CHANGES IN BENTHIC PREY AVAILABILITY AND QUALITY SUGGEST LESS FAVORABLE FORAGING CONDITIONS FOR THREATENED STELLER'S EIDERS (*POLYSTICTA STELLERI*) MOLTING AT IZEMBEK LAGOON, ALASKA

by

Anastasia M. Maliguine, B.S.

A Thesis Submitted in Partial Fulfillment of the Requirements

for the Degree of

Master of Science

in

Marine Biology

University of Alaska Fairbanks

May 2024

APPROVED:

Dr. Tuula E. Hollmén, Committee Chair
Dr. Courtney L. Amundson, Committee Member
Dr. Brenda H. Konar, Committee Member
Dr. Lara Horstmann, Chair
    Department of Marine Biology
Bradley Moran, Dean
    College of Fisheries and Ocean Sciences
Richard Collins, Director
    Graduate School

Abstract

Izembek Lagoon, located in the Alaskan southern Bering Sea, is designated as critical molting and wintering habitat for the Alaska-breeding population of Steller's eiders (*Polysticta stelleri*), listed as Threatened under the United States Endangered Species Act. During the nonbreeding season, the lagoon also hosts a large proportion of the Pacific population of Steller's eiders that nest along the coast of northeastern Russia, and the lagoon is an important stopover site for many other species of migratory water birds. Since the early 1980s, there has been a decline of Steller's eiders in their known nonbreeding range in the southern Bering Sea, but especially in Izembek Lagoon during their remigial molt in the fall. The cause of this decline is unknown; however, in recent years, higher sea temperatures have been observed in Izembek Lagoon and warming ocean temperatures have been associated with shifts in benthic community structure elsewhere. If forage conditions are less favorable in Izembek Lagoon, Steller's eiders may need to redistribute to other locations, or the population at Izembek Lagoon may decline due to reduced survival. To determine if forage conditions have changed, we replicated a 1998 benthic sampling effort in fall of 2018 and 2019 to understand if prey availability has become less favorable to Steller's eiders during their molt in Izembek Lagoon. We compared forage conditions based on the relative biomass (%), overall biomass (g/m^2), and size (mm) of organisms belonging to the marine benthic groups: Bivalvia, Gastropoda, Crustacea, and Polychaeta between the two time points. The results suggest a shift in these taxa with an associated change in their biomass and size. The community shifted from being dominated by bivalves in 1998 to more predominantly polychaetes in 2018 and 2019. In addition to a significant reduction of bivalve and crustacean biomass in 2019 as compared to 1998 ($p = 0.04$, $p = 0.02$, respectively), bivalves and gastropods were significantly smaller ($p < 0.01$, $p < 0.01$, respectively). The decline of Steller's eiders' use of this critical habitat may reflect shifting benthic prey availability. As it has been suggested that Steller's eiders may prefer hard-shelled prey (e.g., bivalves, gastropods) and larger sized bivalves during the molt period specifically, contemporary foraging conditions at Izembek Lagoon may be less favorable or insufficient for supporting historical numbers of Steller's eiders during an energetically taxing time in their annual cycle. Therefore, the molting Steller's eider population at Izembek Lagoon may have difficulty recovering to historical numbers if available forage conditions are of inadequate quality and abundance.

Acknowledgements

This research was made possible by many funding and supporting agencies. Firstly, the North Pacific Research Board (NPRB) Core Project #1814 supported funding for data collection, travel, laboratory analysis, and so much more. I would like to thank the NPRB team who led this project forward: Dr. Tuula Hollmen, Dr. Paul Flint, Dr. Peter Winsor, Sadie Ulman, David Ward, Tim Bowman, David Safine, Jason Schamber, and Tyler Lewis. The Izembek National Wildlife Refuge staff housed my colleagues and I, and supported field logistics for many trips; their collaboration was instrumental for this project. All benthic sampling was conducted under appropriate permits with the State of Alaska (Special Area Permits FH19-II-0069-SA, FH22-II-0128-SA; Use of Motorized Vessels in Special Area: FH21-II-0079-GP-SA) and U.S. Fish and Wildlife Service (Special Use Permits 2018-10, 2021-10). The Alaska SeaLife Center staff and interns spent countless hours processing and sorting through benthic samples in the laboratory, which was an extraordinary task. Support for my graduate stipend, education, and travel was funded by the NPRB Graduate Student Award, the Sea Duck Joint Venture Graduate Student Research Award, the University of Alaska Fairbanks (UAF) Foundation Angus Gavin Migratory Bird Grant, the Calvin J. Lensink Memorial Award, the UAF Graduate School's Thesis Completion Award, the Ken Turner Memorial Scholarship, the Washington Brant Foundation Scholarship, the Dieter Family Marine Science Research Scholarship, and the Dennis Raveling Scholarship. I want to acknowledge travel funding I received from Alaska NSF EPSCOR #OIA-1757348 and the State of Alaska to present my findings at the North American Duck Symposium. I would also like to thank the UAF Marine Biology Department for covering a tuition credit. I am so thankful to these funding sources for supporting me as a student.

My thesis would not have been possible without the contribution of my committee members, Dr. Tuula Hollmen, Dr. Courtney Amundson, and Dr. Brenda Konar, who all provided important feedback on the content of this thesis and proposals to support this work. I am incredibly grateful to my advisor, Tuula, for initially letting me help on her project in 2019 and introducing me to many connections in this field. Thanks for accepting me as a student on this project in 2021 and advising me throughout this journey. I appreciate her passion about the ecology and conservation of Steller's eiders, and I am honored to have had opportunities to learn from and work with her as an expert in this field of study. I appreciate her continuous support. Courtney spent many hours regularly meeting with me the last several semesters. In the absence of taking classes, these meetings helped me stay motivated and her statistical guidance was invaluable. Brenda helped me simplify complicated ideas and stay on track to completion. Her professional perspective on benthic systems was vital for this project, and I always appreciated her feedback.

As mentioned earlier, many supporting agencies made completion of this project possible. I want to specifically thank the staff at Izembek National Wildlife Refuge: Alison Williams, Leticia Melendez, Matt Nielson, Maria Fosado, James Fess, and Patrick Fitzmorris. Their collaboration was instrumental for collecting benthic samples by allowing use of their facilities, boats, and gear, and guiding the logistical planning throughout COVID-19 challenges. I want to specifically thank Matt Nielson, Alison Williams, James Fess, Matt Wilson, Eliana Ardila Ardila, Jeff Wasley, Peter Winsor, and Joel Markis for assisting with the field work associated with this project. I also want to thank the staff and interns from the Alaska SeaLife Center. Sadie Ulman and Jenna Schlener both led and oversaw the laboratory team in Seward for processing the many benthic samples that were collected and making sure data was entered and proofed. The interns spent immeasurable hours sorting through samples and identifying organisms under microscopes and entering and checking data, which can be tedious and time-consuming work. Thanks to the help of many people assisting in the laboratory, including Wynne Larson, Jessica Pollack, Sean Paulin, Sam Kent, Kara Bolander, Riley Temkin, Elisabeth Rintamaa, Sam Artaiz, Emmylou Kidder, Stephanie Gunter, and Katrina Counihan. Also, I want to thank Aleutia Peters from UAF for helping process and sort benthic samples and enter laboratory data.

Equally important to the development of my thesis was Dr. Margaret Petersen and Dr. Paul Flint, former United States Geological Survey (USGS) Alaska Science Center Research Biologists, who both set the foundation for this temporal comparison of forage habitat conditions at Izembek Lagoon for Steller's eiders by initially collecting and analyzing benthic samples in 1998. Works by Dr. Petersen and Keith Metzner have served as the basis of our knowledge for molting Pacific Steller's eiders along the Alaska Peninsula, and the interpretations of my findings are more insightful because of their scientific contributions. I also want to thank Dr. David Ward, USGS Alaska Science Center Emeritus Research Fish Biologist, who led the continuous monitoring of the eelgrass beds at Izembek Lagoon for many years; he is an expert on the eelgrass system at Izembek Lagoon and shared unpublished data he collected there with me.

There are several other individuals I would like to acknowledge who have supported me as a student. I want to thank Dr. Jim Lovvorn, Professor at Southern Illinois University, who enthusiastically shared suggested readings and discussed my research findings at great length with me. I want to thank the U.S. Fish and Wildlife Service Fairbanks Field Office (Neesha Stellrecht and Nathan Graff) for giving me the opportunity to work in Utqiaġvik (formerly Barrow), Alaska on the Steller's Eider Project during the summer of 2022; I learned so much about the breeding ecology of Steller's and spectacled eiders from this opportunity. I also want to thank Dr. Micah Miller, who provided continuous support, had insightful conversations with me about eider ecology, and gave me feedback on practice presentations. I also want to thank Dr. Katrin Iken for her thoughtful feedback in the proposal writing stage. I learned so much from her course, and I believe the knowledge I gained from it helped produce successful proposals when applying for funding. I also want to thank Dr. Chris Latty and Dan Skalos for writing letters of support for my proposal applications. Christina Sutton, the CFOS Academic Program Manager, was extremely helpful throughout my time as a student and provided guidance.

Table of Contents

List of Figures

List of Tables

Introduction

Steller's eiders (*Polysticta stelleri*) have been described as the rarest sea duck in the world, and their population has declined precipitously over the last 40 years across breeding, staging, and wintering areas (Bustnes & Systad, 2001; Kertell, 1991; H. M. Wilson, 2019b). The specific causes for these declines are largely unknown; the main recognized threats to the species are effects of climate change, habitat loss relating to exploitation of oil and gas along their breeding range, and lead poisoning (BirdLife International, 2018; U.S. Fish and Wildlife Service, 2019). The global population, consisting of Pacific (>80%) and Atlantic populations (Rosenberg et al., 2014), is considered "Vulnerable" by the International Union for Conservation of Nature (BirdLife International, 2018). The species is a "Category 2 Decreasing Species" in Russia (Ministry of Natural Resources of the Russian Federation, 2020) and limited work studying Pacific Steller's eiders in Russia has occurred. The Alaska-breeding population was listed as "Threatened" in 1997 (U.S. Fish and Wildlife Service, 1997), and the only extant breeding population occurs on the North Slope of Alaska, which represents less than 1 percent of the Pacific population (Hodges & Eldridge, 2001).

Every fall, Pacific Steller's eiders (eiders hereafter) migrate from breeding areas along the north-eastern Arctic coast of Russia and Utqiaġvik (formerly Barrow), Alaska (Fig. A1), to productive shallow, nearshore habitats and allocate energy to the molting process, in which the eiders drop and re-grow their body and remigial (flight) feathers and are flightless for approximately three weeks (Petersen, 1980). Eiders have been documented molting in Russian coastal waters off eastern Chukotka, the Kamchatka Peninsula, and the Commander Islands in the western Bering Sea (Fig. A1; Kistchinski, 1973; U.S. Fish and Wildlife Service, 2019). In Alaska, eiders have molted in coastal waters from St. Lawrence Island to Nunivak Island and the Yukon-Kuskokwim Delta to the southern Alaska Peninsula and Kodiak Island (Fig. A1; Dau, 1987; Jones, 1965; Rosenberg et al., 2016), with the highest concentration of Pacific Steller's eiders molting along the Alaska Peninsula (Petersen, 1981), where both Russia- and Alaska-breeding populations intermix. In 2001, four marine areas in Alaska (Izembek Lagoon, Nelson Lagoon, Seal Islands, and Kuskokwim Shoals; Fig. 1) were designated as critical habitat for the Alaska-breeding population by the U.S. Fish and Wildlife Service (U.S. Fish and Wildlife Service, 2001), and they are important molting locations for Steller's eiders in the fall. Combined eider abundance counts from fall aerial surveys conducted across the Alaska Peninsula during the molting period showed significant decline—from 135,000 eiders observed in 1979 (Petersen, 1981), to recent surveys (2012-2016) observing between 30,000-70,000 eiders (Williams et al., 2016). Izembek Lagoon and Nelson Lagoon (Fig. 1) have been considered two of the most important molting locations for the Pacific population of

Steller's eiders (Dau et al., 2000), and banding studies show strong site-fidelity to these lagoons (Flint et al., 2000). Specifically, Izembek Lagoon was previously identified as the most important molting location used by adult females among the major molting sites along the Alaska Peninsula (Petersen, 1981). Izembek Lagoon contains some of the largest eelgrass (*Zostera marina*) beds in the world (Ward et al., 1997), which are thought to support a rich and diverse benthic food supply for eiders (Metzner, 1993), as well as other migratory waterfowl (Petersen, 1981).

The bulk of Steller's eiders' diet during the nonbreeding season in Izembek Lagoon has historically been composed of benthic marine invertebrates from within Polychaeta, Crustacea, Bivalvia, and Gastropoda, ranging in size from 3 to 22 mm (Metzner, 1993; Petersen, 1980). The opportunistic and diverse diet of eiders suggests that prey may be consumed based on availability (Metzner, 1993; U.S. Fish and Wildlife Service, 2019). Besides overall abundance of prey, the interaction of other factors, such as prey digestibility, size, size-dependent nutrient content, and burial depth, could be important for understanding quality of benthic prey available for eiders, like for other sea ducks (Richman & Lovvorn, 2003), when evaluating long-term benthic change. Steller's eiders are smaller-sized sea ducks, having greater energy and nutrient requirements relative to their body mass than larger eider species (*Somateria spp.*), and a lower capacity to withstand prolonged periods without food (Ouellet et al., 2013). Energetic costs are thought to be at their highest during remigial molt, as the molting of the remiges (flight feathers) overlaps with molting of body plumage, and ducks are typically flightless, have an impaired diving capacity, and have reduced insulation (Howell et al., 2003; Savard & Petersen, 2015). To offset the expense of regrowing feathers (which are mostly made of proteins), eiders can meet energetic requirements by reducing their energy expenditure and relying on highly productive areas with abundant and high-quality prey (Savard & Petersen, 2015). A previous study conducted in Nelson Lagoon, Alaska, a lagoon largely characterized by its high density of blue mussels (*Mytilus edulis)*, found that Steller's eiders modified their diet during this time by feeding primarily on these bivalves throughout remigial molt and incorporated more crustaceans in their diet again after flight was regained (Petersen, 1981). Similarly, at Izembek Lagoon, relative consumption of bivalves and gastropods was highest for molting birds, and eiders increased their consumption of shell-free prey (crustaceans) following the molt period (Metzner, 1993). Flightless Steller's eiders may minimize the high energy expenditure utilized when diving by instead foraging for prey that settle on the eelgrass leaf blades at the water surface at Izembek Lagoon. Other eiders, such as spectacled eiders (*Somateria fischeri*), which also occur in the Bering Sea, have undergone shifts in their core distribution within molting areas, and their distribution during the molting period likely reflects the distribution of preferred bivalve prey (Sexson et al., 2016). Therefore, the abundance and quality of marine invertebrates seem to be especially important for eiders while undergoing the remigial molt, and shifts in benthic prey abundance or community composition likely have consequences to eider body condition or survival.

The benthic ecosystem of the Bering Sea is vulnerable to species loss or regime shifts as a response to environmental variation (Grebmeier et al., 2006a; Liu et al., 2019). A reduction of sea ice and increased air and ocean temperatures have coincided with major ecosystem shifts observed in the Northern Bering Sea, resulting in less benthic prey available for other sea ducks (Grebmeier et al., 2006b). Current forage conditions for Steller's eiders in Izembek Lagoon have not been assessed; however, a recent assessment of Important Bird Areas (Smith et al., 2019) projected substantial declines of benthic infauna in Izembek Lagoon in coming decades associated with warming seawater temperatures and sea ice loss. Within the last decade, some of the warmest September average seawater temperatures recorded in this lagoon occurred in the years 2014, 2016, 2018, and 2019 (Ward unpubl. data, 2007-2021), and warming ocean temperatures have been associated with shifts in benthic community structure elsewhere (Schiel et al., 2004). The shallow waters in the lagoon are already subject to warmer temperatures, especially in eelgrass-laden tide pools at low tide (Cooper, 1989; McRoy, 1966; Metzner, 1993). At critical molting locations, such as Izembek Lagoon, warming temperatures could have major impacts on the benthic invertebrates that eiders rely on during this vulnerable stage of their annual cycle. Less favorable forage conditions during Steller's eiders' molt may result in declines in eider numbers in the lagoon, due to dispersal to other molting areas or lower survival. Furthermore, low annual survival rates of Steller's eiders in Izembek Lagoon have been associated with warming events (Frost et al., 2013). The average count of eiders observed at Izembek Lagoon during the fall aerial surveys has declined significantly; between 1980-1988 approximately 35,000 eiders (S.D. = 22,700) were observed and between 2009-2018 approximately 5,800 eiders (S.D. = 2,015) were observed (Wilson, 2019; Fig. 2). The proportional change in use of Izembek Lagoon among other molting areas along the Alaska Peninsula from 1979 surveys (43%) (Petersen, 1981) to recent (16%) (Williams et al., 2016) suggests that redistribution or lowered survival is occurring, concurrent with the decline of the whole Pacific population (BirdLife International, 2018). Marine factors affecting the quantity and quality of food (e.g., nearshore shallow habitat, eelgrass habitat) (U.S. Fish and Wildlife Service, 2019) have indirect implications for eider body condition and their survival likelihood and are likely influential to other stages of the annual cycle outside of the molting or wintering stages.

The overall goal of this study was to determine if benthic prey availability has changed coincident with the observed eider decline at Izembek Lagoon. Changing benthic prey composition, biomass, and/or size may help explain observed declines of eiders using Izembek Lagoon. This study analyzed prey availability for benthic groups: Polychaeta, Crustacea, Bivalvia, and Gastropoda, which are recognized as the most common prey groups of Steller's eiders during the nonbreeding season (Metzner, 1993). Benthic surveys were conducted in 2018 and 2019 and compared to historical data from 1998 to examine changes in benthic prey metrics (community composition, relative biomass, overall biomass, and size) between the two time points. Furthermore, results of this study will provide a contemporary assessment of benthic prey availability in a critical habitat for Steller's eiders that can inform future status assessments (i.e., U.S. Endangered Species Act Species Status Assessment or 5-year reviews) and Steller's eider management decisions for recovery.

Methods

Study area

Izembek Lagoon (55°18'57" N, 162°50'43" W) is a 48 km long, shallow embayment of the Bering Sea, located on the north side of the Alaska Peninsula near Cold Bay, Alaska (Fig. 1). The lagoon lies within the boundaries of Izembek National Wildlife Refuge and Izembek State Game Refuge, with a total area of approximately 322 km^2 (Bowman et al., 2022). Izembek Lagoon is characterized by shallow mudflats, intertidal eelgrass beds, and deep channels, and is sheltered from the ocean by long, narrow, partially vegetated barrier islands and spits (Petrich et al., 2014; Ward et al., 1997). Much of the lagoon is < 2 m deep, while the tidal range in the lagoon is greater than 1.5 m (Petrich et al., 2014). In the channels, water depths can be as deep as 10 m, with depths greatest in openings among main points and the barrier islands, where water flows between the lagoon and the Bering Sea (Alaska Department of Fish and Game, 2010). Izembek Lagoon has a polar maritime climate denoted by cool temperatures (-4-16 °C), high winds, and frequent precipitation and cloud cover (Alaska Department of Fish and Game, 2010). The nearby weather station at the Cold Bay Airport (ID: USW00025624) reports wind speeds with an annual mean of 26 km/h (absolute max = 153 km/h; 1971-2020) (NOAA National Centers for Environmental Information, 2023) and a mean annual precipitation of 107 cm (based on data between 1991-2020) (Menne et al., 2012a; Menne et al., 2012b). Salinity in the lagoon varies from 10-37 psu by location (lower salinities near freshwater inputs), but typically ranges from 26-32 psu (McRoy, 1966; Ward, 2021). Water temperatures in the lagoon range between 6-18 °C and average close to 11 °C in September (Ward, unpubl. data) when eiders arrive to molt after the breeding season. In the summer months, water temperatures can be 1-10 °C higher in the shallow eelgrass beds than the deeper channels (McRoy, 1966). In the winter, there is interannual variability in ice conditions at Izembek Lagoon, and ice extent in the lagoon is largely correlated with the position and strength of the Aleutian Low-Pressure System (Petrich et al., 2014). Izembek Lagoon is often ice-free, but ice can cover >75% of the lagoon for 1-2 months between December and March (Ward et al., 1997).

Izembek Lagoon is characterized for its extensive eelgrass beds, which make up 50-75% of the lagoon (168.16 km^2) and are typically found in soft-bottom substrates (Hogrefe et al., 2014). The mean substrate depth (i.e., depth of silt and clay layers until hitting sandy bottom) for the lagoon is 7 cm, and substrate in the lagoon is made up of mud (69%) and sand (31%) (Hogrefe et al., 2014). The dominant sediment type is dark basaltic sand, primarily fine- to very-fine-grained (2-4 phi) between the sand flats and eelgrass beds (McRoy, 1966). The percentage of silt and clay (4-12 phi) sediment types is larger in the eelgrass beds and channel bottoms (8% and 18%, respectively) than in sand flats (<1%) (McRoy, 1966). Eelgrass is a foundation species, forming important habitat that stabilizes and enriches sediments, and provides important nursery and habitat functions for many estuarine organisms (Phillips, 1984). Eelgrass growth occurs primarily during the summer, followed by senescence and sloughing of the leaves in the fall (McConnaughey, 1978). Some of the eelgrass-associated invertebrates found settling on, clinging to, or crawling on blades of eelgrass are: *Caprella* shrimp, gastropods (*Margarites* spp., *Lacuna* spp.), bivalves (*Turtonia minuta*), and polychaetes (McConnaughey, 1978; Metzner, 1993; Ward & Amundson, 2019).

Benthic sample collection and laboratory analysis

Between September 28th and October 1st, 1998, the U.S. Geological Survey (USGS) collected 32 benthic samples among three areas of Izembek Lagoon, where high concentrations of eiders were observed consistently over several years (Petersen, 2021). Area 1 (n = 11 stations) is located along the northeastern edge of Neumann Island (Fig. 3); stations are distributed along sand flats parallel to a major channel and largely exposed to the Bering Sea (Fig. 4). In contrast, Area 2 (n = 15 stations) is protected in the south-western corner of the lagoon in Norma Bay (Fig. 3); stations are located at the edge of a dense eelgrass bed along a narrow channel, where the substrate is siltier and soft-bottomed (Fig. 4). Area 3 (n = 5 stations) is in the center of the eastern side of the lagoon (Fig. 3) at the end of a major channel; stations are near dense eelgrass beds, on bare substrate, and along a channel (Fig. 4). Across Izembek Lagoon, 5-15 samples were collected at stations along a transect in each area, where one benthic sample per station was collected. Stations within an area were spaced approximately 110 m apart (range: 40-284 m).

In this study, the same stations sampled in 1998 were resampled between October 9th and 12th, 2018, and September 14th-15th, 2019. In September 2019, 12 additional samples were collected from randomly selected points, where annual eelgrass monitoring is conducted by the USGS (Ward, 2021; Fig. 3); these samples were included for size comparisons. All sampling was conducted during high tide to access locations by boat within the shallow lagoon. The timing of benthic sampling occurred earlier in 2019 than the previous time points, which aligned with the timing of eiders molting at Izembek Lagoon. It was assumed that the 2-week shift in timing between mid- and late- September would not account for significant differences in macrofaunal benthic biomass. Samples from 2018 were collected with a weighted (600-g messenger weight) Ekman grab (6” x 6”, 0.023 m^2); 1998 and 2019 samples were collected with a Petite Ponar grab (6” x 6”, 0.023 m^2). Both the Petite Ponar and Ekman samplers have similar sampling efficiency when weights are attached to the lighter Ekman grabs (Caires & Chandra, 2012). The samplers differ in that a messenger weight is sent down the line with the Ekman grab after hitting the bottom to close the jaws of the sampler, while the jaws of the Petite Ponar sampler clamp when the line is given slack after hitting the substrate. In addition, while the area of the Ekman and Petite Ponar grabs are the same, the depth and shape of the “bite,” or grab, depends on sediment hardness and weight of the grab sampler (Wilson & Fleeger, 2023). After sample collection, the 1998 and 2019 samples were immediately frozen. The 2018 samples were chilled until returning to the lab, where they were preserved in 70% ethanol (EtOH) solution. To account for the difference in preservation techniques used in 2018 and 1998, extra samples collected in summer 2019 were split in half, preserving each half of the sample either frozen or in 70% EtOH, and no difference in community composition was found based on preservation technique (A. Maliguine, unpubl. data, PERMANOVA test, N = 33 samples, *Pseudo-F* = 1.05, $p = 0.38$).

All lab processing for 2018 and 2019 samples was conducted at the Alaska SeaLife Center in Seward, Alaska. In the lab, sample contents were poured through a 250 µm sieve, washed, and transferred into collection jars. Wet weights of entire samples were recorded to the nearest gram and stored in EtOH. Samples from 2018 and 2019 were split into four subsets of equal weight and one randomly selected quarter was selected for analysis. The remainder of the sample was retained in case a re-analysis is warranted in the future. Prior to analysis, selected samples were stained with a few drops of a Rose Bengal/EtOH mixture (1.3 g Rose Bengal/100 mL 70% EtOH) before organisms were sorted to aid in identification and separated using a dissecting scope with a fiber optic light source. Organisms were classified to order- or class-level for most groupings and sometimes to the family- or genus-level. The number of partial and whole organisms and their wet weight (g) was recorded for each identified taxonomic group in a sample. The length of whole organisms was measured to the nearest mm for 1998 and 2019 samples. For quartered-split samples, wet weights of each taxonomic group were multiplied by 4 to standardize weights by area. Overall biomass (g/m^2) was defined as the total wet weight (g; partial + whole) of organisms within a taxonomic group in each grab divided by the grab area (0.023 m^2). Relative biomass (%) was defined as the total wet weight (g; partial + whole) of each taxonomic group divided by the overall wet weight (g) of all taxa detected in the same sample.

Statistical analysis

Analyses were restricted to four groups of marine benthic invertebrates: Polychaeta, Crustacea, Bivalvia, and Gastropoda, because these represent known prey groups for Steller's eiders (Metzner, 1993; Petersen, 1980, 1981) and comprised the overwhelming majority of invertebrate biomass in samples (mean = 86.5%; range 2-100%). For hard-shelled prey only (bivalves and gastropods), the partial weight was excluded from all overall biomass totals, because 1) bivalve fragments took up most of the wet weight biomass (>75%) in 1998 and <25% in 2019, and 2) shell fragments do not reflect available prey for Steller's eiders. It was assumed that softer-bodied prey (crustaceans and polychaetes) were more likely to get damaged during the laboratory processing, so both partial and whole organisms were combined in overall biomass totals. Partial weights were included in the relative biomass estimates to include year 2018, and partial vs. whole organisms were not separately weighed for all samples in 2018. Unclassified organisms were not reported in the 1998 baseline dataset (Petersen, 2021) and unclassified organisms from this study were not included in the analyses. Pearson's chi-square tests and linear regression models were used to test for differences in relative frequency (%) of occurrence (presence vs. absence) and biomass among years for each taxon (Polychaeta, Crustacea, Bivalvia, and Gastropoda) using R version 4.2.3 (R Core Team, 2023). Temporal trends in both relative (%) and overall (g/m^2) biomass were analyzed. Data were examined for all years for relative biomass, and only 1998 and 2019 for overall biomass, because a different sampler was used in 2018, which led to differences in total grab sample mass (Table 1), which could bias trends. Data contained a high proportion of zeroes, so the effects of Year on proportion of the total biomass was modeled in each sample using a Bayesian zero-inflated beta (ZIB) regression model ("zoib" package) (F. Liu & Kong, 2023) and on overall biomass using a Tweedie regression model ("glmmTMB" and "emmeans" packages) (Brooks et al., 2017; Lenth, 2023). The Bayesian ZIB model ran with 500,000 iterations discarding the first 200,000 as burn-in and retaining every second value. Convergence was checked by verifying that the Gelman-Rubin convergence diagnostic (Rc) was ≤ 1.1 (S. P. Brooks & Gelman, 1998). Area was not included as a covariate, because when included, the model indicated nonconvergence on area parameters regardless of the number of iterations ran (i.e., $Rc > 1.1$).

Changes in community composition were examined through space and time using both relative biomass (%) and overall biomass (g/m^2) as metrics in PRIMER v7 software (Anderson et al., 2008). The Bray-Curtis distance measure was used to build pairwise dissimilarity matrices on standardized relative biomass (%) data for comparing community composition among the three sampling areas (1, 2, 3; see Fig. 3) and years (1998, 2018, and 2019). Because the analysis was restricted to four prey groups, the Euclidean distance measure was used to build a resemblance matrix on the square root overall biomass

(g/m^2) to assess differences in dominant groups based on their total biomass between years 1998 and 2019 (Özkundakci et al., 2016). To test statistical differences in species composition among years and areas, a permutational multivariate analysis of variance (PERMANOVA) was performed using the PERMANOVA+ add-on of PRIMER v7. The maximum number of permutations was set to 9,999 for all tests. After conducting main tests, pairwise PERMANOVA tests were performed for Year, Area, and the interaction of Year and Area to identify which groupings contributed to differences from PERMANOVA main tests. For each year that benthic sampling took place, all samples within each of the three areas were treated as replicates. Prior to conducting PERMANOVA tests, homogeneity of multivariate dispersions was tested using the PERMDISP function to ensure within-group dispersion was similar among groups (Anderson et al., 2008). Non-metric multidimensional scaling (nMDS) plots were created to visualize differences in community composition and biomass among years and areas. To construct ordination plots, the average relative biomass (%) and overall biomass (g/m^2) were calculated for each benthic group by factor Year-Area (e.g., 1998-1, 1998-2, 1998-3, etc.) prior to building resemblance matrices. The ordinations ran until the lowest global stress was found, and stress scores were sufficiently low (<0.05) that data could be interpreted in two dimensions (Clarke et al., 2014).

The mean size (mm) of taxonomic groups (Polychaeta, Crustacea, Bivalvia, and Gastropoda) was also compared between 1998 and 2019. Organism size was not recorded for samples collected in 2018. When organisms were identified in the lab in 2019, individual sizes were not recorded; rather, the size range (minimum and maximum) and/or mean size of all like organisms (i.e., organisms sorted under the same category) was recorded. The mean size was used for size comparisons between years, and the median size for samples, where only the range of sizes was recorded. In addition, as organisms were variably identified (genus, family, order, class, etc.), the mean sizes were aggregated to fall under respective groups: Polychaeta, Crustacea, Bivalvia, and Gastropoda for each benthic sample. Prior to aggregating, the weighted mean sizes were calculated for the four groups based on the number of like organisms identified under a “subgroup” (i.e., genus, family, order) that were measured and identified belonging to one of the four groups. The effect of Year was modeled on the average size of each taxonomic group using weighted generalized linear regression models with the Gamma distribution (log-link; “glmmTMB” package) (Brooks et al., 2017). As each sample had varying total numbers of individuals for each benthic group, the Gamma model was weighted by the number of total individuals per benthic group in each sample. The model fit was examined from Q-Q residual plots (“DHARMa” package) (Hartig, 2022) and the mean size of taxonomic groups was predicted between years using marginal means (“emmeans” package) (Lenth, 2023). All analyses were completed using R version 4.3.2 (R Core Team 2023).

Results

When accounting for all data years (1998, 2018, and 2019), chi-square tests revealed relative frequency of occurrence (i.e., % present; Table 2) of partial and whole organisms at sample stations of polychaetes, crustaceans, and bivalves, but not gastropods, varied significantly among years ($p < 0.01$, $p = 0.01$, $p < 0.01$, for each benthic group respectively). The relative frequency of occurrence of bivalves was highest in 2018 (100%) and lowest in 2019 (~81%; Table 2). The relative frequency of occurrence of polychaetes and crustaceans was highest in 2018 (80%) and 2019 (~77%), and lowest in 1998 (~38%, ~47%, respectively; Table 2). The relative frequency of occurrence of gastropods was highest in 1998 (~75%) and lowest in 2019 (~52%; Table 2). When only accounting for Area (1, 2, 3), chi-square tests revealed relative frequency of occurrence (Table 2) of partial and whole organisms of all groups (polychaetes, crustaceans, bivalves, and gastropods) varied significantly among areas ($p < 0.01$, $p < 0.01$, $p = 0.04$, $p = 0.02$, respectively) across all sample stations. Area 1 had the highest relative frequency of occurrence of polychaetes (~84%), crustaceans (~79%), and bivalves (100%), and Area 2 had the highest occurrence of gastropods (~78%; Table 2). Area 3 had the lowest relative frequency of occurrence for all prey groups (Table 2). For all years and areas, bivalves had the highest occurrence out of all prey groups (Table 2). For size comparisons of whole organisms (partial organisms excluded) between years 1998 and 2019, chi-square tests revealed presence of polychaetes and crustaceans to vary significantly between years ($p < 0.01$, $p = 6.07e^{-7}$, respectively) with whole organisms of these groups occupying fewer sampling stations in 1998 than 2019 (23% vs. 71% for polychaetes and 20% vs. 81% for crustaceans).

Results from the ZIB regression model suggested bivalves comprised most of the benthic biomass in all years of this study, but they accounted for a lower percentage of total biomass in 2018 and 2019 than 1998, while relative polychaete biomass increased in recent years (Fig. 5). Overall biomass (g/m^2) of crustaceans and bivalves was lower in 2019 than in 1998 (Table 3). Results from the Tweedie regression model predicted the overall biomass of crustaceans and bivalves to be significantly lower in 2019 ($p = 0.02$ and $p = 0.04$, respectively), but biomass was similar between years for polychaetes and gastropods (Table 4; Fig. 6).

Based on the Bray-Curtis dissimilarity matrix (used for relative biomass comparisons), there were differences in multivariate dispersion among groups between 1998 and 2018 (PERMDISP, $p = 0.01$) and between 1998 and 2019 ($p < 0.01$), but no differences in dispersion between 2018 and 2019 ($p = 0.12$). Based on relative biomass, significant differences in benthic community composition were associated with Year (PERMANOVA, $p < 0.01$) and Area ($p = 0.03$; Table 5). The ordination plot and vector overlay (Fig. 7) suggests 1998 having more of a bivalve-structured community, while 2018 and 2019 having more of a polychaete-structured community. Pairwise PERMANOVA results found a significant difference in benthic community composition between 1998 and more recent years ($p_{2018} = 0.05$, $p_{2019} < 0.01$), and that composition was similar in 2018 and 2019 ($p = 0.10$; Table 6). Pairwise PERMANOVA results suggest community composition was different between Area 1 and 2 ($p = 0.02$; Table 7). Within Area 1 and 2, pairwise PERMANOVA results generally found 1998 to be different than both 2018 and 2019, but community composition was similar between 2018 and 2019 (Table 8). Within Area 3, pairwise PERMANOVA results found significant differences in community composition between 1998 and 2019 ($p = 0.03$), and 2018 and 2019 ($p = 0.03$), but not 1998 and 2018 ($p = 0.32$; Table 8).

Based on the Euclidean dissimilarity matrix (used for overall biomass comparisons), there was no difference in multivariate dispersion between 1998 and 2019 (PERMDISP, $p = 0.25$). Based on overall biomass, significant differences in benthic community composition were associated with Year (PERMANOVA, $p = 0.02$; Table 9), but not Area ($p = 0.30$) or the interaction of Year and Area ($p = 0.63$). For the pairwise PERMANOVA test on the interaction of Year and Area paired by Year, significant differences in community composition between 1998 and 2019 were detected within Area 3 ($p = 0.05$), but not Area 1 or 2 (Table 10). Ordination plots also suggested lower biomass of bivalves and crustaceans in 2019 and differences in composition between Area 2 and 3 within the Year factor (Figs. 8, 9).

The mean size of all available prey groups examined in this study was smaller in 2019 than 1998 (Fig. 10), and specifically bivalves and gastropods were significantly smaller ($p < 0.01$, $p < 0.01$, respectively; Table 11). Bivalves in 1998 ranged between 2-24 mm in size, (mean = 6.37 mm; 95% CI: 5.98 – 6.77 mm), whereas, in 2019, bivalves ranged between 1-15 mm in size (mean = 2.38 mm; 95% CI: 2.31 – 2.45 mm; Table 12). Gastropods ranged between 2-6 mm in size in 1998 (mean = 3.95 mm; 95% CI: 3.73 – 4.19 mm) and 1-4 mm in 2019 (mean = 3.18 mm; 95% CI: 3.10 – 3.26 mm; Table 12).

Discussion

The biomass, size distribution, and community composition of benthic invertebrate prey (namely polychaetes, crustaceans, bivalves, and gastropods) available to Steller's eiders during the fall remigial molt is likely critical for eider populations to persist at important molting areas like Izembek Lagoon. This study demonstrates evidence of a shift in proportionally dominant taxa, from largely bivalve-dominant towards more of a polychaete-dominant community in 2018 and 2019, compared to 1998. There were also significant reductions in total crustacean and bivalve biomass and in mean size of shelled prey (bivalves and gastropods) available to Steller's eiders in 2019 compared to 1998. In addition to differences detected between years, there was variation in community composition among the sampled areas when accounting for relative biomass. These findings suggest that foraging conditions for molting Steller's eiders have changed at Izembek Lagoon from 1998 to 2018/2019, reflecting less optimal conditions for eiders during the most recent sampling period. As a result, eiders may redistribute to other areas with higher benthic biomass or eiders may consequently face lowered body condition or survival. This is the first study to assess the available forage in a critical marine area used by Steller's eiders during the fall remigial molt and to document changes in benthic prey composition, size, and availability for Steller's eiders in a designated critical habitat. Importantly, the findings did not explore forage quality throughout the nonbreeding season but suggest that conditions may be less suitable for eiders undergoing the remigial molt, as eiders face additional nutritional requirements and have limited mobility due to feather growth at this stage of their annual cycle.

Shifting benthic prey community and changes in biomass

Eelgrass beds are among the most productive marine benthic ecosystems, and eelgrass beds act as "ecosystem engineers" providing important habitat structure for many marine organisms like benthic invertebrates (Hemminga & Duarte, 2000). Macrofaunal communities have been well-documented in high-latitude eelgrass-dominated systems (Bostrom & Bonsdorff, 1997; Fredriksen et al., 2010; Kindeberg et al., 2022; Möller et al., 2014; Wong, 2018), but long-term dynamics of their benthic communities are less understood. Benthic biomass can be highest in eelgrass zones relative to adjacent unvegetated areas (Baldwin & Lovvorn, 1994; Bostrom & Bonsdorff, 1997; Fredriksen et al., 2010) and declines of benthic productivity have been associated with eelgrass loss (Seitz & Ewers Lewis, 2018); however, the eelgrass biomass at Izembek Lagoon appears to be stable (Ward et al., 1997; Ward & Amundson, 2019).

While Izembek Lagoon's eelgrass beds appear to have been stable, their associated benthic communities do not reflect similar stability. In both time points of this study, bivalves dominated the benthic biomass in Izembek Lagoon; however, in 2018 and 2019, there was a significant reduction in the proportional and total biomass of bivalves, and the relative contribution of polychaete biomass was more prominent in 2018/2019 compared to 1998. In this analysis, the partial fragments of shelled-prey (bivalves and gastropods) were removed from overall biomass estimates, as their proportional biomass of partial vs. whole organisms between 1998 and 2019 were different. Other work in the Bering Sea found discordance in living vs. dead bivalve assemblages and identified shifts in dominance to smaller-bivalve taxa in living assemblages potentially linked to climate change (Meadows et al., 2019). In this study, the reductions in bivalve biomass of dead assemblages (partial shell fragments) in 2019 relative to 1998 agreed with simultaneous reductions in assumed-living biomass of bivalves (whole organisms) in 2019, further supporting that bivalve biomass has declined. This shift could reflect that observed differences may not be an artifact of events or conditions in 2018 or 2019 specifically but could be an ongoing shift over a longer duration of time towards reduced bivalve biomass, and/or their size distribution. However, the timing and causes of ecological shifts of benthic community responses are difficult to identify without long-term monitoring. Other work surveying benthic invertebrates in Izembek Lagoon found differences in the abundance of organisms between two time points suggesting that significant community reorganization took place (Tippery, 2013). These authors collected benthic invertebrates near Grant Point in Izembek Lagoon (an area not recognized as an important foraging location in the lagoon for Steller's eiders; Fig. 3) and found bivalves to be approximately 77 times more abundant in 2008 than 1977 (Tippery, 2013). It has been suggested that these higher densities could be related to changes in eelgrass morphology, such as increased leaf surface area; however, changes in benthic invertebrate biomass or size were not analyzed in previous work (Tippery, 2013). Biomass is not necessarily directly comparable to density; total benthic biomass can decline simultaneously with increases in total organism abundance, if there is a high proportion of younger or smaller organisms (Azovsky & Kokarev, 2019; Paalme et al., 2020). Overall, studies on the benthic fauna in Izembek Lagoon found the biomass and abundance of benthic fauna to vary between sampling time points (1998 vs. 2018/2019, this study; 1977 vs. 2008) (Tippery, 2013), warranting for longer-term monitoring to understand the sources of the observed variability in the benthos, as it provides an important role in the local marine food web and a source of food for Steller's eiders.

Spatial and temporal patterns in benthic community composition

Benthic community composition also showed spatial variability in the temporal patterns. Izembek Lagoon is a productive system covering a large area with various habitat landforms (Fig. 4) to support benthic communities among the eelgrass beds, sand flats, and deeper water channels, which could respond variably under different environmental conditions and by location (Bostrom & Bonsdorff, 1997; Millet & Guelorget, 1994). Other studies in high-latitude eelgrass systems have found significant differences in abundance of benthic fauna within eelgrass beds compared to adjacent bare sand (Bostrom & Bonsdorff, 1997; Fredriksen et al., 2010; Wong, 2018). As the three sampled areas varied by landform types (Fig. 4), it was expected that variation in community composition would be observed among the three areas, and each area may respond differently to variation in environmental conditions. Among all areas, Area 1 varied in composition between the 1998 and recent time points based on relative biomass metrics. Area 2 followed a similar trend; however, the differences in community composition between 1998 and 2019 were not significant in this study. Unlike Areas 1 and 2, Area 3 varied in composition between 2019 and the other years based on relative biomass metrics but did not vary between 1998 and 2018. In addition, while benthic community composition based on the overall biomass did not vary among the areas, it varied temporally between 1998 and 2019 for Area 3. Area 3 also had the fewest number of replicate samples (N = 4-6; Tables 2, 3), and sample stations in this area are distributed both along the edge of eelgrass beds and on unvegetated bare substrate (Fig. 4). Trends in Area 3 could be influenced by the smaller sample sizes or have more compositional variability associated with the diverse landform types (Bostrom & Bonsdorff, 1997; Fredriksen et al., 2010; Millet & Guelorget, 1994).

When accounting for temporal differences between benthic sampling, benthic community composition based on relative biomass varied between Areas 1 and 2. In lagoons, benthic community composition and substrate types near the entrances vary relative to sheltered sites farther from the lagoon entrance (Rodrigues et al., 2012). In Izembek Lagoon, the sand flats are distributed along the barrier islands, and the silt and clay substrates dominate in the eelgrass beds and channel bottoms (McRoy, 1966). Finding variability in community composition between Areas 1 and 2 was not unexpected as Area 2 is in a sheltered bay on the opposite end of the lagoon (Fig. 3), characterized by its shallow, dense eelgrass beds with a lower tidal range than Area 1 (Maliguine, unpubl. data). Benthic assemblages are influenced by tide-induced hydrodynamics and distance from sea inlets (Millet & Guelorget, 1994). Area 1 is near one of the three main lagoon entrances, and the community may be more adapted to variable conditions, as the storm tides annually shape and move sediments near these entrances (Ward et al., 1997). Area 2, being more sheltered from lagoon entrances, may be better suited to host different benthic community composition associated with softer-substrate eelgrass beds. Overall, benthic community composition was expected to vary among areas, because each area represents different habitats in the lagoon, with varying hydrography, vegetation, and substrates. Different areas within the lagoon may represent varying suitability or quality of habitat among years for Steller's eiders.

Reduced size of benthic prey

Steller's eiders forage on smaller bivalves that range between 1-16 mm (mean = 6 mm) and gastropods ≤ 5 mm (mean ≤ 2.5 m) (Bustnes & Systad, 2001). The understanding of prey selection by Pacific Steller's eiders during the molting period is limited to a few diet studies conducted in the late 1970s and early 1980s (Metzner, 1993; Petersen, 1980, 1981). Previous work suggested that Steller's eiders consume smaller bivalves (*Macoma spp.* and *Turtonia minuta*) in Izembek Lagoon relative to other areas where *Mytilus edulis* is more common (e.g., Nelson Lagoon, Fig. 1), but unfortunately did not report sizes of prey consumed (Metzner, 1993). Diet analyses from collected Steller's eiders from nearby Nelson Lagoon found eiders to select larger mussels (*M. edulis;* 9-10 mm range) in the fall than summer months (1-10 mm range), although the commonly available mussels in the fall were smaller (~5 mm) than mussels eaten by eiders (Petersen, 1980). Therefore, the presence of larger bivalves may be important for molting Steller's eiders. Most of the bivalves detected in 2019 were smaller than 5 mm (IQR = 1-3 mm; mean = 2.38 mm), with 3 outlier samples containing bivalves ranging 8-15 mm in size, whereas most bivalves in 1998 ranged between 3.5-10.75 mm (IQR; mean = 6.37 mm). While larger-sized bivalves were more commonly available in 1998, they were scarcer among samples in 2019 (Fig. 10). If bivalve abundance has not changed, declines in the mean body sizes of bivalves or shifting species composition could explain reductions in both relative and overall bivalve biomass detected in 2018/2019. Overall, all benthic invertebrate groups were smaller in 2019 than 1998, but sample sizes of whole crustacean and polychaetes were too low in 1998 for adequate size comparisons between the years. Differences in the benthic prey size composition suggest changes in prey availability and quality for molting eiders using Izembek Lagoon between time points.

Forage profitability

There are several factors to consider when determining the profitability of bird foraging on various prey types, such as prey size, nutrient content, digestibility, and the intake rate and gut retention time of food items (Richman & Lovvorn, 2003). Optimal foraging theory states that organisms forage in a way as to maximize their net energy intake per unit time (MacArthur & Pianka, 1966). Generally, smaller sea duck species, like Steller's eiders, have a less specialized and more diversified diet than larger sea ducks, like common eiders (*Somateria mollissima)*, where bivalve prey largely dominates their diet (Ouellet et al., 2013). However, previous work has suggested that Steller's eiders may select more (and larger) shelled prey during the remigial molt and switch to a mixed diet of crustaceans and shelled prey after flight is regained (Metzner, 1993; Petersen, 1980, 1981).

Steller's eiders may optimize their foraging during the molt to maximize their net energy intake per unit time by 1) selecting larger prey, 2) selecting higher-protein prey, or 3) utilizing feeding strategies that minimize energy expenditure (e.g., surface-feeding, feeding at low tide, and selecting less-mobile prey). Steller's eiders may optimize their foraging strategy during the molt by selecting larger-sized bivalves (Petersen, 1980). Sea ducks commonly eat bivalves of lengths 10-30 mm (Žydelis & Richman, 2015); while size composition of prey varies in energy content, many ducks prefer "small" bivalves when larger bivalves are readily available, because the costs are lower for crushing smaller-sized shells in the gizzard (Žydelis & Richman, 2015). Many studies have analyzed the profitability of various sized bivalves from the perspective of a diving duck (Bustnes & Erikstad, 1990; De Leeuw & Van Eerden, 1992; Draulans, 1982, 1984; Richman & Lovvorn, 2003); however, it is important to note that these studies define "small" as being in the 10-15 mm range—much larger than the mean size of bivalves detected in this study. Bivalves must be a certain size threshold to be considered "profitable". According to profitability curves from prey selection studies conducted on other duck species (Bustnes & Erikstad, 1990; De Leeuw & Van Eerden, 1992; Draulans, 1982, 1984), bivalves < 5 mm in size appear to be among the least profitable size classes, and most of the bivalves found in 2019 in this study fall into this category. Previous work on the size selection of mussels by common eiders found that eiders would require consumption of 116 times more mussels in the smallest size range (7-9 mm) compared to eating the largest mussels available (41-43 mm) (Bustnes & Erikstad, 1990). While Steller's eiders eat smaller bivalves than common eiders, they would similarly require consuming significantly more bivalves, if they were to feed on bivalves ranging 1-3 mm rather than 9-10 mm in size. The difference in mean sizes of bivalves between years was approximately 4 mm (63% decline), so feeding solely on the available-sized bivalves would have required much more effort in 2019 relative to 1998. Furthermore, the available mean size of bivalves in 2019 may be unprofitable especially when eiders require foods of higher quality during the molt.

During the molt, eiders require protein-rich foods for feather growth and body maintenance and may optimize their foraging strategy by selecting prey with the most profitable protein gain. Total energetic content of marine organisms depends on the amount of carbohydrates, proteins, and lipids contained in their bodies. The energy content of organisms can vary by geographic area (Beukeuma, 1997), as more calorie-rich benthic taxa are found at higher latitudes associated with colder water temperatures (Wilt et al., 2014). Bivalves and gastropods can have among the lowest caloric values compared to crustaceans and polychaetes (Ouellet et al. 2013); however, most caloric values have been derived from studies conducted outside of the North Pacific Ocean. In the Bering Sea, few studies have assessed the caloric value of benthic fauna; however, one summer study found mollusks (bivalves and gastropods) to have the highest caloric content (Hondolero et al., 2012), and another in the Chukchi Sea found the highest mean caloric values among polychaetes, gastropods, and bivalves, in descending order (Wilt et al. 2014). The relative energy value could also vary due to time of year, with seasonality of reproductive cycles and sources of food (Hondolero et al., 2012). While gastropods are high in protein, they have a low flesh-shell ratio and require extra work to digest in the gizzard (Metzner, 1993). For blue mussels (*M. edulis*) collected from Nelson Lagoon in summer and fall 1979, protein levels were highest in July and September, while fat levels were highest in July (Petersen, 1981). Male Steller's eiders require 104 kcal/day and females require 116 kcal/day to meet their daily requirements of feather growth (Petersen, 1981), assuming the energetic cost during molt is similar to mallard ducks (*Anas platyrhynchos*) (Prince, 1979). Eiders would need to eat at least three times more in wet weight of amphipods (0.47 kcal/g whole wet weight) (Tyler, 1973) than blue mussels (1.52 kcal/g whole wet weight) (Petersen, 1981) to meet their daily energetic needs during the molt, and eiders would have to feed more times a day on a diet composed of amphipods compared to a diet of blue mussels (Petersen, 1981). Therefore, it would be more profitable for eiders to increase their caloric intake by eating higher-protein foods during the molt (Metzner, 1993; Petersen, 1981). However, if higher-protein foods require more foraging effort due to their reduced biomass and size (as observed for bivalves in 2019), eiders may need to alter their foraging strategy to meet nutritional requirements, which may not be equally profitable. Izembek Lagoon may not represent optimal foraging habitat for molting eiders in recent years, which may explain why less eiders are observed molting there than historically.

Steller's eiders could also optimize foraging during the molt by utilizing feeding strategies that minimize energy expenditure. Calculations of prey profitability incorporate the caloric yield (calories) or gross intake of organic material (ash-free dry weight) per unit handling time (seconds) (De Leeuw & Van Eerden, 1992; Draulans, 1982, 1984), or is thought of as the total energy gain minus the cost (Richman & Lovvorn, 2003). Therefore, eiders can utilize feeding strategies that minimize the foraging time or reduce their energy expenditure which would increase profitability of any prey item. During the remigial molt, eiders have limited mobility, because they cannot dive well or fly. Steller's eiders feed more at low tide, and they often utilize a "head-dipping" or "upending" foraging strategy (Petersen, 1981), which may potentially minimize handling time, if there is plentiful prey available close to the water surface or in the shallows. Foraging by head-dipping can offset the energy expenditure required to dive for food; in fact, a larger proportion of eelgrass was found in eider diets during the remigial molt relative to other nonbreeding stages (Metzner, 1993), suggesting that eiders likely feed more at the water's surface and target sessile organisms on the eelgrass blades. Bivalves and gastropods are sessile hard-shelled organisms, can occur in high densities in suitable habitat, and require a shorter search and capture time than more mobile, energy rich prey (Ouellet et al., 2013). Steller's eiders may select these prey to minimize energy expenditure, because they require less energy to forage for them than more mobile prey (crustaceans and polychaetes) and are a predictable food source. Gastropods and small bivalves (*T. minuta*) can be found in abundance attached to the blades of eelgrass (McConnaughey, 1978) and *Macoma spp.* dominate the sandy bottoms that are more exposed at low tide (Metzner, 1993). This study found significantly less bivalve biomass and smaller-sized shelled prey available in 2019 compared to 1998, so eiders molting at Izembek Lagoon may have had to spend more time foraging in 2019 to acquire these foods. When shelled prey shift to smaller sizes (< 5 mm) and represent less biomass, the foraging profitability of shelled prey decreases overall, as smaller-sized prey is less visible and has lower nutritional value. Under such conditions, eiders would need to spend more time and energy searching for larger, more profitable bivalves (6-12 mm), consume very large quantities of smaller prey, or rely on a wider diversity of prey types to maintain energy balance. It has been suggested that Steller's eiders may have little flexibility in their feeding ecology in terms of the type and size of prey they eat, potentially due to bill shape (Bustnes & Systad, 2001). A comparative foraging study on long-tailed ducks (*Clangula hyemalis*) and Steller's eiders found that the eiders selected smaller prey and did not opportunistically exploit abundant capelin (*Mallotus villosus*) as does their long-tailed duck counterpart (Bustnes & Systad, 2001). If Steller's eiders require larger, shelled prey to meet their nutritional requirements for molt (Petersen, 1980, 1981), the decline of eiders molting in Izembek Lagoon could be explained by less profitable prey sources available for molting eiders at Izembek Lagoon. Understanding both the diet and relative body condition of eiders using Izembek Lagoon (and other molting areas) would be insightful for understanding habitat suitability with available conditions.

Potential factors influencing benthic prey availability

Without long-term monitoring of the associated benthic communities, it is difficult to attribute causal factors to observed variability. Many factors can influence the benthic community composition and biomass and a few of these factors relevant to Izembek Lagoon are listed in Figure 11. Studies in the Bering Sea have observed changes associated with warming sea temperatures and reduced winter ice cover (Goethel, 2021; Grebmeier, 2012; Grebmeier et al., 2006a; Grebmeier et al., 2018; Grebmeier et al., 2006b; Meadows et al., 2019), and warmer conditions were observed in Izembek Lagoon in 2018 and 2019 compared to 1998. Some of the warmest average seawater temperatures across September months (when many eiders molt) occurred in 2018 and 2019, and sea temperatures were warmer than average across all months of 2019 (Ward unpubl. data from HOBO logger stationed in Grant Point, Izembek Lagoon, 2007-2021). In the winter preceding the 1998 fall sampling, Izembek Lagoon had approximately 20 days of significant-severe ice cover based on modeled ice cover (Petrich et al., 2014); however, in February of 2018 and 2019, there was no ice cover observed in Izembek Lagoon or the surrounding areas during aerial surveys (Wilson, 2018, 2019a). In addition, winter air temperatures (January – March) were mostly ≥ 2°C warmer than the mean temperature normal in the adjacent town, Cold Bay, in both 2018 and 2019; it is likely there was minimal to no ice cover in the lagoon in the winters preceding fall sampling (Table A1). Concurrent with warming conditions observed in the larger Bering Sea, changes in benthic invertebrate availability include lower bivalve biomass (Coyle et al., 2007), shifting dominance from bivalves to polychaetes (Grebmeier et al., 2018; Grebmeier & Cooper, 2016), and species distribution shifts (Goethel, 2021; Grebmeier, 2012; Grebmeier et al., 2018; Yeung & McConnaughey, 2006). Outside of the Bering Sea, other trends have been observed coincident with warming temperatures; among bivalves *Macoma balthica*, *Mytilus* spp., and *Mya* spp., all of which previously occurred at Izembek Lagoon (Table A2), higher recruitment follows cold winters relative to milder winters (Beukema et al., 1993, 1998, 2009; Jensen & Jensen, 1985). In addition, higher temperatures correlated with lower survival of *Macoma balthica* in years with warmer summers (Beukema et al., 2009), and *M. balthica* have narrower temperature thresholds compared to other bivalves (Freitas et al., 2007; Jansen et al., 2007; van der Veer et al., 2006). If invertebrate fauna at Izembek Lagoon are colder-adapted and have narrow temperature thresholds, one might expect lower biomass to occur in warmer years.

As this study did not report bivalve species in 2018 and 2019, the observed differences in size structure of bivalves could be explained by 1) a shift in species composition, 2) a younger bivalve community, and/or 3) rates of growth. The dominant bivalves identified in fall 1998 across the three sampling areas in Izembek Lagoon were *Macoma moesta, Macoma golikovi, Axinopsida serricata*, and *Clinocardium nuttallii*, respectively, which made up 94% of the whole bivalve biomass (excluding fragments) (Petersen, 2021). The dominant bivalves detected in diets of nonbreeding Steller's eiders at Izembek Lagoon in 1980-1981 were *Macoma* spp., specifically *M. balthica,* and *T. minuta* (Metzner, 1993). *Turtonia minuta* is a small bivalve that settles on eelgrass blades at Izembek Lagoon (McConnaughey, 1978; Metzner, 1993), and their maximum body length is 3 mm (World Register of Marine Species Editorial Board, 2024); this species was not reported in 1998 (Petersen, 2021), although it was present in other studies at Izembek Lagoon (Table A2). Other work has suggested that *M. balthica* is sensitive to high temperatures (Freitas et al., 2007; Jansen et al., 2007; van der Veer et al., 2006), and they may avoid the lethal temperature limits by moving to deeper waters or burrowing deeper into the sediments (Zwarts & Wanink, 1993). Other *Macoma* clams have shifted their range northward in other areas of the Bering Sea (Goethel, 2021). It is possible that *Macoma* spp. may be less common or accessible than previously thought, and the majority of benthic biomass in 2019 could have been attributable to more available *T. minuta,* as most bivalves detected were approximately 2 mm. It is unlikely that larger bivalves would have remained undetected during the sorting process. Future work should identify invertebrates at a finer taxonomic resolution to monitor potential differences in species composition, as it may explain the differences in size composition and have important implications for available food quality for Steller's eiders.

A younger bivalve-structured community also may be explained by mortality of larger, older bivalves, by mechanisms such as predation, environmental conditions, and/or disturbance. Of some of the bivalve species found in Izembek Lagoon (Table A2), many are long-lived *(Mactromeris* spp., *Macoma* spp., *Siliqua* spp., *Mya truncata, Hiatella arctica*), with maximum ages of over 20 years, and they can grow to be relatively large (20-145 mm) (Sejr et al., 2002; Selin, 2010). The absence of ice cover could allow benthic predators to feed throughout the winter in Izembek Lagoon, instead of forcing them to forage in deeper ice-free waters, thus exposing larger bivalves to predation for longer durations of the year. In the absence of ice cover, 20,000-30,000 Steller's eiders and other sea ducks (e.g., scoters, eiders, long-tailed ducks) will continue to use Izembek Lagoon throughout the winter (Wilson, 2018, 2019a, 2019b) when otherwise the lagoon would be >75% ice-covered (Ward et al., 1997). In addition to sea ducks, sea otters (*Enhydra lutris*) are common in Izembek Lagoon (Wilson, 2018, 2019a), and their major prey in the lagoon are bivalves (10-40 mm) (Green & Brueggeman, 1991). Sea otters can significantly influence the size-structure of intertidal prey communities in similar soft-sediment habitats, resulting in fewer larger bivalves over time (Weitzman, 2013). Increased winter predation by benthivores could potentially explain why the common sizes of bivalves available in the fall are similarly sized to first-year recruits or second-year bivalves (based on data from *Macoma calcarea* on the Bering/Chukchi Shelf) (Stoker, 1978). Besides predation, disturbance, such as ice scouring resulting from severe winter ice formation, can cause indirect mortality to eelgrass (Ward et al., 1997) and benthic fauna (Strasser et al., 2001). It is possible that older bivalves experience lower winter survival under warming conditions or disturbance, which may influence their availability for eiders in the following fall.

The prevalence of larger-sized bivalves depends on individual growth that may take several years, and increases in disturbance regimes can interrupt growth or other ecosystem processes (Norkko et al., 2013). *Clinocardium nuttalii* and *Hiatella arctica* can take less than 1 year to grow to lengths of 10 mm (Ratti, 1978; Sejr et al., 2002; Table A2). The rate of growth can vary depending on latitude, temperatures, and length of growing seasons. Recent studies found reductions in adult body sizes among bivalves in the Bering Sea coincident with warmer sea temperatures (Goethel, 2021; Meadows et al., 2019). For *M. balthica,* growing to lengths of 10 mm can vary between 1 and 16 years (Gilbert, 1973). At warmer temperatures, *M. balthica* can grow faster and have a shorter lifespan (Gilbert, 1973), but recruitment may be lower following warmer winters (Beukema et al., 1998). Large bivalves play important roles in ecosystem function in the form of nutrient and organic matter processing, and the loss of large bivalves have unknown consequences for the overall ecosystem functionality (Norkko et al., 2013), but their presence and availability for Steller's eiders during the molt could be important.

Coastal marine benthic communities are expected to face many changes in the coming decades due to climate change. Both increasing seawater temperatures and loss of sea ice in the Bering Sea are probably already impacting benthic prey communities (Grebmeier et al., 2018; Grebmeier et al., 2006b; Meadows et al., 2019). In addition, the combination of sea level rise, reduced ice coverage in the Bering Sea, and higher frequency of storm surges will likely negatively impact the habitat at Izembek Lagoon in the coming decades (Bowman et al., 2022; Fujii, 2012). These factors make the barrier islands separating the lagoon from the Bering Sea more vulnerable to coastal erosion. Other molting areas protected by barrier islands are also at risk of coastal erosion, such as Nelson Lagoon. Nelson Lagoon is likely the most important molting area currently used by the Pacific population of Steller's eiders in Alaska (Williams et al., 2016). It is characterized by its dense *Mytilus* spp. beds that may provide eiders a reliable protein source during the molt (Petersen, 1981). The potential future loss of land barriers that protect lagoons will impact the benthic invertebrate communities and entire estuarine ecosystems of lagoon mudflats and intertidal areas, as well as reduce refugia habitat used by eiders to forage during the molt. As a large proportion of the Pacific population of Steller's eiders uses the Alaska Peninsula to molt

(Petersen, 1981), ecosystem changes in these nearshore waters could have major impacts to their population dynamics.

Challenges and future directions with benthic monitoring

Comparisons of benthic samples collected across long time intervals may be confounded by short-term variation (Morrisey et al., 1992), and shallow, benthic habitats can show variation over small temporal and spatial scales (Bostrom & Bonsdorff, 1997; Kindeberg et al., 2022). The time points in which benthic sampling occurred in Izembek Lagoon are isolated by two decades (1998 vs. 2018/2019), limiting the ability to attribute sources of observed variability to long-term change, a single natural or climate-related event, or sampling bias. While detecting causal factors for temporal trends is difficult without long-term studies, habitat suitability modelling can predict patterns of species distribution, when species occurrence data are paired with important environmental covariates to understand environmental drivers of observed spatial variability. Previous work has modeled the distribution of the benthos across the broader Bering Sea (Feng et al., 2021; Grebmeier et al., 2006a; Oppel & Huettmann, 2010), but fine-scale modelling of the shallow nearshore habitats used by nonbreeding Steller's eiders has not been done. Findings from this study suggest there may be spatial drivers that affect the relative biomass of benthic prey groups on a finer scale, as the communities across three areas in Izembek Lagoon varied from one another through space and time. Fine-scale modelling may reveal habitat patches, which may be important to consider as molting eiders forage synchronously in large, dense flocks (>1,000 birds) (Metzner, 1993). Temperature, salinity, and primary production are considered among the most important causal predictors for distribution of benthic fauna, while substrate and water depth are useful factors for determining presence of certain bottom fauna (Reiss et al., 2015). Water temperatures in Izembek Lagoon vary among the water channels and the shallow eelgrass-laden tide pools, and some areas of the lagoon near freshwater inputs are less saline (McRoy, 1966). Future work to model how various environmental factors (e.g., temperature, salinity, primary production, substrate type, water depth) relate to the observed benthic biomass, and how factors vary spatially across the lagoon, could be insightful for understanding the drivers of community compositional changes and identifying "hotspots" of benthic productivity in the lagoon (Fig. A2). In addition, predictions of "benthic hotspots" could be verified by concurrent observations of eiders from fall aerial surveys.

While collecting benthic samples is relatively simple, a challenge for marine monitoring is the labor-intensive manual sorting and visual identification that requires specialized taxonomic knowledge (Goodwin et al., 2017). In addition, soft-bodied organisms often become unidentifiable after processing (Schiaparelli et al., 2016). Only *Cistenides* spp. polychaetes were detected in 1998 samples; as polychaetes are difficult to identify (Zhou et al., 2010), it could be possible that unknown polychaetes were not recorded in 1998, and the total polychaete biomass was underestimated that year in community analyses. It seems unlikely that only *Cistenides* spp. were present in 1998, as other polychaete species have been identified at Izembek Lagoon (Table A2), and other studies in eelgrass-dominated systems in higher latitudes have reported high numbers of polychaete species (Fredriksen et al., 2010). As there were fewer whole polychaetes and crustaceans among the 1998 samples for the size comparison analyses, it is possible that these smaller soft-bodied prey were damaged by freezing, sieving, or the sorting process and therefore were not identifiable or reported that year. In addition, the common *Turtonia minuta* was not reported in the 1998 dataset although other studies in Izembek Lagoon consider this species to be among one of the most abundant bivalves in the eelgrass beds (McConnaughey, 1978; Metzner, 1993; Tippery, 2013; Table A2). Alternative methods to streamline benthic monitoring are worth considering for future work. For example, environmental DNA (eDNA) methods are becoming more popular for marine research and monitoring, because it is non-invasive and samples collected from water, sediments, or scat samples can be easily identified (Goodwin et al., 2017). While eDNA would be a useful tool for identifying organisms and quantifying community composition from benthic samples, it may still be of importance to continue conventional sampling, because the size distribution of prey is a key factor that would not be captured with eDNA methods. However, eDNA methods could be a practical tool for monitoring benthic species composition (and potentially biomass, as eDNA quantification methods continue to evolve) across various habitats and would ease future studies to assess habitat quality for the broader groups of sea ducks, as many sea ducks in North America are declining (North American Bird Conservation Initiative, 2022).

Long-term studies are useful for monitoring changes in ecosystem dynamics and identifying causal factors to observed variability. The continuous ongoing long-term eelgrass monitoring effort at Izembek Lagoon conducted by the USGS has been essential for understanding lagoon stability and environmental change. This effort assesses the annual eelgrass cover and biomass across hundreds of sampling stations in the lagoon in the summer and collects data on local sea temperature, salinity, substrate, depth, invertebrate presence, and various other data (Ward & Amundson, 2019). Extending this ongoing effort to include additional benthic invertebrate monitoring, aside from existing visual surveys of invertebrate presence (Ward & Amundson, 2019), could be important for understanding complex ecosystem interactions, as benthic fauna affect sedimentary environments. Extending this effort would fill data gaps on marine invertebrates available before eiders arrive at the lagoon to molt and allow for direct comparisons of habitat variables collected during the eelgrass survey. Continuation of benthic monitoring during the fall months of the key taxonomic groups consumed by Steller's eiders would be informative for understanding forage conditions relative to lagoon use by eiders, when they arrive to molt. Future fall sampling in Izembek Lagoon should also consider additional samples outside of historically sampled areas, representing areas not used by eiders, to improve spatial resolution and reduce sampling bias. A longer-term dataset of both forage conditions and eider habitat use could help ascertain drivers of habitat use changes and potential habitat changes that may be co-occurring.

In summary, future work should aim to understand drivers of habitat changes (Fig. A2), further monitor benthic communities at important molting areas used by Steller's eiders and aim to understand diet preferences of molting eiders to determine the quality and suitability of these marine areas. Expanding benthic monitoring to other key areas along the coast of Alaska used by Steller's eiders during the molting period (e.g., Nelson Lagoon, Seal Islands, Kuskokwim Shoals, Port Heiden) could be insightful for comparison of various marine areas to understand quality of foraging habitat. Expanding monitoring of the distribution of Steller's eiders during the fall molt across their molting areas in conjunction with examining the flocks' demographics relative to the areas used would be informative for determining if eiders are redistributing to different locations or if eider populations are experiencing lowered survival within certain areas. In addition, future work should evaluate the energetic composition of prey sources, and the feeding habits and diet composition of Steller's eiders before, during, and after the fall molt at molting areas. This would improve the knowledge of prey quality and potential prey preferences of Steller's eiders during the fall molt to determine habitat suitability among various marine areas. Understanding highly suitable and high-quality areas will be increasingly important to designate critical habitats in the future, as previously significant areas may become no longer suitable under the future climate change scenarios.

Conclusion

The findings of this study provide insight on the benthic availability in a critical habitat used by molting Steller's eiders in 2018 and 2019 compared to conditions in 1998. In summary, the benthic prey availability in 2018 and 2019 suggested less favorable forage for molting Steller's eiders compared to 1998. These findings can be used as a reference for future comparisons of benthic change at Izembek Lagoon, especially for assessing habitat for Steller's eiders or other benthivores. Steller's eiders molting in Izembek Lagoon have strong site fidelity (Flint et al., 2000) and may rely on the predictability and stability of marine food resources there to meet their nutritional needs during the remigial molt. Likely due to the additional energetic costs during molt, eiders consume proportionally more and larger bivalve prey during this stage (Metzner, 1993; Petersen, 1980, 1981). Although Steller's eiders could be considered diet generalists by feeding on diverse benthic taxa, they are likely food-limited (due to mobility constraints) and may need a specialized (higher protein) diet during the molting stage particularly, thus requiring reliable and productive food sources. Therefore, the observed variability in crustacean and bivalve biomass, and reduced size of gastropods and bivalves are not optimal for Steller's eiders, as all prey groups are large components of nonbreeding Steller's eiders' diet, and especially if eiders prefer bivalve-type prey during the molt (Metzner, 1993; Petersen, 1980, 1981). Izembek Lagoon has previously been considered the most important molting location for adult females (Petersen, 1981), so the quality of benthic prey available there is important for eider body condition and survival, and therefore, the overall population dynamics of the Pacific population of Steller's eiders. If benthic community resources from year-to-year are variable and unreliable for molting eiders, which exhibit strong site fidelity to their molting habitats, the observed decline in Steller's eiders use of Izembek Lagoon in the fall over time may be a result of variable foraging conditions. However, insights into the causes of decline of Steller's eiders at Izembek Lagoon and beyond could be informed by future diet and body condition studies, in addition to simultaneous habitat and population monitoring.

References

Alaska Department of Fish and Game. (2010). Izembek state game refuge management plan. Divisions of Habitat and Wildlife Conservation, Anchorage, AK.

Anderson, M. J., Gorley, R. N., & Clarke, K. R. (2008). PERMANOVA+ for PRIMER: guide to software and statistical methods. PRIMER-E Ltd, Plymouth, UK.

Azovsky, A. I., & Kokarev, V. N. (2019). Stable but fragile: long-term dynamics of arctic benthic macrofauna in Baydaratskaya Bay (the Kara Sea). *Polar Biology*, *42*(7), 1307–1322.

Baldwin, J. R., & Lovvorn, J. R. (1994). Habitats and tidal accessibility of the marine foods of dabbling ducks and brant in Boundary Bay, British Columbia. *Marine Biology*, *120*, 627–638.

Beukema, J., Dekker, R., & Jansen, J. (2009). Some like it cold: populations of the tellinid bivalve *Macoma balthica (L.)* suffer in various ways from a warming climate. *Marine Ecology Progress Series*, *384*, 135–145.

Beukema, J. J., Essink, K., Michaelis, H., & Zwarts, L. (1993). Year-to-year variability in the biomass of macrobenthic animals on tidal flats of the Wadden Sea: how predictable is this food source for birds? *Netherlands Journal of Sea Research*, *31*(4), 319–330.

Beukema, J. J., Honkoop, P. J. C., & Dekker, R. (1998). Recruitment in *Macoma balthica* after mild and cold winters and its possible control by egg production and shrimp predation. *Hydrobiologia*, *375/376*, 23–34.

Beukeuma, J. J. (1997). Caloric values of marine invertebrates with an emphasis on the soft parts of marine bivalves. In A. D. Ansell, R. N. Gibson, & M. Barnes (Eds.), *Oceanography and Marine Biology: An Annual Review* (Vol. 35, pp. 387–414). UCL Press.

BirdLife International. (2018). *Polysticta stelleri*, Steller's eider. The IUCN Red List of Threatened Species 2018: e.T22680415A132527232.

Bostrom, C., & Bonsdorff, E. (1997). Community structure and spatial variation of benthic invertebrates associated with *Zostera marina (L.)* beds in the northern Baltic Sea. *Journal of Sea Research*, *37*, 153–166.

Bowman, T. D., Churchill, J. L., Lepage, C., Badzinski, S. S., Gilliland, S. G., McLellan, N. R., & Silverman, E. (2022). Atlas of sea duck key habitat sites in North America. Publication, Sea Duck Joint Venture March 2022.

Brooks, M. E., Kristensen, K., Benthem, K. J., van, Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Mächler, M., & Bolker, B. M. (2017). glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. *The R Journal*, *9*(2), 378.

Brooks, S. P., & Gelman, A. (1998). General methods for monitoring convergence of iterative simulations. *Journal of Computational and Graphical Statistics*, *7*(4), 434.

Bustnes, J. O., & Erikstad, K. E. (1990). Size selection of common mussels, *Mytilus edulis*, by common eiders, *Somateria mollissima*: energy maximization or shell weight minimization? *Canadian Journal of Zoology*, *68*(11), 2280–2283.

Bustnes, J. O., & Systad, G. H. (2001). Comparative feeding ecology of Steller's eider and long-tailed ducks in winter. *Waterbirds: The International Journal of Waterbird Biology*, *24*(3), 407–412.

Caires, A. M., & Chandra, S. (2012). Conversion factors as determined by relative macroinvertebrate sampling efficiencies of four common benthic grab samplers. *Journal of Freshwater Ecology*, *27*(1), 97–109.

Clarke, K. R., Gorley, R. N., Somerfield, P. J., & Warwick, R. M. (2014). Change in marine communities: an approach to statistical analysis and interpretation. 3rd edition. PRIMER-e: Plymouth, UK.

Cooper, L. W. (1989). Patterns of carbon isotopic variability in eelgrass, *Zostera marina L.,* from Izembek Lagoon, Alaska. *Aquatic Botany*, *34*(4), 329–339.

Coyle, K. O., Konar, B., Blanchard, A., Highsmith, R. C., Carroll, J., Carroll, M., Denisenko, S. G., & Sirenko, B. I. (2007). Potential effects of temperature on the benthic infaunal community on the southeastern Bering Sea shelf: possible impacts of climate change. *Deep Sea Research Part II: Topical Studies in Oceanography*, *54*(23–26), 2885–2905.

Dau, C. P. (1987). Birds in nearshore waters of the Yukon-Kuskokwim Delta, Alaska. *The Murrelet*, *68*(1), 12–23.

Dau, C. P., Flint, P. L., & Petersen, M. R. (2000). Distribution of recoveries of Steller's eiders banded on the lower Alaska Peninsula, Alaska. *Journal of Field Ornithology*, *71*(3), 541–548.

De Leeuw, J. J., & Van Eerden, M. R. (1992). Size selection in diving tufted ducks *Aythya fuligula* explained by differential handling of small and large mussels *Dreissena polymorpha*. *ARDEA*, *80*(3), 353–362.

Draulans, D. (1982). Foraging and size selection of mussels by the tufted duck, *Aythya fuligula*. *Journal of Animal Ecology*, *51*(3), 943–956.

Draulans, D. (1984). Sub-optimal mussel selection by tufted ducks *Aythya fuligula*: test of a hypothesis. *Animal Behaviour*, *32*(4), 1192–1196.

Feng, Z., Ji, R., Ashjian, C., Zhang, J., Campbell, R., & Grebmeier, J. M. (2021). Benthic hotspots on the northern Bering and Chukchi continental shelf: spatial variability in production regimes and environmental drivers. *Progress in Oceanography*, *191*, 102497.

Flint, P. L., Petersen, M. R., Dau, C. P., Hines, J. E., & Nichols, J. D. (2000). Annual survival and site fidelity of Steller's eiders molting along the Alaska Peninsula. *The Journal of Wildlife Management*, *64*(1), 261–268.

Fredriksen, S., De Backer, A., Boström, C., & Christie, H. (2010). Infauna from *Zostera marina L.* meadows in Norway. Differences in vegetated and unvegetated areas. *Marine Biology Research*, *6*(2), 189–200.

Freitas, V., Campos, J., Fonds, M., & Van der Veer, H. W. (2007). Potential impact of temperature change on epibenthic predator–bivalve prey interactions in temperate estuaries. *Journal of Thermal Biology*, *32*(6), 328–340.

Frost, C. J., Hollmen, T. E., & Reynolds, J. H. (2013). Trends in annual survival of Steller's eiders molting at Izembek Lagoon on the Alaska Peninsula, 1993-2006. *Arctic*, *66*(2), 173–178.

Fujii, T. (2012). Climate change, sea-level rise and implications for coastal and estuarine shoreline management with particular reference to the ecology of intertidal benthic macrofauna in NW Europe. *Biology*, *1*(3), 597–616.

Gilbert, M. A. (1973). Growth rate, longevity and maximum size of *Macoma balthica (L.). The Biological Bulletin*, *145*(1), 119–126.

Goethel, C. L. (2021). Time-series focused assessments of changing marine bivalve communities in the Bering and Chukchi seas [PhD Dissertation]. University of Maryland.

Goodwin, K. D., Thompson, L. R., Duarte, B., Kahlke, T., Thompson, A. R., Marques, J. C., & Caçador, I. (2017). DNA Sequencing as a tool to monitor marine ecological status. *Frontiers in Marine Science*, *4*(107): 1–14.

Grebmeier, J. M. (2012). Shifting patterns of life in the Pacific Arctic and sub-Arctic seas. *Annual Review of Marine Science*, *4*(1), 63–78.

Grebmeier, J. M., & Cooper, L. W. (2016). The Saint Lawrence Island polynya: a 25-Year evaluation of an analogue for climate change in polar regions. In P. M. Gilbert & T. M. Kana (Eds.), *Aquatic Microbial Ecology and Biogeochemistry: A Dual Perspective* (pp. 171–183). Springer International Publishing.

Grebmeier, J. M., Cooper, L. W., Feder, H. M., & Sirenko, B. I. (2006a). Ecosystem dynamics of the Pacific-influenced northern Bering and Chukchi seas in the Amerasian Arctic. *Progress in Oceanography*, *71*(2–4), 331–361.

Grebmeier, J. M., Frey, K. E., Cooper, L. W., & Kedra, M. (2018). Trends in benthic macrofaunal populations, seasonal sea ice persistence, and bottom water temperatures in the Bering Strait region. *Oceanography*, *31*(2), 136–151.

Grebmeier, J. M., Overland, J. E., Moore, S. E., Farley, E. V., Carmack, E. C., Cooper, L. W., Frey, K. E., Helle, J. H., McLaughlin, F. A., & McNutt, S. L. (2006b). A major ecosystem shift in the northern Bering Sea. *Science*, *311*(5766), 1461–1464.

Green, G. A., & Brueggeman, J. J. (1991). Sea otter diets in a declining population in Alaska. *Marine Mammal Science*, *7*(4), 395–401.

Hartig, F. (2022). DHARMa: residual diagnostics for hierarchical (multi-level / mixed) regression models (R package version 0.4.6). https://CRAN.R-project.org/package=DHARMa

Hemminga, M. A., & Duarte, C. M. (2000). Seagrass ecology. Cambridge University Press.

Hodges, J. I., & Eldridge, W. D. (2001). Aerial surveys of eiders and other waterbirds on the eastern Arctic coast of Russia. *Wildfowl*, *52*, 127–142.

Hogrefe, K. R., Ward, D. H., Donnelly, T. F., & Dau, N. (2014). Establishing a baseline for regional scale monitoring of eelgrass (*Zostera marina*) habitat on the lower Alaska Peninsula. *Remote Sensing*, *6*(12), 12447–12477.

Hondolero, D., Bluhm, B. A., & Iken, K. (2012). Caloric content of dominant benthic species from the northern Bering and Chukchi seas: historical comparisons and the effects of preservation. *Polar Biology*, *35*(4), 637–644.

Howell, M. D., Grand, J. B., & Flint, P. L. (2003). Body molt of male long-tailed ducks in the near-shore waters of the North Slope, Alaska. *The Wilson Bulletin*, *115*(2), 170–175.

Jansen, J. M., Pronker, A. E., Kube, S., Sokolowski, A., Sola, J. C., Marquiegui, M. A., Schiedek, D., Wendelaar Bonga, S., Wolowicz, M., & Hummel, H. (2007). Geographic and seasonal patterns and limits on the adaptive response to temperature of European *Mytilus spp.* and *Macoma balthica* populations. *Oecologia*, *154*(1), 23–34.

Jensen, K. T., & Jensen, J. N. (1985). The importance of some epibenthic predators on the density of juvenile benthic macrofauna in the Danish Wadden Sea. *Journal of Experimental Marine Biology and Ecology*, *89*, 157–174.

Jones, R. D. (1965). Returns from Steller's eiders banded in Izembek Bay, Alaska. *The Wildfowl Trust*, *16*, 83–84.

Kertell, K. (1991). Disappearance of the Steller's eider from the Yukon-Kuskokwim Delta, Alaska. *Arctic*, *44*(3), 177–187.

Kindeberg, T., Severinson, J., & Carlsson, P. (2022). Eelgrass meadows harbor more macrofaunal species but bare sediments can be as functionally diverse. *Journal of Experimental Marine Biology and Ecology*, *554*, 151777.

Kistchinski, A. A. (1973). Waterfowl in north-east Asia. *Wildfowl*, *24*, 88–102.

Lenth, R. V. (2023). emmeans: estimated marginal means, aka least-squares means (R package version 1.8.7). https://CRAN.R-project.org/package=emmeans

Liu, F., & Kong, Y. (2023). zoib: bayesian inference for beta regression and zero-or-one inflated beta regression (R package version 1.6). https://CRAN.R-project.org/package=zoib

Liu, K., Lin, H., He, X., Huang, Y., Li, Z., Lin, J., Mou, J., Zhang, S., Lin, L., Wang, J., & Sun, J. (2019). Functional trait composition and diversity patterns of marine macrobenthos across the Arctic Bering Sea. *Ecological Indicators*, *102*, 673–685.

MacArthur, R. H., & Pianka, E. R. (1966). On optimal use of a patchy environment. *The American Naturalist*, *100*(916), 603–609.

McConnaughey, T. (1978). Ecosystems naturally labeled with carbon-13: applications to the study of consumer food-webs [M.S. Thesis]. University of Alaska Fairbanks.

McRoy, C. P. (1966). The standing stock and ecology of eelgrass (*Zostera marina L.*) in Izembek Lagoon, Alaska [M.S. Thesis]. University of Washington.

Meadows, C. A., Grebmeier, J. M., & Kidwell, S. M. (2019). High-latitude benthic bivalve biomass and recent climate change: testing the power of live-dead discordance in the Pacific Arctic. *Deep Sea Research Part II: Topical Studies in Oceanography*, *162*, 152–163.

Menne, M. J., Durre, I., Korzeniewski, B., McNeill, S., Thomas, K., Yin, X., Anthony, S., Ray, R., Vose, R., Gleason, B., & Houston, T. (2012a). Global historical climatology network - daily (GHCN-daily), version 3. NOAA National Climatic Data Center. Accessed 4 February 2024.

Menne, M. J., Durre, I., Korzeniewski, B., McNeill, S., Thomas, K., Yin, X., Anthony, S., Ray, R., Vose, R., Gleason, B., & Houston, T. (2012b). An overview of the global historical climatology network-daily database. *Journal of Atmospheric and Oceanic Technology*, *29,* 897-910.

Metzner, K. (1993). Ecological strategies of wintering Steller's eiders on Izembek Lagoon and Cold Bay, Alaska [M.S. Thesis]. University of Missouri.

Millet, B., & Guelorget, O. (1994). Spatial and seasonal variability in the relationships between benthic communities and physical environment in a lagoon ecosystem. *Marine Ecology Progress Series*, *108*(1), 161–174.

Ministry of Natural Resources of the Russian Federation. (2020). On approval of the list of wildlife objects listed in the Red Book of the Russian Federation (57940). Order, Red Data Book of the Russian Federation, Moscow, RU.

Möller, T., Kotta, J., & Martin, G. (2014). Spatiotemporal variability in the eelgrass *Zostera marina L.* in the north-eastern Baltic Sea: canopy structure and associated macrophyte and invertebrate communities. *Estonian Journal of Ecology*, *63*(2), 90.

Morrisey, D. J., Underwood, A. J., Howitt, L., & Stark, J. S. (1992). Temporal variation in soft-sediment benthos. *Journal of Experimental Marine Biology and Ecology,164*(2), 233–245.

National Oceanic and Atmospheric Administration National Centers for Environmental Information. (2023). Integrated surface dataset (global). https://registry.opendata.aws/noaa-isd

Norkko, A., Villnäs, A., Norkko, J., Valanko, S., & Pilditch, C. (2013). Size matters: implications of the loss of large individuals for ecosystem function. *Scientific Reports*, *3*(1), 2646.

North American Bird Conservation Initiative. (2022). The state of the birds, United States of America: 2022. U.S. State of the Birds Report.

Oppel, S., & Huettmann, F. (2010). Using a random forest model and public data to predict the distribution of prey for marine wildlife management. In *Spatial Complexity, Informatics, and Wildlife Conservation* (pp. 151–163). Springer Japan.

Ouellet, J. F., Vanpé, C., & Guillemette, M. (2013). The body size-dependent diet composition of North American sea ducks in winter. *PLoS ONE*, *8*(6).

Özkundakci, D., Gsell, A. S., Hintze, T., Täuscher, H., & Adrian, R. (2016). Winter severity determines functional trait composition of phytoplankton in seasonally ice-covered lakes. *Global Change Biology*, *22*(1), 284–298.

Paalme, T., Torn, K., Martin, G., Kotta, I., & Suursaar, Ü. (2020). Littoral benthic communities under effect of heat wave and upwelling events in the NE Baltic Sea. *Journal of Coastal Research*, *95*(sp1), 133.

Petersen, M. R. (1980). Observations of wing-feather moult and summer feeding ecology of Steller's eiders at Nelson Lagoon, Alaska. *Wildfowl*, *31*, 99–106.

Petersen, M. R. (1981). Populations, feeding ecology and molt of Steller's eiders. *The Condor*, *83*(3), 256–262.

Petersen, M. R. (2021). Benthos sample data from Izembek and Nelson lagoons, Alaska, 1998: U.S. Geological Survey data release. In *U.S. Geological Survey, Alaska Science Center.*

Petrich, C., Tivy, A. C., & Ward, D. H. (2014). Reconstruction of historic sea ice conditions in a sub-Arctic lagoon. *Cold Regions Science and Technology*, *98*, 55–62.

Phillips, R. C. (1984). Ecology of eelgrass meadows in the Pacific Northwest: a community profile. Federal Government Series Technical Report FWS/OBS-84/24, USGS Publications Warehouse, United States.

Prince, H. H. (1979). Bioenergetics of postbreeding dabbling ducks. In T. A. Bookhout (Ed.), *Waterfowl and Wetlands—an integrated review: Vol. Proc. 1977 Symp.* (pp. 103–117).

R Core Team. (2023). R: a language and environment for statistical computing. R Foundation for Statistical Computing. https://www.R-project.org/

Ratti, F. D. (1978). Reproduction and growth of the Pacific basket-cockle, *Clinocardium nuttallii Conrad*, from intertidal and subtidal environments of Netarts Bay [M.S. Thesis]. Oregon State University.

Reiss, H., Birchenough, S., Borja, A., Buhl-Mortensen, L., Craeymeersch, J., Dannheim, J., Darr, A., Galparsoro, I., Gogina, M., Neumann, H., Populus, J., Rengstorf, A. M., Valle, M., van Hoey, G., Zettler, M. L., & Degraer, S. (2015). Benthos distribution modelling and its relevance for marine ecosystem management. *ICES Journal of Marine Science*, *72*(2), 297–315.

Richman, S. E., & Lovvorn, J. R. (2003). Effects of clam species dominance on nutrient and energy acquisition by spectacled eiders in the Bering Sea. *Marine Ecology Progress Series*, *261*, 283–297.

Rodrigues, A. M., Quintino, V., Pereira, F., & Freitas, R. (2012). Alterations in macroinvertebrate spatial patterns in coastal lagoons: Óbidos (NW coast of Portugal) 1984 versus 2002. *Estuarine, Coastal and Shelf Science*, *110*, 176–189.

Rosenberg, D. H., Petrula, M. J., Schamber, J. L., Zwiefelhofer, D., Hollmén, T. E., & Hill, D. D. (2014). Seasonal movements and distribution of Steller's eiders (*Polysticta stelleri*) wintering at Kodiak Island, Alaska. *Arctic*, *67*(3), 347–359.

Rosenberg, D. H., Petrula, M. J., Zwiefelhofer, D., Hollmen, T., Hill, D. D., & Schamber, J. (2016). Seasonal movements and distribution of Pacific Steller's eiders (*Polysticta stelleri*). Final Wildlife Research Report ADF&G/DWC/WRR-2016-7, Alaska Department of Fish and Game, Division of Wildlife Conservation, Juneau, AK.

Savard, J.-P. L., & Petersen, M. R. (2015). Remigial molt of sea ducks. In J.-P. L. Savard, D. V Derksen, D. Esler, & J. M. Eadie (Eds.), *Ecology and Conservation of North American Sea Ducks* (pp. 305–336). CRC Press.

Schiaparelli, S., Schnabel, K. E., de Forges, B. R., & Chan, T. (2016). Sorting, recording, preservation and storage of biological samples. In *Biological Sampling in the Deep Sea* (pp. 338–367). Wiley.

Schiel, D. R., Steinbeck, J. R., & Foster, M. S. (2004). Ten years of induced ocean warming causes comprehensive changes in marine benthic communities. *Ecology*, *85*(7), 1833–1839.

Seitz, R. D., & Ewers Lewis, C. J. (2018). Loss of seagrass results in changes to benthic infaunal community structure and decreased secondary production. *Bulletin of Marine Science*, *94*(4), 1273–1292.

Sejr, M. K., Sand, M. K., Jensen, K. T., Petersen, J. K., Christensen, P. B., & Rysgaard, S. (2002). Growth and production of *Hiatella arctica* (Bivalvia) in a high-Arctic fjord (Young Sound, northeast Greenland). *Marine Ecology Progress Series*, *244*, 163–169.

Selin, N. I. (2010). The growth and life span of bivalve mollusks at the northeastern coast of Sakhalin Island. *Russian Journal of Marine Biology*, *36*(4), 258–269.

Sexson, M. G., Petersen, M. R., Breed, G. A., & Powell, A. N. (2016). Shifts in the distribution of molting Spectacled eiders (*Somateria fischeri*) indicate ecosystem change in the Arctic. *The Condor*, *118*(3), 463–476.

Smith, M. A., Sullender, B. K., Koeppen, W. C., Kuletz, K. J., Renner, H. M., & Poe, A. J. (2019). An assessment of climate change vulnerability for important bird areas in the Bering Sea and Aleutian Arc. *PLoS ONE*, *14*(4).

Stoker, S. W. (1978). Benthic invertebrate macrofauna of the eastern continental shelf of the Bering and Chukchi seas [PhD Dissertation]. University of Alaska, Fairbanks.

Strasser, M., Reinwald, T., & Reise, K. (2001). Differential effects of the severe winter of 1995/96 on the intertidal bivalves *Mytilus edulis, Cerastoderma edule* and *Mya arenaria* in the northern Wadden Sea. *Helgoland Marine Research*, *55*(3), 190–197.

Tippery, A. C. (2013). A temporal comparison of the eelgrass *(Zostera marina L.)* food web and community structure at Izembek Lagoon, Alaska from the mid-1970's to 2008 [M.S. Thesis]. University of Alaska, Fairbanks.

Tyler, A. V. (1973). Caloric values of some North Atlantic invertebrates. *Marine Biology*, *19*, 258–261.

U.S. Fish and Wildlife Service. (1997). Threatened status for the Alaska breeding population of the Steller's eider. In *Federal Register* (Vol. 62, Issue 112).

U.S. Fish and Wildlife Service. (2001). Final determination of critical habitat for the Alaska-breeding population of the Steller's eider. In *Federal Register* (Vol. 66, Issue 23, pp. 8850–8884).

U.S. Fish and Wildlife Service. (2019). Status assessment of the Alaska-breeding population of Steller's eiders. Published Report, U.S. Fish and Wildlife Service, Fairbanks Fish and Wildlife Field Office, Fairbanks, AK.

van der Veer, H. W., Cardoso, J. F. M. F., & van der Meer, J. (2006). The estimation of DEB parameters for various northeast Atlantic bivalve species. *Journal of Sea Research*, *56*(2), 107–124.

Ward, D. H. (2021). Point sampling data for eelgrass (*Zostera marina*) and seaweed distribution and abundance in bays adjacent to the Izembek National Wildlife Refuge, Alaska. In *U.S. Geological Survey,* Alaska Science Center.

Ward, D. H., & Amundson, C. L. (2019). Monitoring annual trends in the abundance of eelgrass (Zostera marina) at Izembek National Wildlife Refuge in 2018. Open-File Report 2019-1042, U.S. Geological Survey, Reston, VA.

Ward, D. H., Markon, C. J., & Douglas, D. C. (1997). Distribution and stability of eelgrass beds at Izembek Lagoon, Alaska. *Aquatic Botany*, *58*, 229–240.

Weitzman, B. P. (2013). Effects of sea otter colonization on soft-sediment intertidal prey assemblages in Glacier Bay, Alaska [M.A. Thesis]. University of California Santa Cruz.

Williams, A. R., Bowman, T. D., & Shults, B. S. (2016). Molting Pacific Steller's eider surveys in southwest Alaska, 2016. Unpublished Report, U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Wilson, H. M. (2018). Aerial survey of wintering Pacific brant and other species at the Izembek Lagoon Complex and the Sanak Islands, Alaska, 2018. Unpublished Report, U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Wilson, H. M. (2019a). Alaska winter brant aerial survey, Izembek Lagoon Complex and Sanak Islands, Alaska, 2019. Unpublished Report, U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Wilson, H. M. (2019b). Fall Izembek brant aerial survey, Alaska, 2018. Unpublished Report, U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, AK.

Wilson, J. G., & Fleeger, J. W. (2023). Estuarine benthos. In B. C. Crump, J. M. Testa, & K. H. Dunton (Eds.), *Estuarine Ecology* (3rd ed., pp. 253–273). John Wiley & Sons, Inc.

Wilt, L. M., Grebmeier, J. M., Miller, T. J., & Cooper, L. W. (2014). Caloric content of Chukchi Sea benthic invertebrates: modeling spatial and environmental variation. *Deep Sea Research Part II: Topical Studies in Oceanography*, *102*, 97–106.

Wong, M. C. (2018). Secondary production of macrobenthic communities in seagrass (*Zostera marina*, eelgrass) beds and bare soft sediments across differing environmental conditions in Atlantic Canada. *Estuaries and Coasts*, *41*(2).

World Register of Marine Species Editorial Board. (2024). World register of marine species. https://marinespecies.org. Accessed 2024-02-04.

Yeung, C., & McConnaughey, R. A. (2006). Community structure of eastern Bering Sea epibenthic invertebrates from summer bottom-trawl surveys 1982 to 2002. *Marine Ecology Progress Series*, *318*, 47–62.

Zhou, H., Zhang, Z., Chen, H., Sun, R., Wang, H., Guo, L., & Pan, H. (2010). Integrating a DNA barcoding project with an ecological survey: a case study on temperate intertidal polychaete communities in Qingdao, China. *Chinese Journal of Oceanology and Limnology*, *28*(4), 899–910.

Zwarts, L., & Wanink, J. H. (1993). How the food supply harvestable by waders in the Wadden Sea depends on the variation in energy density, body weight, biomass, burying depth and behaviour of tidal-flat invertebrates. *Netherlands Journal of Sea Research*, *31*(4), 441–476.

Žydelis, R., & Richman, S. E. (2015). Foraging behavior, ecology, and energetics of sea ducks. In J.-P. L. Savard, D. V Derksen, D. Esler, & J. M. Eadie (Eds.), *Ecology and Conservation of North American Sea Ducks* (pp. 241–265). CRC Press.

Figures

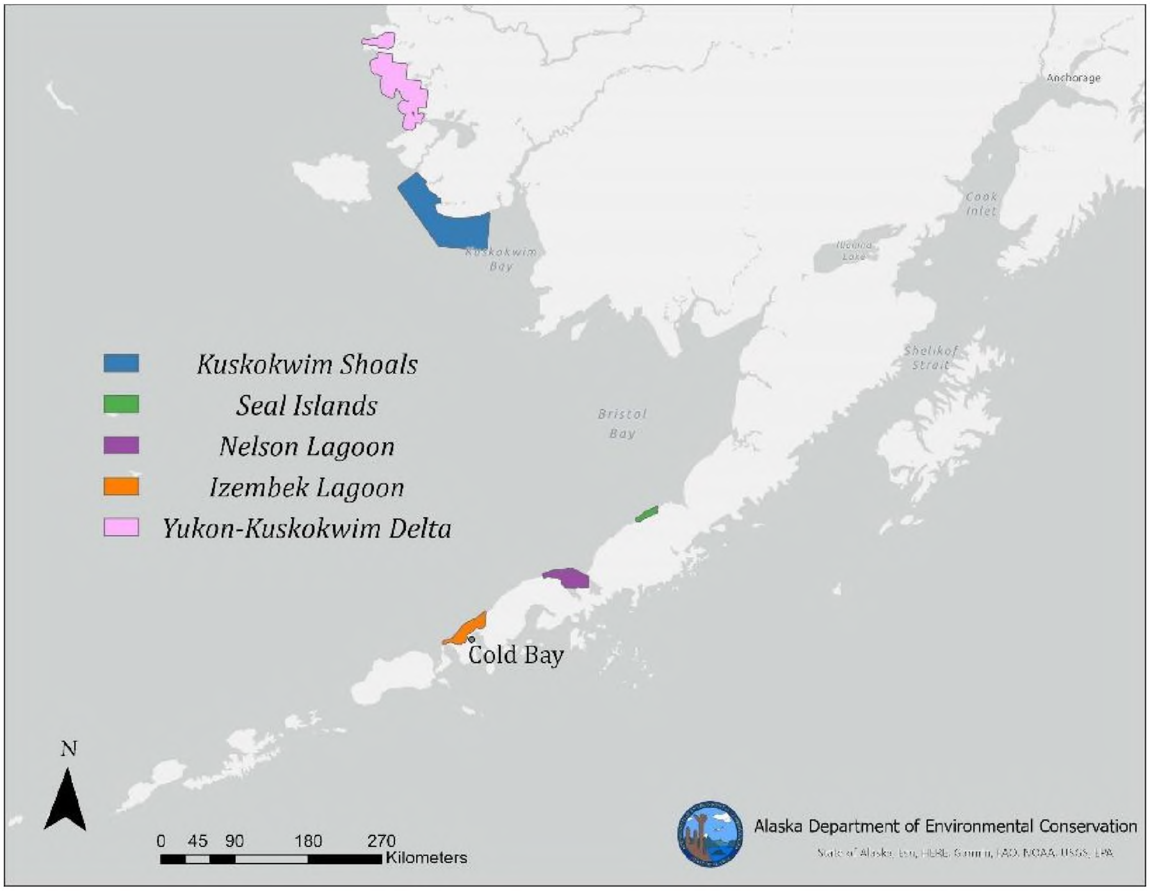

Figure 1. Designated critical habitats for Steller's eiders by the U.S. Fish and Wildlife Service in 2001 (U.S. Fish and Wildlife Service, 2001).

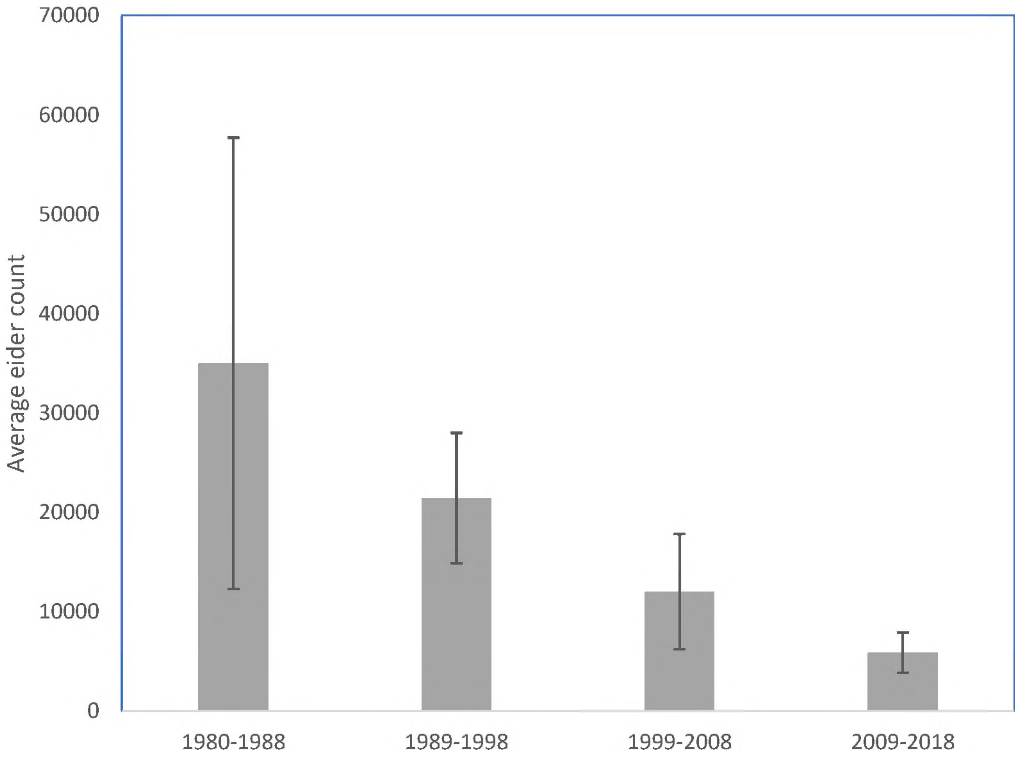

Figure 2. Average Steller's eider counts within 10-year survey periods from fall aerial surveys conducted at Izembek Lagoon, Alaska between September 23 and October 31 (data source: Wilson, 2019b). Error bars represent ± 1 standard deviation.

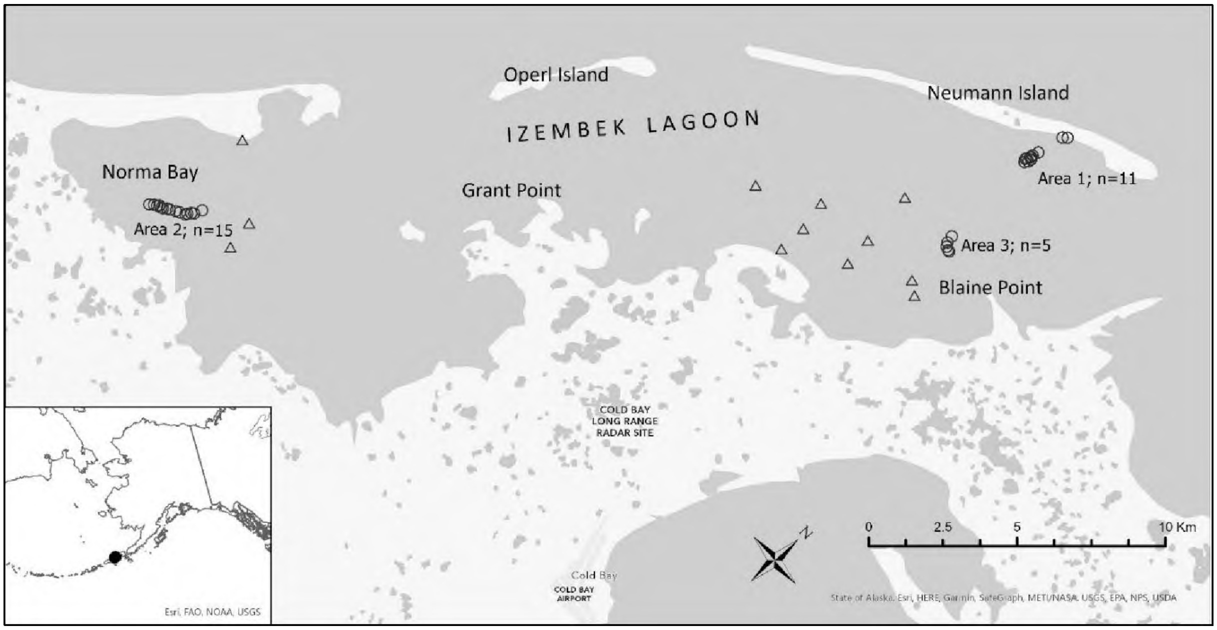

Figure 3. Map of benthic sampling locations in Izembek Lagoon, Izembek State Game Refuge, Alaska, where grab samples were collected in fall 1998, 2018, and 2019. Circles denote areas sampled for community composition and biomass comparisons (1998, 2018, 2019) and triangles represent additional stations added for size comparison analyses (only sampled in 2019).

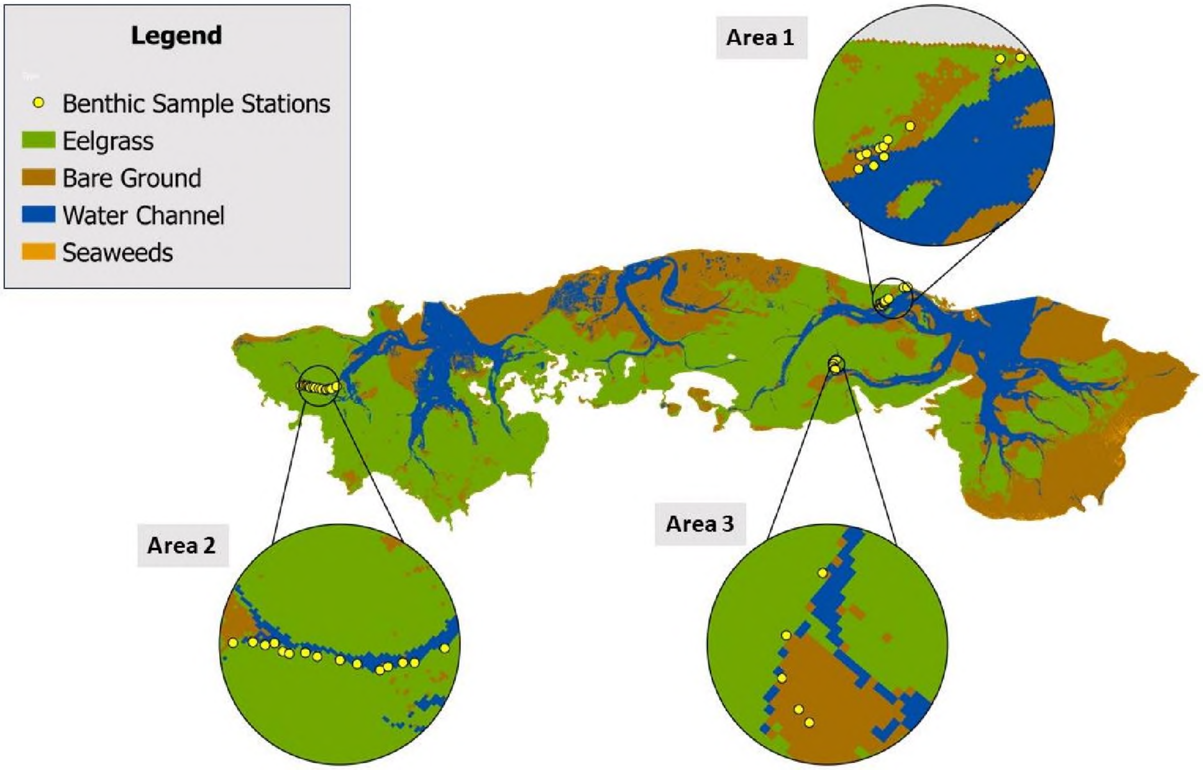

Figure 4. Landform types within Izembek Lagoon, Alaska from layers developed by Hogrefe et al. (2014) for each of the three benthic sampling areas in this study.

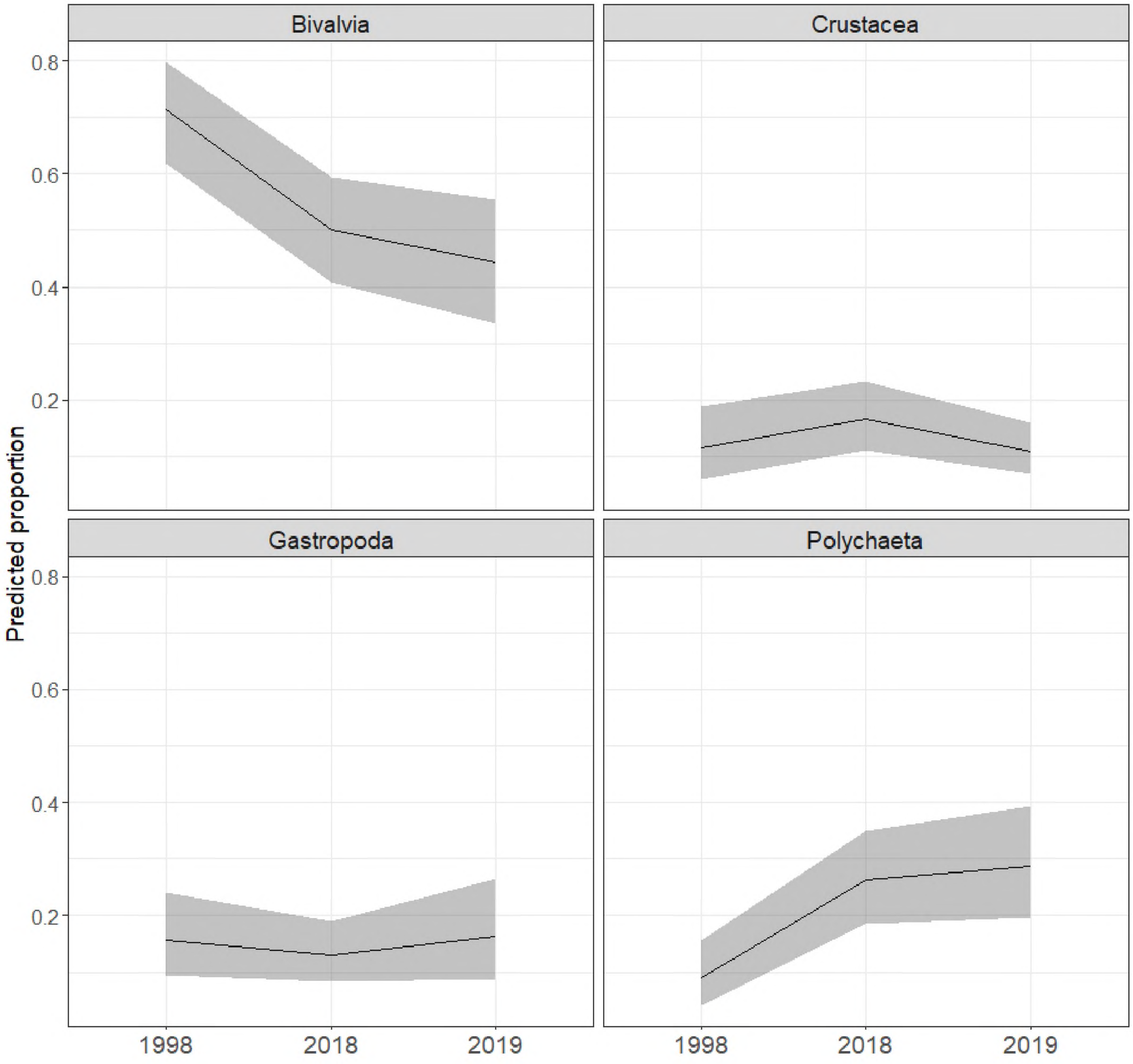

Figure 5. Zero-inflated beta regression model predictions with 95% confidence intervals for trends in relative biomass (%) for groups Bivalvia, Crustacea, Gastropoda, and Polychaeta among years 1998, 2018, and 2019, from benthic samples collected in Izembek Lagoon, Alaska.

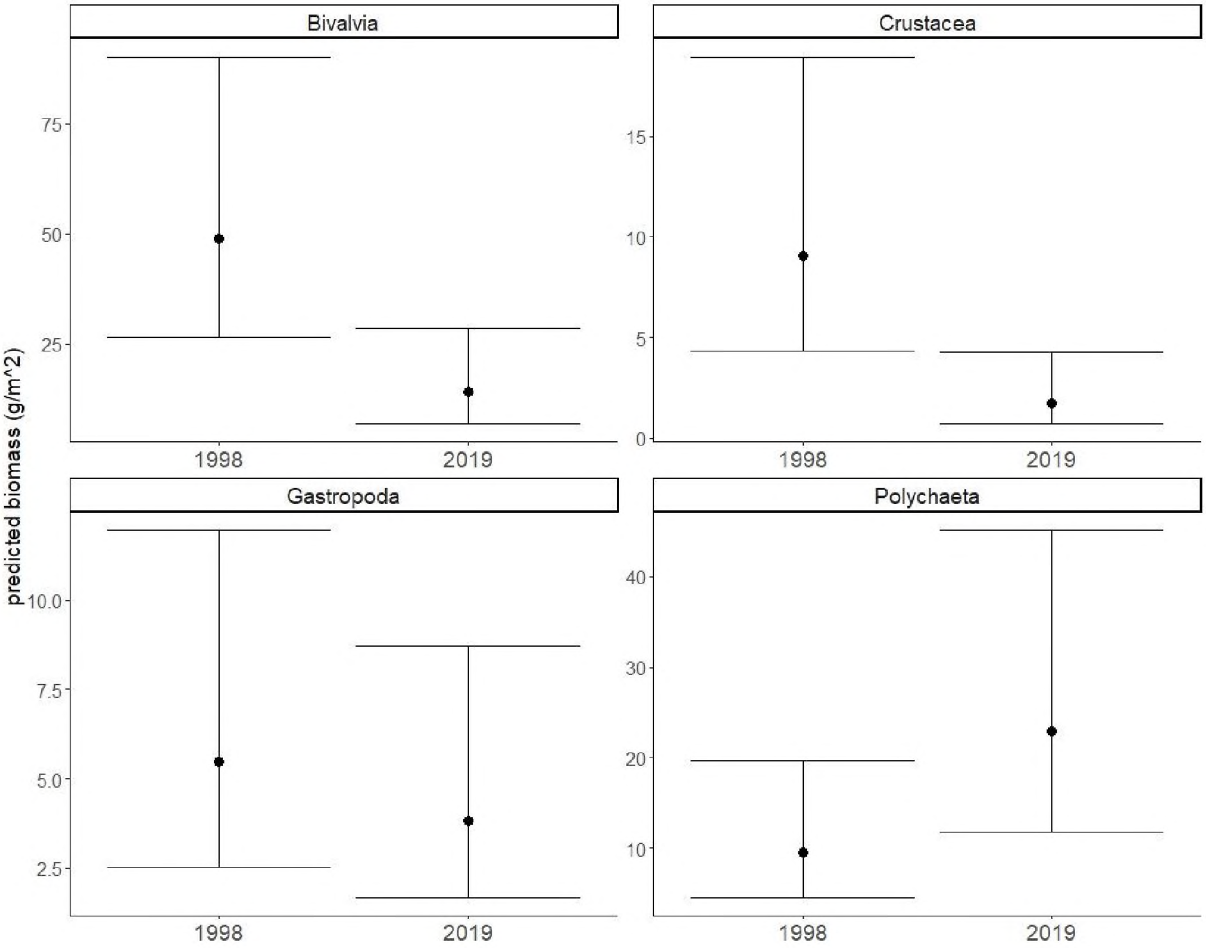

Figure 6. Tweedie model predictions of the overall biomass (g/m^2) of groups Bivalvia, Crustacea, Gastropoda, and Polychaeta between years 1998 and 2019 from benthic samples collected in Izembek Lagoon, Alaska. Error bars represent the 95% confidence intervals.

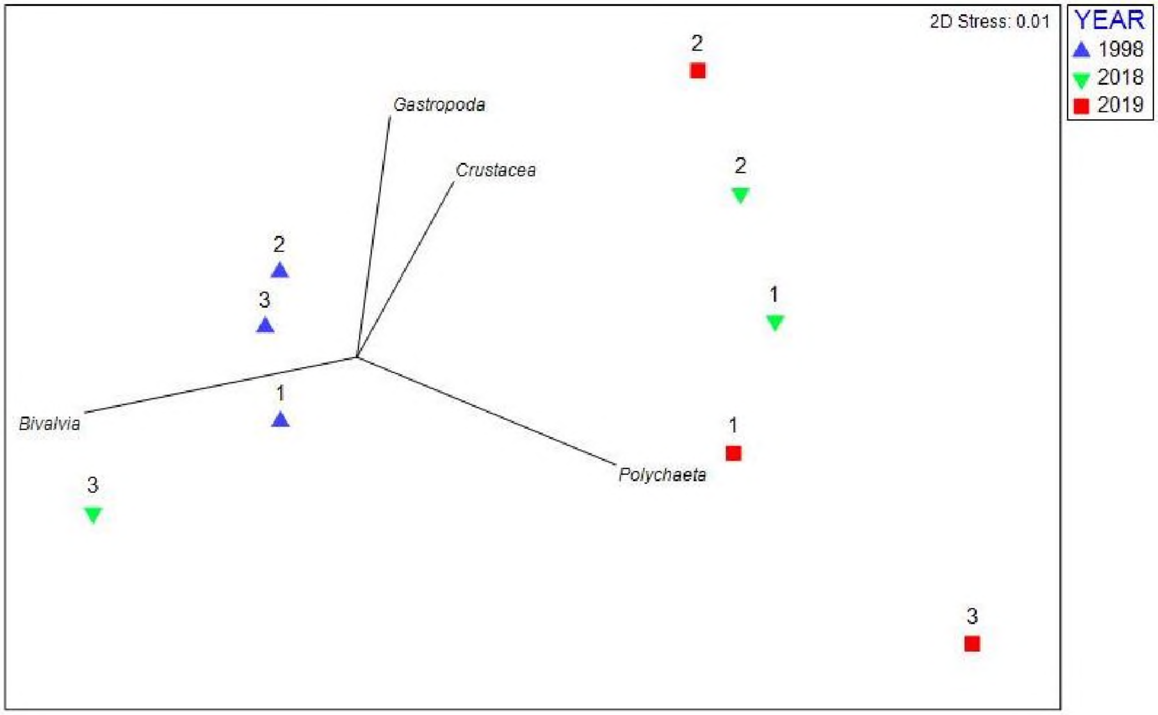

Figure 7. Non-metric multidimensional scaling ordination plot of benthic community composition based on relative biomass (%) for three areas (represented by numbers above shapes) sampled in Izembek Lagoon, Alaska, among years 1998, 2018, and 2019. Colored shapes represent the community composition based on the average relative biomass of each taxonomic group for the Year-Area factor and plotted in 2D space (stress = 0.01) from the Bray-Curtis dissimilarity of average relative biomass values using 500 iterations. Vector overlay indicates compositional grouping contributing most to separation of data.

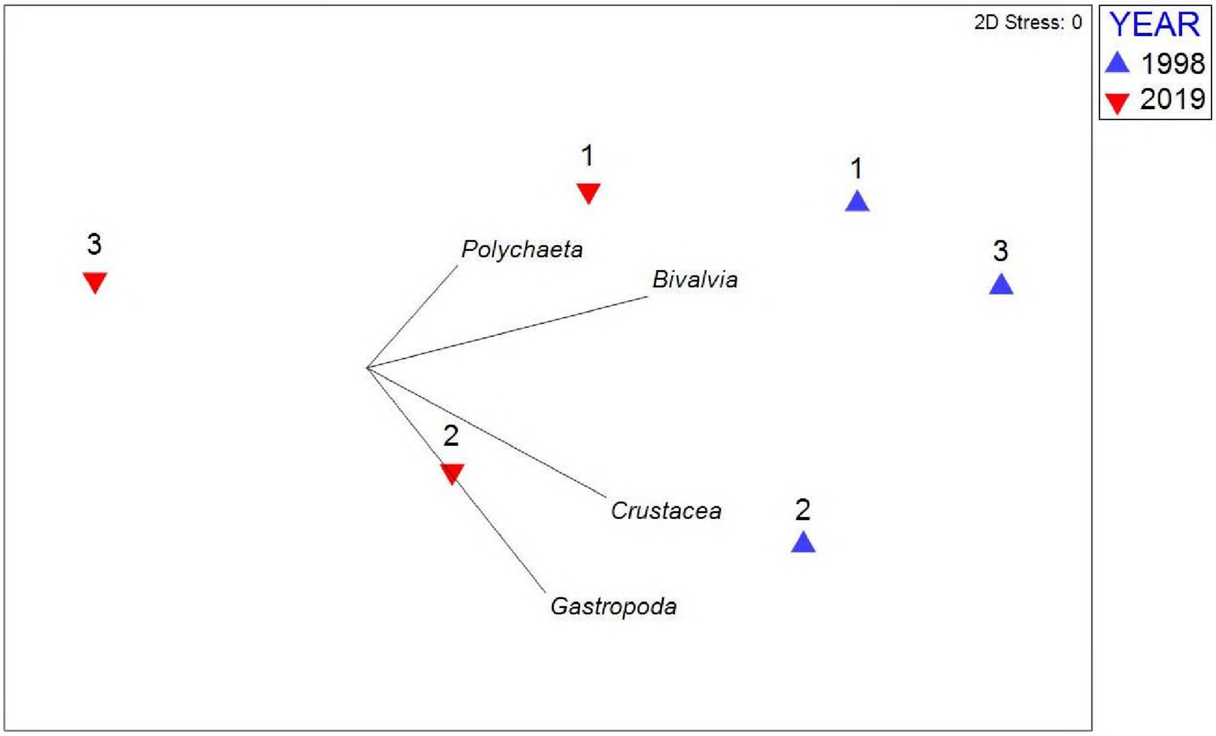

Figure 8. Non-metric multidimensional scaling ordination plot of benthic community composition based on overall biomass (g/m^2) for three areas (represented by numbers above shapes) sampled in Izembek Lagoon, Alaska, between years 1998 and 2019. Colored shapes represent the community composition based on the average overall biomass of each taxonomic group for the Year-Area factor and plotted in 2D space (stress = 0) from Euclidean distances of average overall biomass values using 500 iterations. Vector overlay indicates compositional grouping contributing most to separation of data.

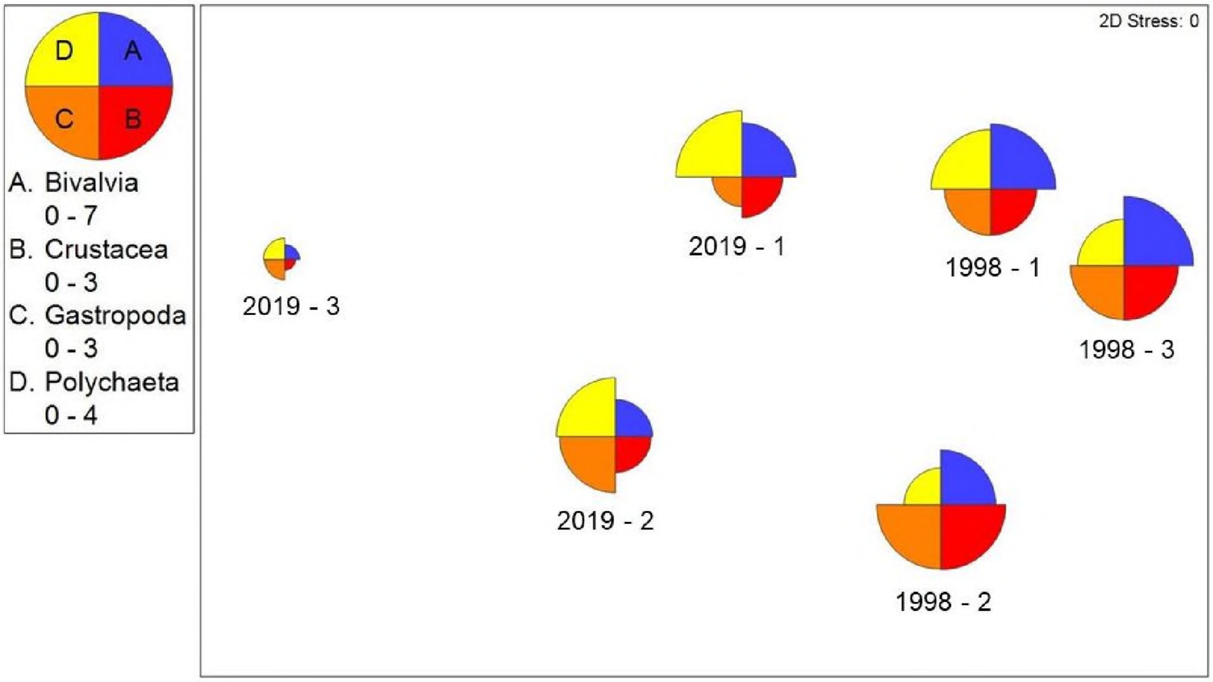

Figure 9. Non-metric multidimensional scaling ordination plot of benthic community composition based on overall biomass (g/m^2) for three areas (1, 2, 3) sampled in Izembek Lagoon, Alaska, between years 1998 and 2019. Bubble plots display the resemblance in community composition for factor 'Year – Area'. Colors correspond to taxonomic groups: Bivalvia (A), Crustacea (B), Gastropoda (C), and Polychaeta (D); size of pie slices is scaled to the maximum value of the square root mean overall biomass for each prey group. Plots were constructed from Euclidean distances of average square root overall biomass values using 500 iterations.

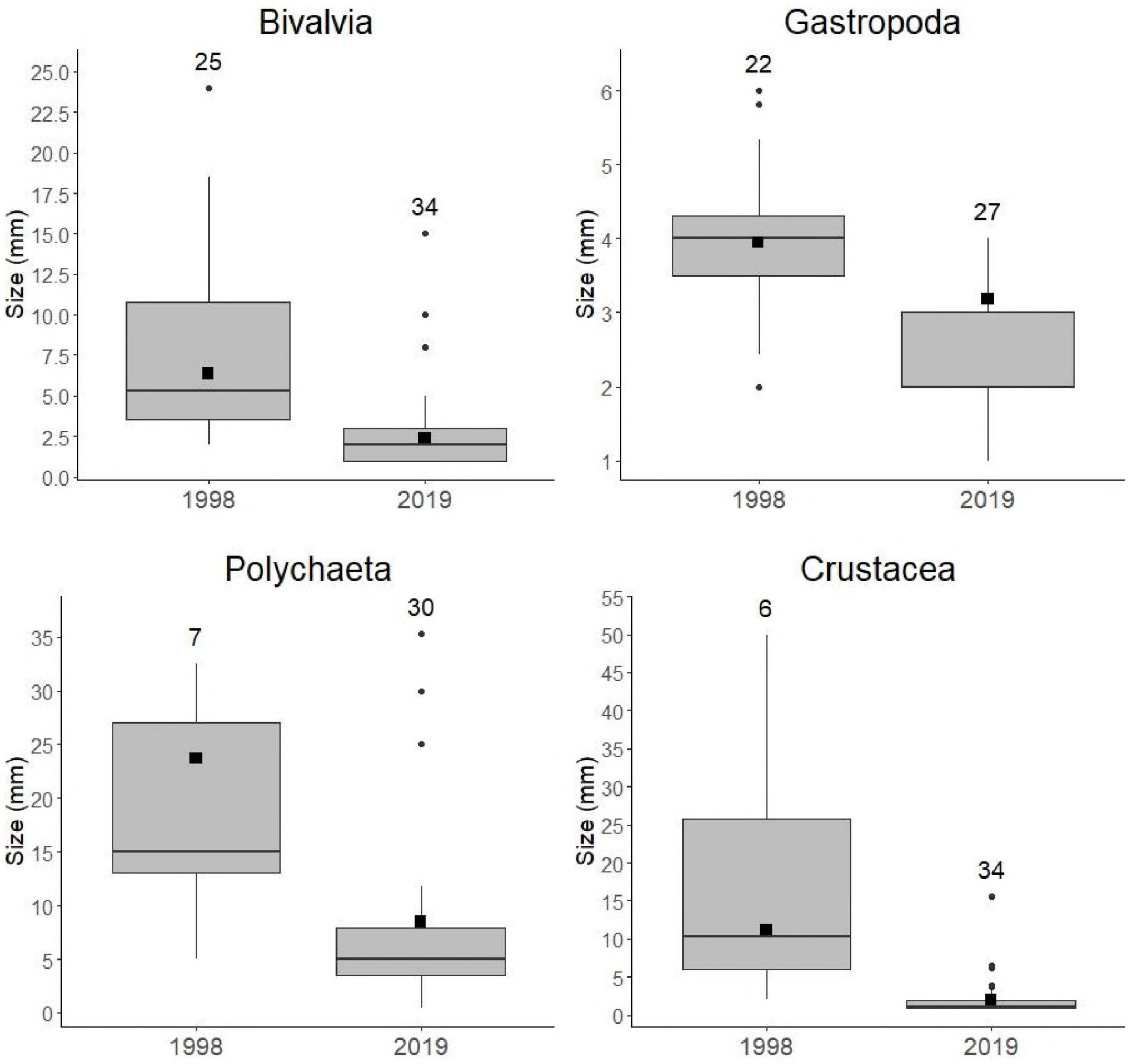

Figure 10. Observed size (mm) of bivalves, gastropods, polychaetes, and crustaceans in 1998 and 2019 from benthic samples collected in Izembek Lagoon, Alaska. Boxplots show the interquartile range, with bolded horizontal line representing the median, and black circles representing outliers. Text above boxplots displays the number of samples containing the taxonomic group (representing whole organisms) for each year. Black squares represent the weighted mean (adjusted by the number of whole organisms per sample).

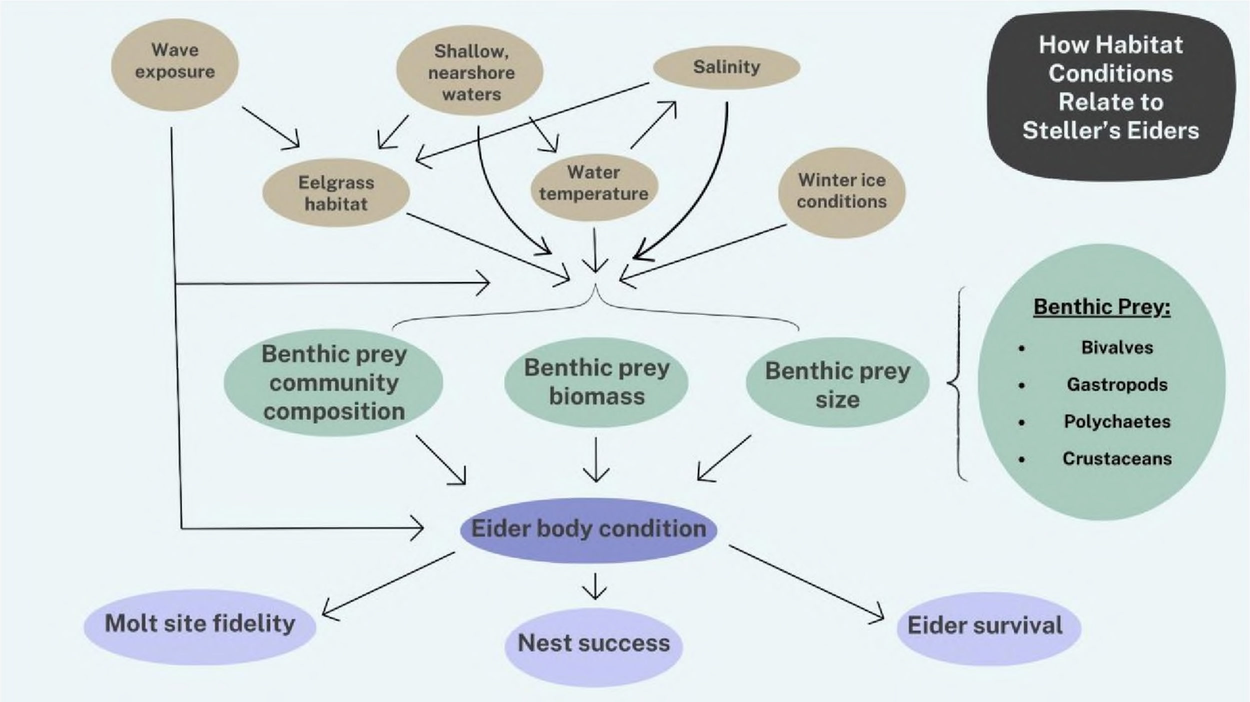

Figure 11. Conceptual model linking some habitat variables to various metrics of benthic prey in Izembek Lagoon, Alaska, which could impact Steller's eiders.

Tables

Table 1. Summary statistics for total sample weights of benthic samples collected from Izembek Lagoon, Alaska, using Petite Ponar (0.023 m^2; 1998 and 2019) and Ekman (0.023 m^2; 2018) grab samplers.

	Fall 1998	Fall 2018	Fall 2019
Number of samples	32	36	31
Min (g)	6	114.6	1.3
Max (g)	1512	1108.3	1956.88
Mean (g) ± 1 S.D.	205.5 ± 290.92	546.7 ± 235.22	275.76 ± 405.61
Median (g)	107	533.8	126.47
Combined total sample weight (g)	6575	19,679.87	8548.71

Table 2. Frequency of occurrence (%) of marine benthic groups Bivalvia, Crustacea, Gastropoda, and Polychaeta between factors Year and Area in benthic samples collected at Izembek Lagoon, Alaska. N = number of samples.

Factor		N	Bivalvia (%)	Crustacea (%)	Gastropoda (%)	Polychaeta (%)
Year	1998	32	96.88	46.88	75.00	37.50
	2018	35	100.00	77.14	71.43	80.00
	2019	31	80.65	77.42	51.61	77.42
Area	1	38	100.00	78.95	63.16	84.21
	2	45	91.11	68.89	77.78	53.33
	3	15	80.00	33.33	40.00	53.33

Table 3. Wet weight mean biomass (g/m^2) ± 1 standard deviation of bivalves, crustaceans, gastropods, and polychaetes between Years 1998 and 2019, and for Areas 1, 2, and 3 sampled in Izembek Lagoon, Alaska. Mean total biomass for bivalves and gastropods excludes partials (fragments) for mean biomass estimates. N = number of samples.

	Area	Bivalvia	Crustacea	Gastropoda	Polychaeta	N
1998	1	57.75 ± 88.24	3.20 ± 5.53	3.12 ± 4.79	16.80 ± 32.12	11
	2	24.69 ± 73.59	13.33 ± 23.15	6.58 ± 9.46	4.61 ± 13.22	15
	3	65.07 ± 97.95	9.20 ± 18.43	7.10 ± 13.16	8.12 ± 14.20	6
2019	1	29.20 ± 44.10	2.22 ± 4.24	0.94 ± 2.39	32.65 ± 92.91	11
	2	7.63 ± 13.57	1.94 ± 6.19	7.16 ± 14.14	23.50 ± 69.74	15
	3	0.15 ± 0.27	0.01 ± 0.01	0.16 ± 0.37	0.13 ± 0.20	5

Table 4. Predicted overall biomass (g/m^2) of marine benthic invertebrate groups in 1998 and 2019, and contrasts between years from Tweedie regression models testing the fixed effect of Year on total biomass of each benthic group. Overall biomass predictions for bivalves and gastropods are based on whole organism biomass only (partial shell fragments excluded).

	Year	Predicted biomass (g/m^2) and 95% CI	Year comparison	
			z-ratio	*p*
Bivalvia	1998	49.04 (26.63 – 90.30)	2.61	0.04
	2019	14.08 (6.90 – 28.71)		
Gastropoda	1998	4.59 (2.52 – 11.96)	0.62	1.00
	2019	3.82 (1.67 – 8.72)		
Polychaeta	1998	9.46 (4.54 – 19.69)	-1.75	0.32
	2019	22.98 (11.70 – 45.12)		
Crustacea	1998	9.08 (4.35 – 18.96)	2.80	0.02
	2019	1.73 (0.70 – 4.25)		

Table 5. PERMANOVA results testing marginal contribution (Type III) of fixed effects Year (1998, 2018, 2019), Area (1, 2, 3), and the interaction of Year and Area on differences in benthic community composition based on relative biomass (%) among samples collected in Izembek Lagoon, Alaska in fall 1998, 2018, and 2019. Analysis was based on Bray-Curtis dissimilarities from relative biomass data using 9999 permutations.

	df	SS	MS	Pseudo-F	*p*	Unique perms
Year	2	13052.00	6526.20	4.77	< 0.01	9952
Area	2	6807.90	3403.90	2.49	0.03	9948
Year x Area	4	7971.60	1992.90	1.46	0.16	9935
Residuals	87	1.20E5	1368.70			

Table 6. Summary of pairwise PERMANOVA results (Type III) testing for differences in benthic community composition at Izembek Lagoon, Alaska by fixed effects Year (1998, 2018, 2019), Area (1, 2, 3), and the interaction of Year and Area paired by factor Year. Analysis is based on the Bray-Curtis dissimilarity of relative biomass (%) using 9999 permutations.

Year	1998	2018
2018	$p = 0.05$	-
2019	$p < 0.01$	$p = 0.10$

Table 7. Summary of pairwise PERMANOVA results (Type III) testing for differences in benthic community composition at Izembek Lagoon, Alaska by fixed effects Year (1998, 2018, 2019), Area (1, 2, 3), and the interaction of Year and Area and paired by factor Area. Analysis is based on the Bray-Curtis dissimilarity of relative biomass using 9999 permutations.

Area	1	2
2	$p = 0.02$	-
3	$p = 0.38$	$p = 0.10$

Table 8. Summary of Pairwise PERMANOVA results (Type III) testing for differences in benthic community composition at Izembek Lagoon, Alaska with the interaction of terms Year and Area, and paired by the factor Year (1998, 2018, 2019) within Area (1, 2, 3). Analysis is based on the Bray-Curtis dissimilarity of relative biomass (%) using 9999 permutations.

Area	Year	1998	2018
1	2018	$p < 0.01$	-
	2019	$p = 0.05$	$p = 0.54$
2	2018	$p = 0.04$	-
	2019	$p = 0.08$	$p = 0.66$
3	2018	$p = 0.32$	-
	2019	$p = 0.03$	$p = 0.03$

Table 9. PERMANOVA results (Type III) of fixed effects Year (1998, 2019), Area (1, 2, 3), and the interaction of Year and Area on testing the fixed effect year on differences in benthic community composition based on overall biomass (g/m^2) among samples collected in Izembek Lagoon, AK in fall 1998 and 2019. Analysis was based on the Euclidean distance from overall biomass data using 9999 permutations.

	df	SS	MS	Pseudo-F	*p*	Unique perms
Year	1	154.48	154.48	3.97	0.02	9944
Area	2	93.39	46.69	1.20	0.30	9938
Year x Area	2	54.81	27.40	0.70	0.63	9946
Residuals	54	2100.2	38.89			

Table 10. Summary of Pairwise PERMANOVA results (Type III) testing for differences in benthic community composition at Izembek Lagoon, Alaska with the interaction of terms Year and Area, and paired by the factor Year (1998, 2019) within Area (1, 2, 3). Analysis is based on the Euclidean distance from overall biomass (g/m^2) data using 9999 permutations.

Area	Year	1998
1	2019	$p = 0.66$
2	2019	$p = 0.11$
3	2019	$p = 0.05$

Table 11. Results of generalized linear models with a Gamma distribution and 'log' link function testing the effect of Year on size (mm) of individual taxonomic groups, weighted by the number of whole organisms detected per benthic sample collected in Izembek Lagoon, Alaska. Results show the estimate, standard error (S.E.), z-values, p-values, and the residual degrees of freedom (resid df).

Group	Year	Estimate	S.E.	z-value	*p*	resid df
Bivalvia	1998	1.85	0.03	58.68	<0.01	56
	2019	-0.98	0.03	-28.37	<0.01	
Gastropoda	1998	1.37	0.03	47.02	<0.01	46
	2019	-0.22	0.03	-6.76	<0.01	
Polychaeta	1998	3.17	0.14	23.19	<0.01	34
	2019	-1.02	0.14	-7.42	<0.01	
Crustacea	1998	2.41	0.12	19.85	<0.01	37
	2019	-1.72	0.12	-13.98	<0.01	

Table 12. Predicted mean size (mm) for each benthic group for the years 1998 and 2019 in Izembek Lagoon, Alaska from generalized linear models with a Gamma distribution and 'log' link function. Results show the predicted size (mm), standard error (S.E.), and the 95% confidence intervals (95% CI).

Group	Year	Predicted size (mm)	S.E.	95% CI
Bivalvia	1998	6.37	0.20	5.98 – 6.77
	2019	2.38	0.03	2.31 – 2.45
Gastropoda	1998	3.95	0.12	3.73 – 4.19
	2019	3.18	0.04	3.10 – 3.26
Polychaeta	1998	23.74	3.24	18.17 – 31.03
	2019	8.51	0.18	8.17 – 8.88
Crustacea	1998	11.17	1.36	8.80 – 14.18
	2019	2.00	0.04	1.92 – 2.08

Appendix A: Supplemental Information

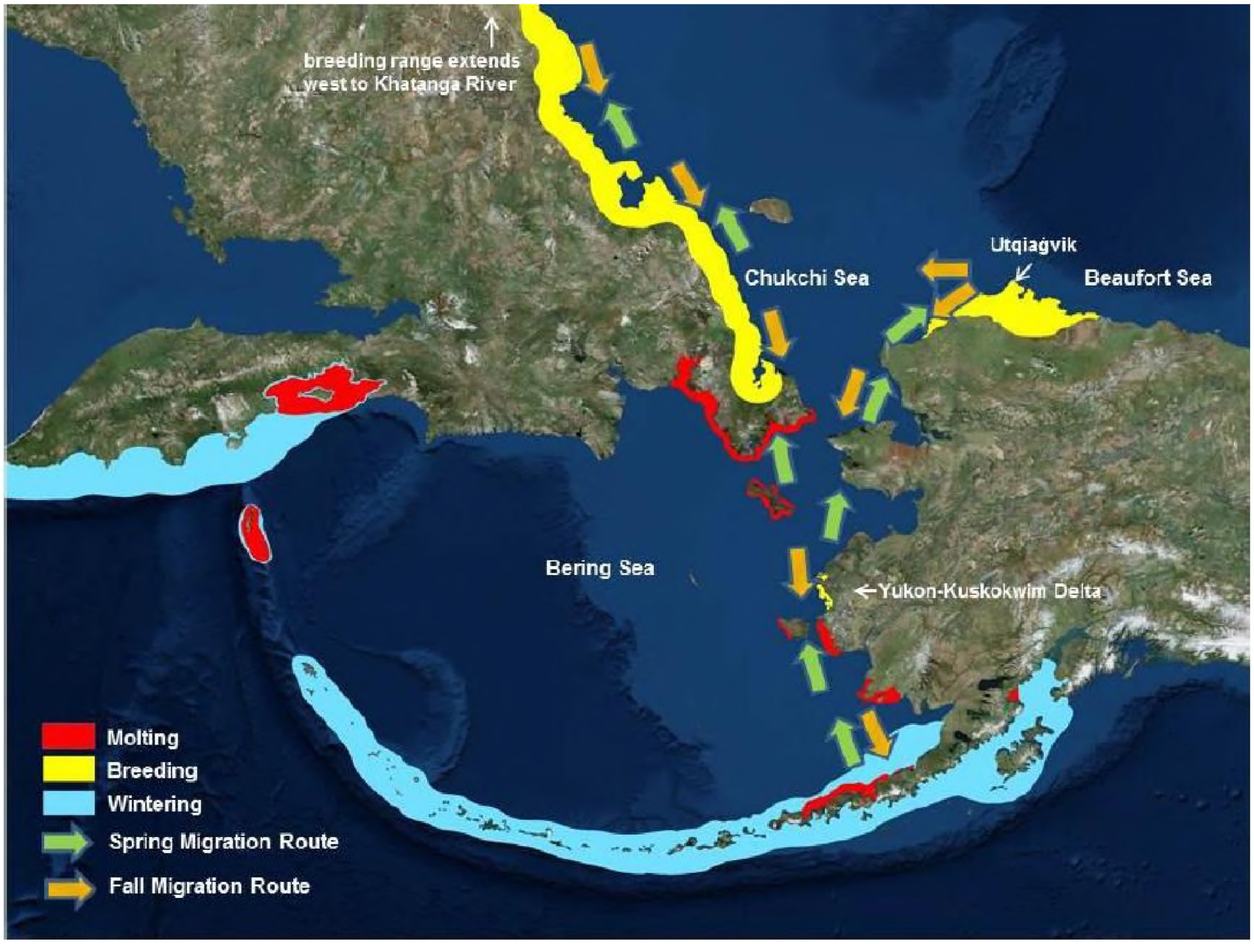

Figure A1. The Pacific population of Steller's eiders' distribution at various stages of the annual cycle (molting, breeding, wintering) and general migration routes (arrows) (Figure from: U.S. Fish and Wildlife Service, 2019).

Table A1. Mean monthly ambient air temperatures (°C) at Cold Bay, Alaska Airport (Station ID: USW00025624) near Izembek Lagoon from NOAA National Centers for Environmental Information (2023). Bolded numbers denote temperatures exceeding 2 °C from the mean temperature normals (1981-2010), with red text indicative of warmer temperatures and blue text indicative of colder temperatures.

	January	February	March	April	May	June	July	August	September	October	November	December
Mean temperature normal 1981-2010	-2.11	-1.67	-1.06	1.11	4.61	7.94	10.5	11.17	8.94	4.67	1.39	-0.5
1998	**-4.16**	-2.27	**2.01**	2.82	4.72	8.57	10.63	10.7	8.12	4.09	1.322	-2.17
2018	-0.64	**2.33**	**1.65**	**3.48**	5.06	8.91	11.2	11.68	10.57	**6.96**	**4.26**	-0.93
2019	**0.56**	**3.22**	**1.98**	**3.63**	**6.39**	**9.97**	**12.84**	**14.09**	**11.08**	**7.06**	**5.19**	0.44

Table A2. Identified marine invertebrates in Izembek Lagoon, Alaska from previous studies. This study was intended to replicate benthic surveys conducted in fall 1998 by Petersen (2021). The marine organisms identified by Metzner (1993) were ingested by collected Steller's eiders at Izembek Lagoon in the fall and winter months between 1979-1981. Tippery (2013) replicated work by McConnaughey (1978), where they collected many marine organisms using various field methods (sediment cores, by hand, seins, push-nets) from Grant Point, Izembek Lagoon for stable isotope analyses. Names of organisms and classification may have been changed to be in accordance with current accepted status by the World Register of Marine Species Editorial Board (2024).

Identified Organisms	**Petersen (2021)** Fall 1998	**Metzner (1993)** Fall /Winter 1979 - 1981	**Tippery (2013)** Summer 2008	**McConnaughey (1978)** Summer 1977
Annelida				
Polychaeta				
Terebillida				
Pectinariidae				
Cistenides	X			
Cistenides granulata		X		
Sabellida				
Serpulidae		X		
Spionida				
Rhynchospio				X
Scolecida				
Arenicolidae				
Abarenicola pacifica			X	
Arenicola marina glacialis				X
Orbiniidae			X	
Leodamas				X
Maldanidae			X	X
Phyllodocida				
Sigalionidae		X		
Phyllodocidae				
Eteone longa			X	
Polynoidae			X	
Harmothoe imbricata			X	
Nephtyidae				
Nephtys caeca				X
Echiuroidea				
Echiurus echiurus alascanus		X		X
Sipuncula			X	
Golfingia			X	

Table A2 cont.

Identified Organisms cont.	**Petersen (2021)** Fall 1998	**Metzner (1993)** Fall /Winter 1979 - 1981	**Tippery (2013)** Summer 2008	**McConnaughey (1978)** Summer 1977
Cnidaria				
Hydrozoa				
Gonionemus vertens				X
Scyphozoa				
Cyanea capillata			X	
Crustacea				
Malacostraca				
Amphipoda	X			
Phoxocephalidae	X			
Uristidae				
Anonyx	X			
Atylidae				
Atylus collingi		X		
Stenothoidae				
Hardametopa nasuta				X
Caprellidae	X			
Caprella		X		
Caprella alaskana			X	X
Ischyroceridae				
Microjassa		X		
Ampithoidae				
Ampithoe	X			X
Anisogammaridae				
Anisogammarus		X	X	X
Anisogammarus pugettensis		X		
Dogielinotidae				
Allorchestes		X		
Talitridae				
Orchestoidea			X	
Pontogeneiidae				
Pontogeneia		X		
Calliopiidae				
Calliopius				
Calliopius laeviusculus				X
Oradarea				X
Mysida				
Mysidae				
Holmesiella anomala			X	
Cumacea		X		
Decapoda				
Caridea			X	
Thoridae				
Heptacarpus camtschaticus				X

Table A2 cont.

Identified Organisms cont.	**Petersen (2021)** Fall 1998	**Metzner (1993)** Fall /Winter 1979 - 1981	**Tippery (2013)** Summer 2008	**McConnaughey (1978)** Summer 1977
Crustacea – Decapoda continued				
Crangonidae				
Crangon	X			
Crangon septemspinosa				X
Crangon dalli				X
Paguridae	X			
Elassochirus tenuimanus	X			
Pagurus hirsutiusculus				X
Epialtidae				
Pugettia gracilis	X			
Majidae		X		
Cheiragonidae				
Telmessus cheiragonus			X	X
Isopoda				
Chaetiliidae				
Saduria entomon	X			
Munnidae				
Munna spinifrons		X		
Idoteidae				
Idotea			X	
Thecostraca				
Balanus	X			X
Balanus glandula			X	X
Hexapoda				
Coelopa frigida			X	
Echinodermata				
Asteroidea				
Asteriidae	X			
Leptasterias				X
Evasterias				X
Evasterias troschelii			X	X
Echinoidea		X		
Echinarachnius parma	X			
Mollusca				
Bivalvia	X			
Adapedonta				
Hiatellidae				
Hiatella arctica	X			
Pharidae				
Siliqua patula	X			
Cardiida				
Cardiidae				
Clinocardium nuttallii	X			

Table A2 cont.

Identified Organisms cont.	**Petersen (2021)** Fall 1998	**Metzner (1993)** Fall /Winter 1979 - 1981	**Tippery (2013)** Summer 2008	**McConnaughey (1978)** Summer 1977
Mollusca – Bivalvia – Cardiida continued				
Tellinidae				
Macoma	X	X		
Macoma balthica	X	X	X	X
Macoma golikovi	X			
Macoma inquinata	X			
Macoma moesta	X			
Lucinida				
Axinopsida serricata	X			
Myida				
Mya truncata	X			
Mya arenaria				X
Venerida				
Mactridae				
Mactromeris	X			
Veneridae				
Turtonia minuta		X	X	X
Mytilida				
Mytilidae	X			
Mytilus trossulus	X			
Mytilus edulis		X		
Gastropoda				
Heterobranchia				
Cylichnidae				
Cylichna alba	X			
Cylichna attonsa	X			
Pyramidellidae				
Odostomia	X			
Caenogastropoda				
Littorinidae				
Lacuna	X			
Lacuna vincta	X			
Lacuna variegata				X
Littorina				
Littorina sitkana			X	X
Rissoidae				
Boreocingula martyni			X	
Naticidae	X			
Cryptonatica affinis	X	X		
Euspira pallida	X			
Mangeliidae				
Obesotoma simplex	X			
Muricidae				
Nucella lima	X			

Table A2 cont.

Identified Organisms cont.	**Petersen (2021)** Fall 1998	**Metzner (1993)** Fall /Winter 1979 - 1981	**Tippery (2013)** Summer 2008	**McConnaughey (1978)** Summer 1977
Mollusca – Gastropoda – Caenogastropoda – Muricidae continued				
Nucella canaliculata			X	
Nucella lamellosa				X
Buccinidae				
Volutopsius		X		
Vetigastropoda				
Margaritidae				
Margarites		X		
Margarites pupillus	X	X		
Margarites helicinus	X		X	X
Patellogastropoda				
Lottiidae				
Lottia digitalis			X	
Lottia persona			X	
Testudinalia testudinalis				X
Nemertea			X	

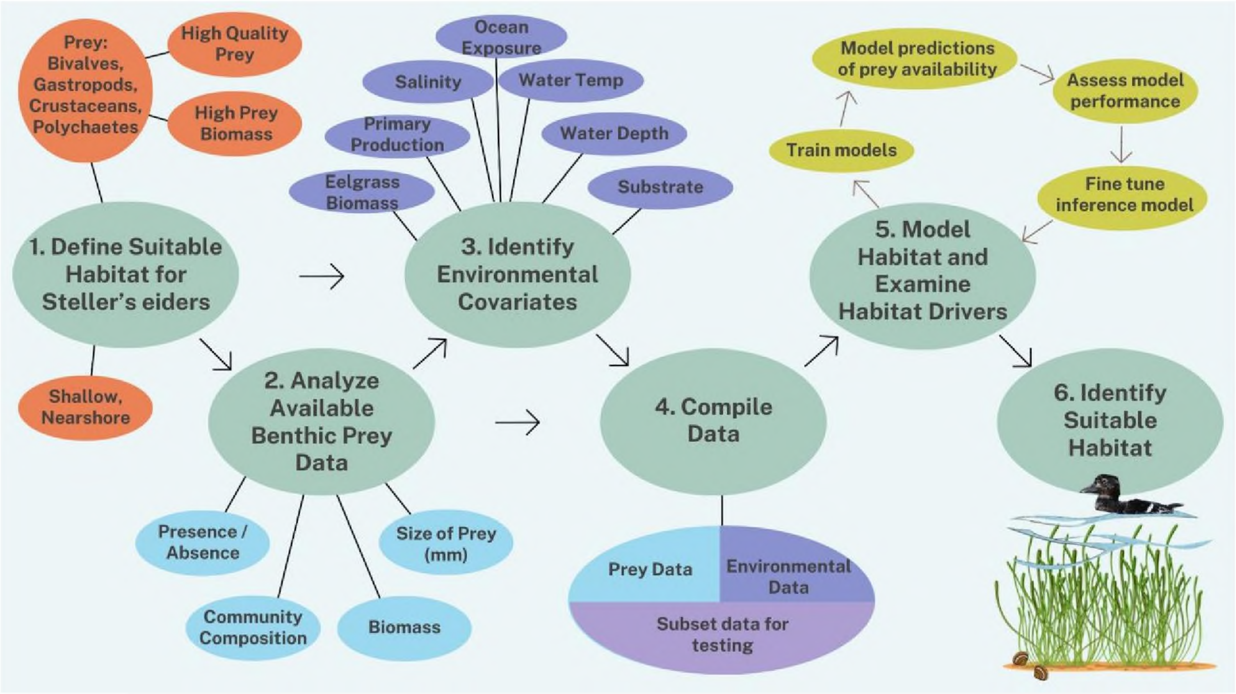

Figure A2. Conceptual model for integrating available benthic prey data from this study (Step 2) to foraging habitat suitability modeling for molting Steller's eiders at Izembek Lagoon, Alaska.