2019.
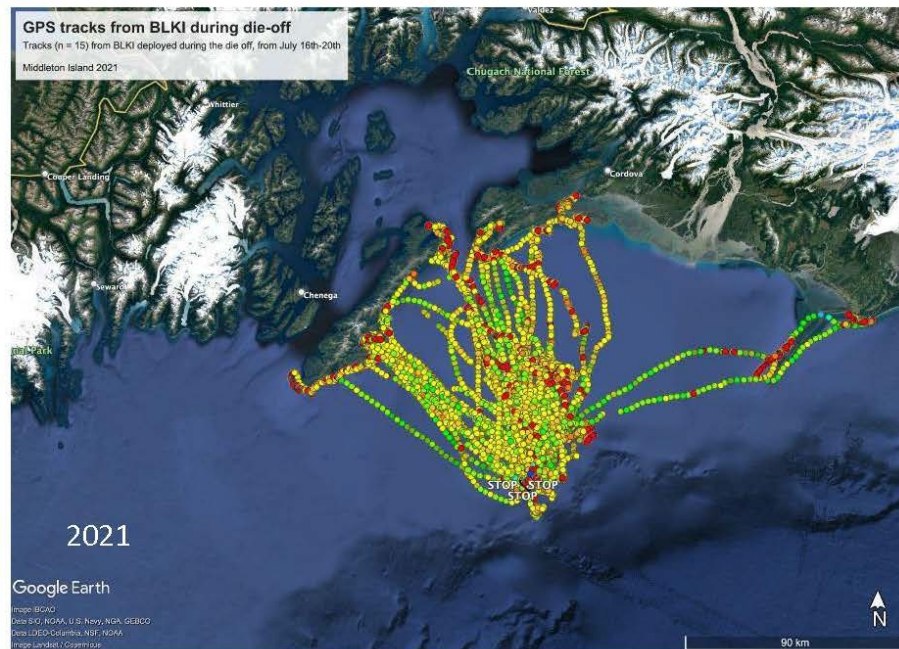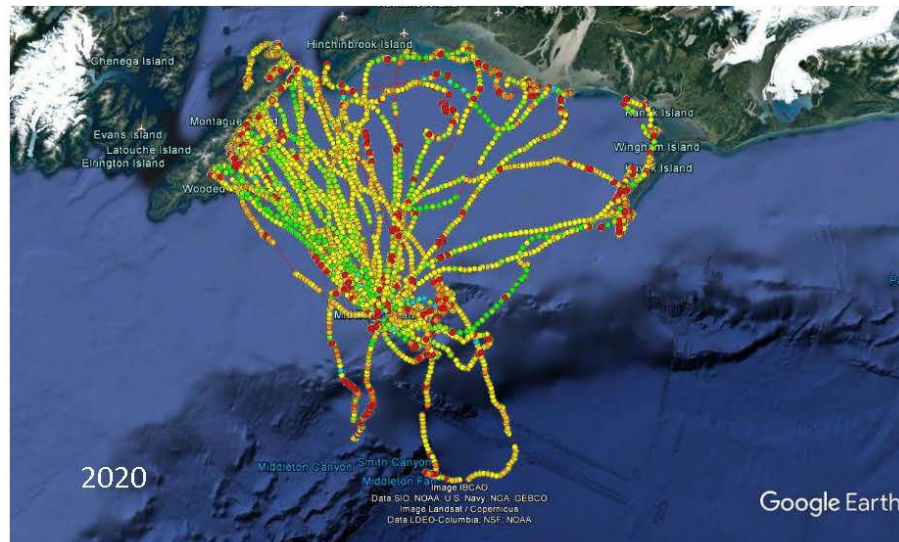
Figure 13. GPS tracking of foraging kittiwakes during the chick-rearing period in 2020 (upper panel, 11 individuals) and 2021 (lower panel, 15 individuals).
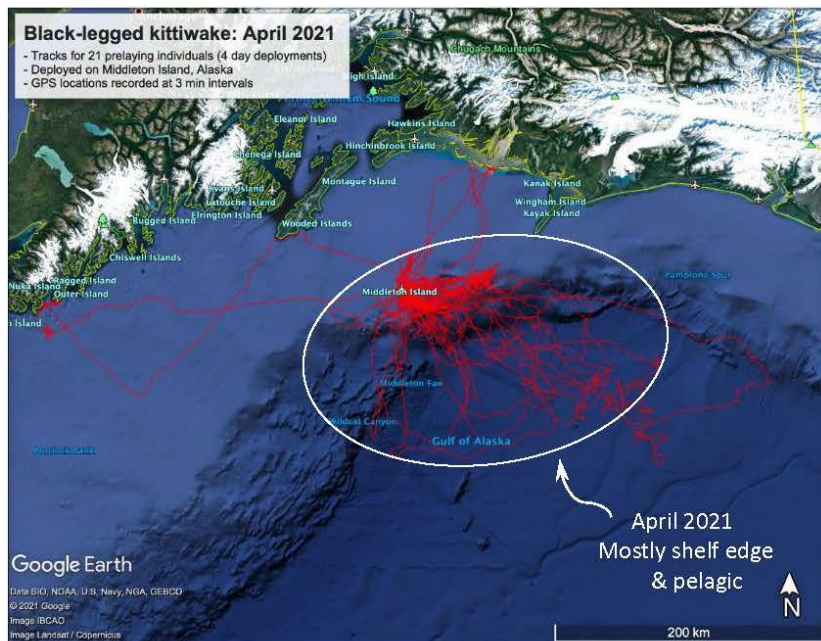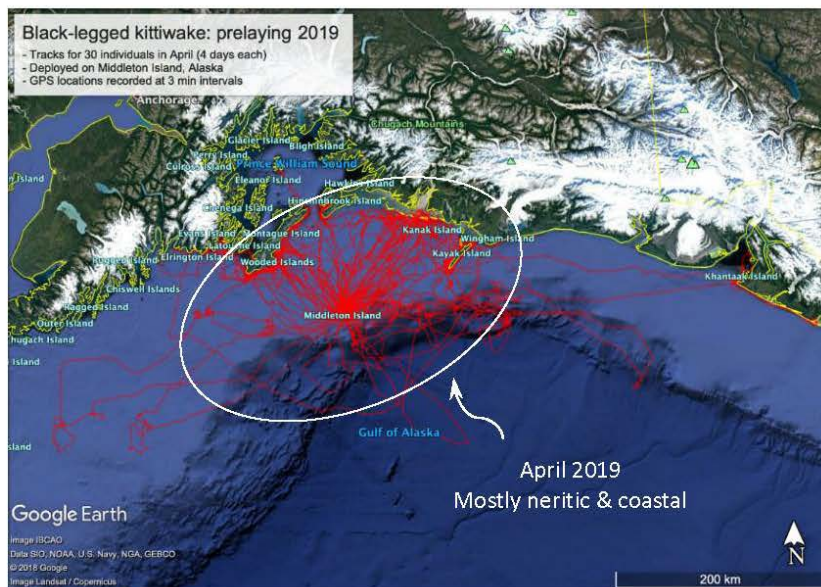
Figure 14. Contrasting patterns of foraging by Middleton kittiwakes during the pre-laying period in 2019 (upper panel) and 2021 (lower panel).
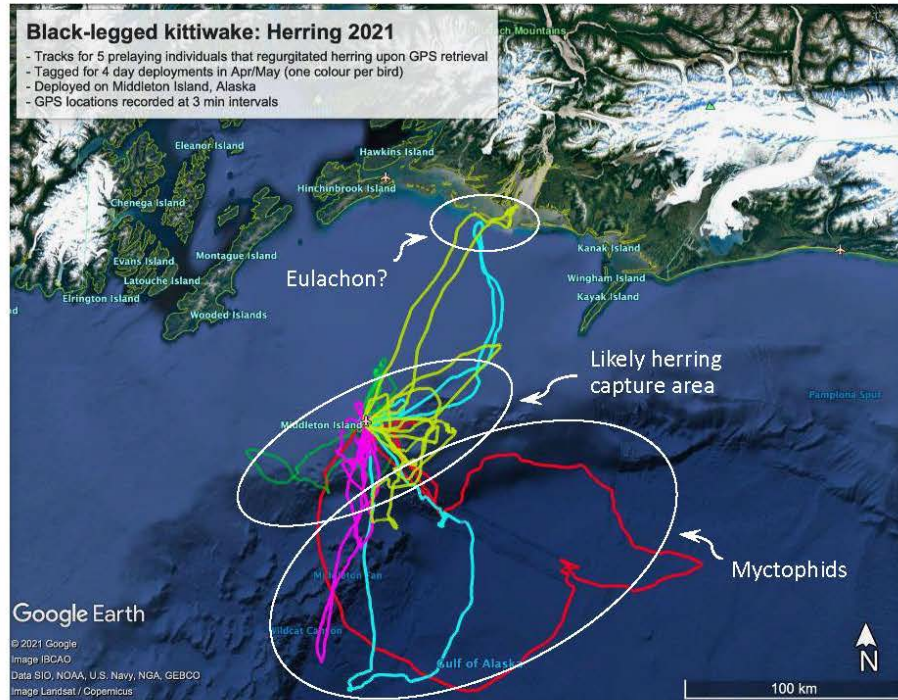
Figure 15. Apparent distribution of large (Age-1+) herring on the outer shelf in spring 2021 as indicated by movements of kittiwakes that regurgitated herring upon return to the Middleton tower.
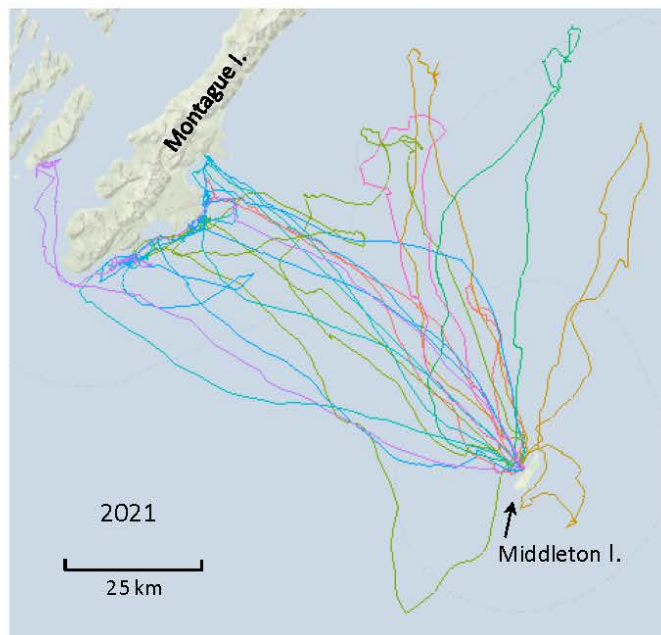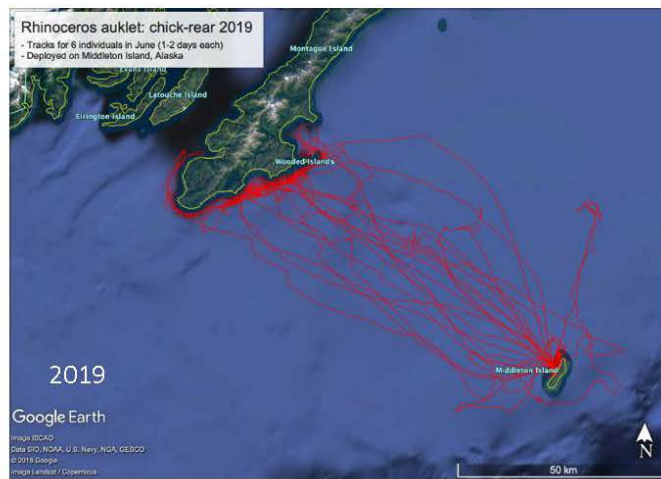
Figure 16. Foraging tracks of rhinoceros auklets during chick-rearing as revealed by GPS devices deployed on 6 individuals in 2019 (upper panel) and 14 individuals in 2021 (lower panel) on Middleton Island.
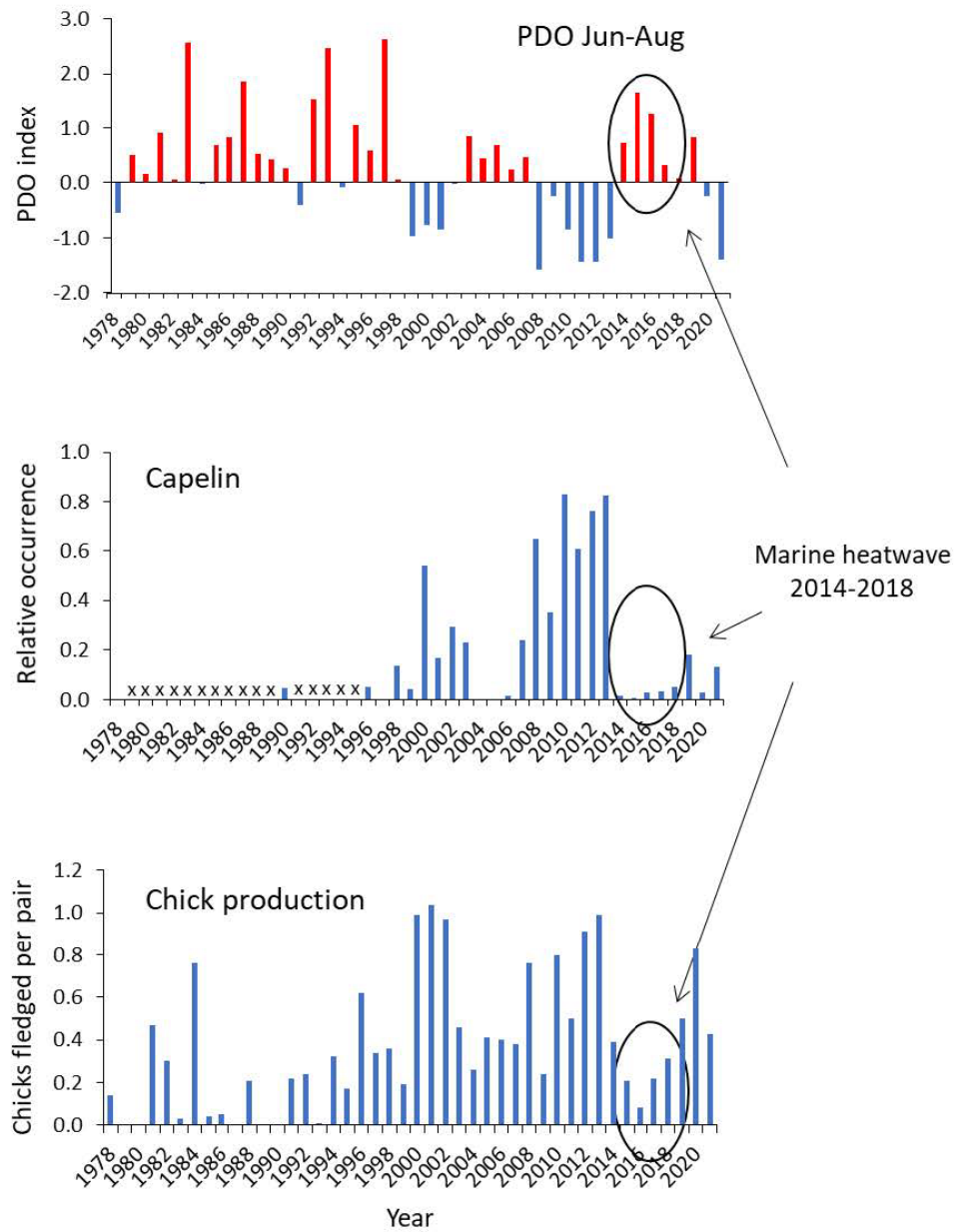
Figure 17. Relations among the Pacific Decadal Oscillation (PDO) index (June – August), relative occurrence of dietary capelin, and the annual production of kittiwake chicks on Middleton Island, 1978 to 2021. Missing data denoted by 'x'.

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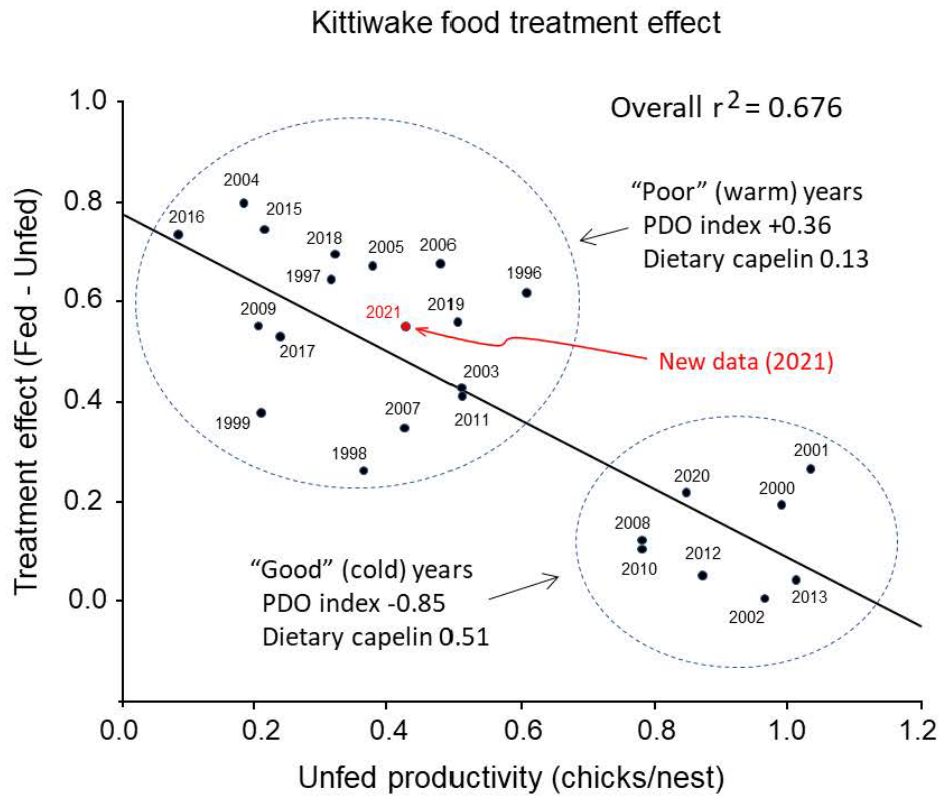
Figure 18. Effect of supplemental food treatment on kittiwake breeding performance on Middleton Island in 24 years since 1996. Productivity of unfed pairs is a proxy for quality of the foraging environment. Treatment effect is the difference in productivity between supplementally fed and unfed pairs. "Bad" years are characterized by warm ocean conditions (PDO index June-August), a low proportion of capelin in the diet, and a marked effect of food treatment on kittiwake production. "Good" years have cool ocean conditions, a higher proportion of dietary capelin, and reduced or no difference in breeding performance of fed and unfed pairs.

RHAU Nest Box Outside Dimensions

14 in
30 in
6 in
12 in
18 in
8 in
10.5 in
24 in
6 in

1/2 in. plywood
1 x 1 in. square dowels
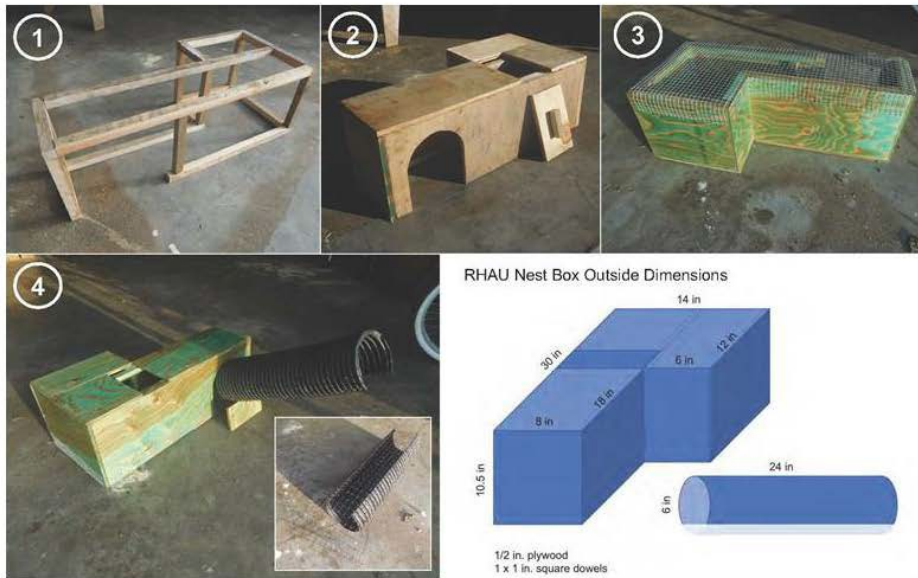
Appendix Figure 1. Nest boxes for rhinoceros auklets and tufted puffins are being installed at the Middleton station to facilitate future research and monitoring of those species.
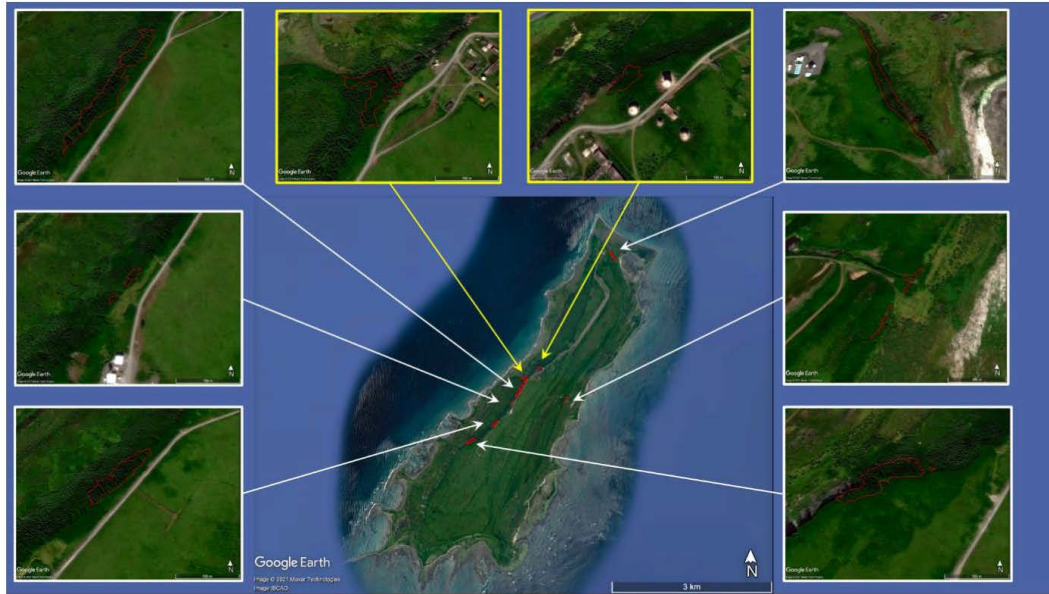
Appendix Figure 2. Mapping of rhinoceros auklet nesting habitat on Middleton Island, Alaska, in spring 2021. Red polygons indicate perimeters of eight different sub-colonies. Two sub-colonies are located on ISRC property (yellow arrows).